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P.S.

CONTENTS

Editorial note

The First International Swan Symposium was held at Slimbridge, England, on 7 and 8 December 1971; it did not prove possible to publish the proceedings in book form, but a number of the major papers were published in 'Wildfowl' 24.

The Second International Swan Symposium, like the first, was held in association with an annual meeting of the Executive Board of the International Waterfowl Research Bureau (IWRB), this time at Sapporo, Japan, on 21 and 22 February 1980. The participants in Sapporo were able to enjoy not only the magnificent facilities and hospitality provided by their Japanese hosts, but the deeply impressive sight of large numbers of wintering swans during excursions to Utonai and Odaito. Concurrently with the Swan Symposium, an International Crane Symposium was held, and its proceedings are being published under the auspices of the International Crane Foundation. The minutes of the IWRB Board Meeting have already been published in a separate volume, and this includes a list of all who participated at the Board Meeting and the two symposia.

The editors' task was an invidious one, since so much excellent material was presented at the symposium or submitted by post. There was simply not room to include all the details. The editorial 'blue-pencil' had to be used ruthlessly and apologies are offered to any who feel that their papers were unduly pruned. Problems arose in reproducing some diagrams and the high cost prohibited use of photographs and reproduction of the discussion. Some of the papers were only submitted in summary form. Within each section, the order is geographical (beginning with the host country, via the New World to the Old World) unless the subject matter, in such sections as behaviour or feeding, dictated otherwise.

In accordance with standard IWRB publishing practice, only scientific names of birds are used. For the swans the following names have been consistently adopted:

Cygnus atratus	Black Swan
Cygnus columbianus columbianus	Whistling Swan
Cygnus columbianus bewickii	Bewick's Swan (includes Jankowski's or Eastern Bewick's Swan)
Cygnus cygnus cygnus	Whooper Swan
Cygnus cygnus buccinator	Trumpeter Swan
Cygnus olor	Mute Swan

The scientific and English vernacular names of other birds are given in the Appendix. The editors thank Mrs J Dunning for help in sub-editing and Miss J Storey for help in typing.

Introduction

On 18 February 1980, His Imperial Highness Prince Hitachi, accompanied by Princess Hitachi, was the special guest at the opening of the IWRB Sapporo Meeting, comprising Executive Board Meeting, Swan Symposium and Crane Symposium. The Second International Swan Symposium was declared open on 21 February 1980 by Dr Shigeru Matsui, President of the Swan Society of Japan. Prof W J L Sladen, Co-ordinator of IWRB's Swan Research Group, then introduced Sir Peter Scott, Honorary Chairman of the Symposium. Sir Peter handed to Dr Matsui a small gift for His Imperial Highness, Prince Hitachi. This consisted of the adoption papers for two Slimbridge Bewick's Swans — one for His Imperial Highness and one for Her Imperial Highness. These were called Lotus and Leaf and each one had a drawing of its face pattern so that they can be recognized in the future.

Sir Peter then went on to say, "You will be hearing more about the Swan Supporter Scheme later in the symposium. The first symposium at Slimbridge received representatives from many countries, including two from Japan, Mr Honda and Mr Yoshikawa from Hyoko.

"For one reason or another, each one of us is an enthusiast about swans and I think it is very appropriate that there should be a double symposium — one about swans and one about cranes — because both of them are part of human mythology, leading to a very happy relationship between man and animal in many, but not alas in all, parts of the world. Swans are more fortunate than cranes in that, although they are edible, they seem to be less hunted. Perhaps this is one of the reasons why no species are seriously endangered although there are problems in some populations. In the case of the crane, however, the great majority are endangered, most directly by man. In both cases, the wetland habitat may be threatened. There is some possibility of over-population of swans in some localities and there has been a demand in some parts of the North American continent for hunting to take place. One of the most important features is the adaptation of all these birds to man-made habitats, but the swans seem in most cases to have to have a relatively undisturbed breeding habitat.

"I would like to mention the question of methodology and standardization. The measurements taken in Japan are in some cases different from those taken in England and some measurements that we think are important are not taken at all as, for example, the length of the skull. I think it is important at this meeting to standardize techniques and also to compare notes on the best methods used in the course of capture and handling. I believe it to be very important that we keep any damage and unnecessary stress to the birds to a minimum. These birds are very fragile creatures. There are three reasons why we should handle them in a very gentle manner. The first is the principle. We really have no right to be rough with birds. The second reason is also very compelling. It is that if we are rough with experimental birds, they will not behave like normal birds and therefore we shall not get the best data from the ringing. The third reason is that there are people who do not believe that birds should be caught at all because it may damage them; we don't want this to be substantiated. It is always right to hold the birds for the shortest possible time in captivity and to handle them very carefully during that time. Swans should not be caught just before having to make a long migratory flight. We know that flight for them is not altogether easy and, indeed, aerodynamics suggest that, theoretically, Whooper Swans cannot fly — they simply don't have large enough wings to overcome the heavy load of their body. The evidence of our eyes indicates that that theory is not correct, but I make the point because I think that the margin between being able to fly easily and not being able to fly at all is narrow and therefore the effect of handling them may be deleterious."

Sir Peter then passed the meeting to the Chairman of the opening session, Prof G V T Matthews, Director of the IWRB. Other sessions were chaired by —

- Dr M Williams (New Zealand)
- Mr P Andersen-Harild (Denmark)
- Prof W J L Sladen (USA)
- Dr J Bartonek (USA)
- Mr N Perret (Canada)
- Dr S Matsui (Japan)

Distribution and Status

TEN YEARS OF SWAN COUNTS IN JAPAN

M HORIUCHI

Introduction

The Environment Agency has made an annual census of waterbirds in the middle of January since 1970 to learn about their wintering conditions in Japan. This census is mainly conducted by the prefectural governments of Japan under the supervision of the Environment Agency.

This census may not cover all the wintering populations of swans in our country, because their habitats range from rivers and lakes to harbours and far out on the sea and if they winter in small numbers some may be overlooked. However, the findings of the census are fairly reliable.

Results

1. The number of wintering places in the country has varied through the years: 82 at the fewest, 154 at the most and 124 average. The total number of swans has been: 11 477 minimum, 16 067 maximum and 13 467 average.

2. The second degree curve of the population trend during these ten years is: $P = 14400.9 + 103.976t - 28.3134t^2$. (The starting point lies midway between 1974 and 1975 and the interval of each year is $t = 2$).

3. The coefficient of correlation of the number of swans and the number of their wintering places is: 0.83 and its regression line is: $Y = 6858.4 + 50.7345x$.

4. 96% of *Cygnus cygnus cygnus* winter in the following five prefectures: Hokkaido 53%, Aomori 18%, Miyagi 13%, Niigata 7% and Yamagata 5%.

5. 91% of *Cygnus columbianus bewickii* winter in the following five prefectures: Fukushima 33%, Shimane 23%, Miyagi 20%, Niigata 9% and Akita 6%.

From these findings of the census a few comments are possible. First of all, there is no indication that the population has increased or decreased in the past ten years. Second, the high correlation between the total number of swans and the number of their wintering places indicates that the populations in the main wintering places have come up to a very reasonable size. Third, the wintering places of *C. c. cygnus* are located somewhat north of those of *C. c. bewickii.*

Summary

The paper reviews the results of swan counts in Japan over ten years and shows that numbers have remained high.

Editorial note

Preliminary data for the national census of 13 January 1980, presented to the Symposium, gave 6797· *C. c. cygnus* and 1954 *C. c. bewickii.* A count of Hokkaido alone on 10 February 1980 gave 5129 *C. c. cygnus,* including 157 on Lake Utonai and 3520 on Notsuke Bay, which were to be visited on the excursions.

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PRESENT STATUS OF THE SWANS WINTERING IN KOREA AND THEIR CONSERVATION

PYONG-OH WON

Introduction

Three species of swan migrate to Korea. They are *Cygnus cygnus cygnus, Cygnus columbianus bewickii* and *Cygnus olor.* The last is a rare winter visitor.

Before World War II, flocks of thousands of swans would winter in Korea and form magnificent spectacles. In early winter, they would arrive in large groups at ponds, lakes and reservoirs on the eastern and the western seashores in the north. When it became colder, they would move down to the south and winter on ponds and wetlands in Geongsang-namdo. Some would move further down to the southern islands, such as Jindo, when waters froze in the rest of the Korean peninsula. Thus, in the south swans began to appear in late October and would stay until they flew northward in late February and early March.

Before World War II, there were many abandoned wetlands which attracted swans in Korea. Among them, Hyopcheon and Changnyong inland areas and Jindo seashore areas were designated and preserved as Natural Monuments, on Professor Tamezo Mori's proposal, from 1934 to 1945. Since then, the wetlands and marshes in these areas have become farm fields. Accordingly, Hyopcheon and Changnyong were released from being Natural Monuments in 1973, and before long Jindo will face a similar situation (see Fig 1).

Causes of wildlife decline in Korea

After World War II, wildlife in Korea met its disaster during the period of the

Fig 1. Wintering grounds of swans in Korea 1960–1970.

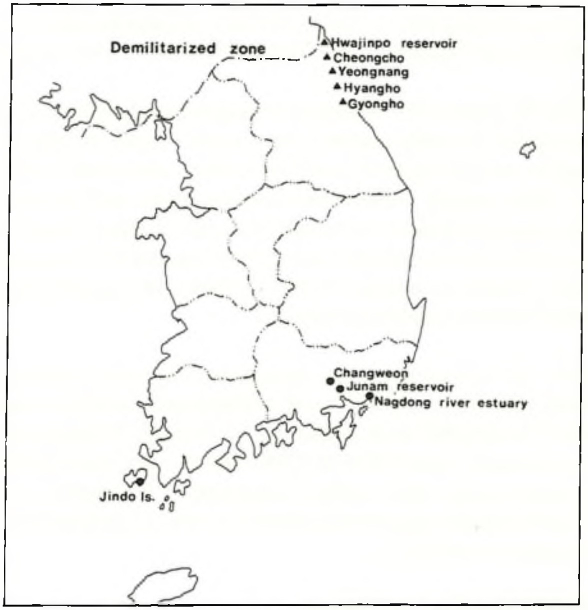

Fig 2. Wintering grounds of swans in Korea 1970–1980.

Korean War, 1950 to 1953, and in the period of social disorder which followed. Soldiers and even civilians illegally hunted wildlife with shotguns, traps and poisons so as to sell it to fur and taxidermy shops. As a result, wildlife greatly decreased and some species faced the danger of extinction.

Since then, the Government planned farm expansion in the 1960s largely by the reclamation of seashore wetlands and inland water, and gave a deadly trial to waterfowl and waders by destroying their habitats. Furthermore, the indiscriminate use of chemical fertilizer and all kinds of insecticide for agriculture has brought about an environmental pollution which allows hardly any wildlife to survive. Again, the recent speedy development of modern industrialism has transformed many inland and seashore areas into sites of mammoth factories with chimneys and pipes pumping out smoke and sewage. These and other human disturbances, such as noise from automobiles and aeroplanes, threaten wildlife virtually everywhere.

Present wintering grounds of swans in Korea

In the Nagdong Delta about 2000 to 3000 *C. c. cygnus* and *C. columbianus bewickii* winter annually. Less than 200 swans winter on the Jindo seashore and on Dunjeon Reservoir on that island. About 260 to 370 swans migrate to Junam Reservoir (210 ha) in Gyeongnam Province and a lesser number arrive at Samnam Reservoir (70 ha) nearby.

On some ponds, streams and newly made reservoirs, several wintering swans, and sometimes up to ten, may be seen. At times, a similar number of wintering swans may be seen on certain southern islands, but none is observed on the western seashore. Some *C. olor* alone winter on lakes on the eastern seashore (see Fig 2).

Wintering grounds of *C. olor*

Before World War II, there were only three records in Korea. Kalinowski collected a young female at Wonsan on 27 February 1888. Then Kuroda reported one from Mogpo, Jeolla-namdo, in January 1916. Finally, Mori collected one in Chungnam Province on 13 December 1918.

After World War II, several new wintering grounds were discovered. On 8 January 1968, 24 *C. olor,* including 4 young, were observed on Gyongho Pond at Gyongpodae, Gangneung in Gangweon-do. On 21 February 1974, 8 and on 22–23 January 1977, 12, including 4 young, were observed on Cheongcho Pond near Sokcho in Gangweon-do. Recently, the author was fortunate enough to discover some 145 wintering on Hwajinpo Reservoir near Geojin, Goseong-gun in Gangweon-do, on 8 January 1980. This must be the largest group of wintering *C. olor* ever recorded in Korea. Hwajinpo Reservoir (202 ha), which was built for agricultural water supply and which overflows into the sea, is one of the least polluted reservoirs.

The distance between Hwajinpo and Gyongho Pond is about 112 km, and there are in between several large and small ponds and small patches of wetland, such as Songjiho Pond (63 ha), Bongpo Pond (10 ha), Yeongnang Pond (101 ha), a piece of wetland near Wolpo seashore in Yangyang (about 20 ha), Maeho Pond (19 ha), Hyangho Pond (104 ha), Cheongcho Pond near Sokcho (135 ha) and Gyongho Pond (99 ha). To these ponds and a wetland, about 250 to 300 swans, including 145 *C. olor,* seem to make regular visits from late October to early March.

These ponds and wetlands with brackish water seem to be the only wintering grounds of *C. olor* and their proper conservation should be established immediately.

The wintering grounds of swans at Nagdong Delta

Nagdong River has a large estuary and a number of deltas which fall under the jurisdiction of the city of Pusan. On the upper estuary there are islets such as Hadan-do and Eulsug-do, and between the main stream of Nagdong River and Jugrim River a huge delta is formed.

Migrants gather and search for food around the ever-changing tidal spits on the mudflats in front of the Nagdong Estuary as there are plenty of aquatic plants and invertebrates at low tide. These huge wetlands become the sanctuary of waterfowl in Korea. In spring and autumn, large flocks of waders stop here. In winter, this area becomes the haunt of ducks, geese, swans, gulls and cormorants. Even in a severe winter when water is frozen in central Korea, the Nagdong Delta usually remains open. Sometimes even Natural Monuments, such as *Grus vipio, Platalea minor,* eagles and vultures, may be seen among the species wintering there and, at times, rare species, such as *Glareola maldivarum* and *Eurynorhynchus pygmaeus,* may be observed. From these areas of the Nagdong Delta, a total of 136 species of bird have so far been recorded, most of the waterfowl, waders and birds of prey hitherto observed in Korea.

Recently, however, the species and the numbers of birds that migrate to the Nagdong Delta have decreased remarkably year by year. This is primarily due to the waste discharged from nearby manufacturing plants into the tributaries of the river and the insecticides widely spread for agricultural use on adjacent areas.

The Office of Forestry prohibited hunting in those areas of the Nagdong River as of 31 October 1962, and the Bureau of Culture Property Preservation designated those areas as a Natural Monument as of 13 July 1966, and the three swan species were designated by the Government as Natural Monument No 201 on 30 May 1968.

General

In Korea, only three wetlands have been preserved as Natural Monuments, being designated by the Government for migrating birds. They are the estuaries of the

Han River and of the Nagdong River and the mudflat of Incheon on the western seashore. These three places (307 km^2) occupy only 0.03% of the total area (98 000 km^2) of South Korea. These three places must be preserved for wildlife by all means.

There are a number of ponds, reservoirs and mudflats where a considerable number of waterfowl regularly visit or winter, such as Paldang Reservoir in Gyeonggi Province, two reservoirs in Changweon-gun, Gyeongnam Province, Dunjeon Reservoir in Chindo-gun, Jeonnam Province, and the mudflat of Suyu-ri in Gunnae-myeon, Jindo-gun, Jeonnam Province, and Seongsanpo and Kosan Reservoirs in Jeju Island, Jeju Province. Proper conservation of these areas should be established soon.

Of all 372 species of birds hitherto recorded in Korea, half, 186 species, rely on water or wetlands for life. Among these, 34 species have nearly lost their habitats and at least 20 are now faced with extinction. Positive measures to save these species by securing their habitats should be undertaken immediately.

Summary

Swan wintering habitat has been greatly reduced in Korea and the principal remaining site is the Nagdong Delta. Details are given of recent sightings of *Cygnus olor.* Three wetlands have been designated Natural Monuments and conservation measures are needed at other sites.

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NUMBERS OF SWANS WINTERING IN THE UNITED STATES

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Introduction

Four swans winter within the United States, ie the native *Cygnus columbianus columbianus, C. cygnus buccinator* and *C. cygnus cygnus* and the feral *C. olor.* In this paper we present summary data on their numbers as measured by Midwinter Waterfowl Surveys and discuss trends of various populations.

Numbers of swans and other waterfowl are estimated generally in January during

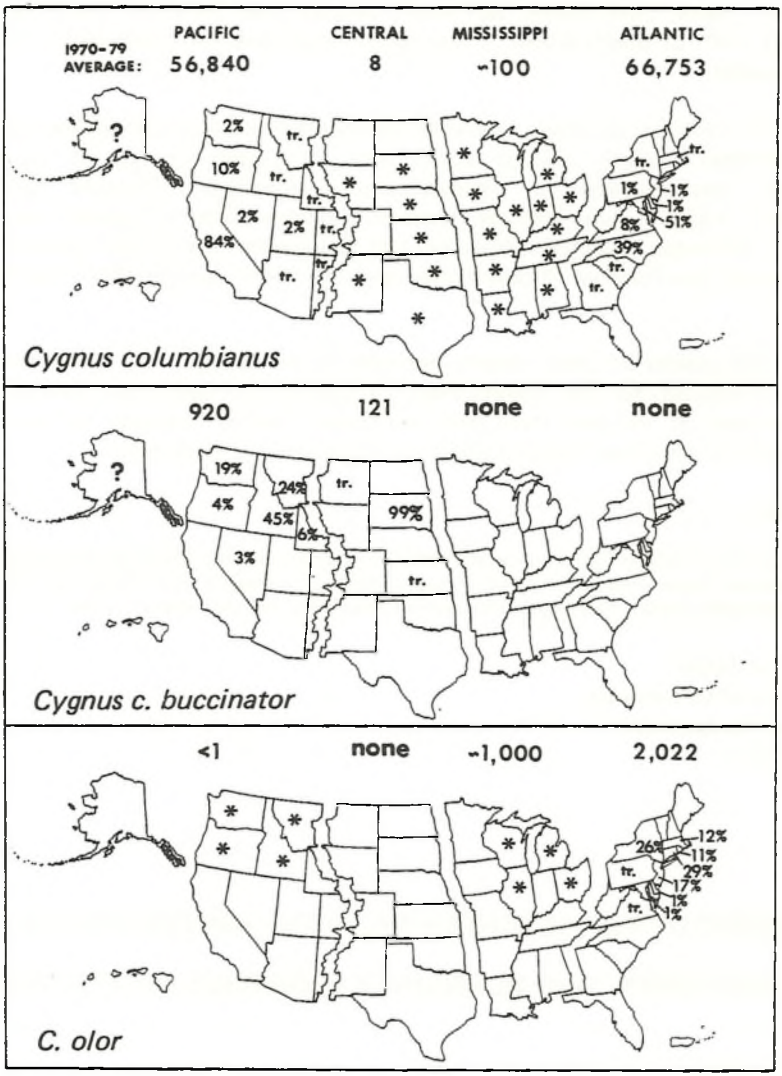

Figure 1. Average numbers and distribution of three swan species in the United States as measured by Midwinter Waterfowl Surveys, 1970–79. Asterisks denote occurrence of swans but data are such that the use of percentages is unwarranted. While Alaska, Hawaii, Puerto Rico and the Virgin Islands are not surveyed, only Alaska is known to winter both *Cygnus c. columbianus* and *Cygnus c. buccinator.*

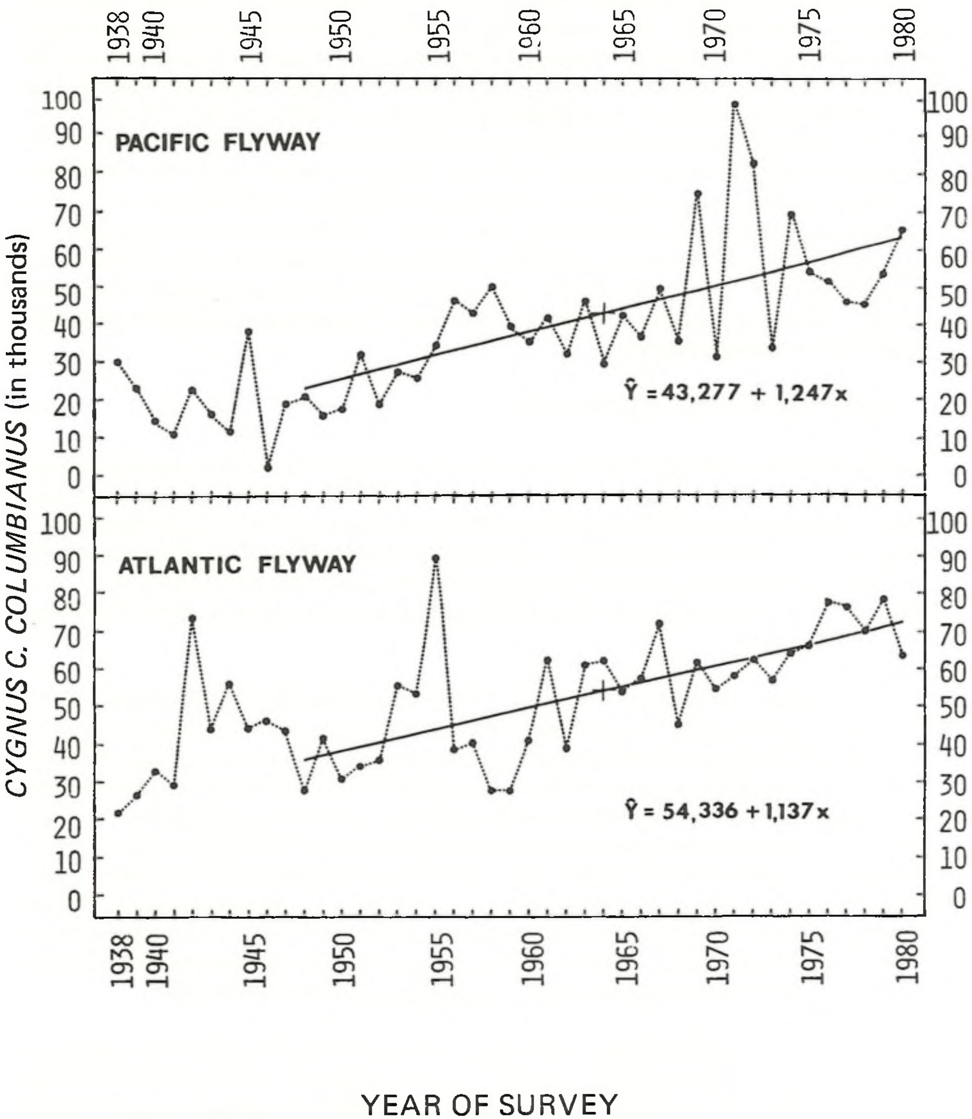

Figure 2. Numbers of *Cygnus c. columbianus* counted in the Pacific and Atlantic Flyways during Midwinter Waterfowl Surveys (usually conducted in January), 1938–80.

the federal-state co-operative Midwinter Waterfowl Survey which has been undertaken throughout the conterminous United States since 1935. Counts of wintering waterfowl in Alaska were attempted for only a few years in the 1950s. Observers count from aeroplanes, automobiles, boats and on foot. While originally intended to enumerate all waterfowl wintering in the nation, this survey proved practical to estimate numbers of waterfowl mainly in areas where they habitually wintered in large numbers. Among its several uses, the survey provides indices to populations of many species, and for *C. c. columbianus* it is believed to provide a reasonable assessment of their total numbers. Coverage of areas, manner of survey, and effort expended have been more or less consistent since 1948; since then data were more reliable for comparisons than those from earlier surveys. Because an unmeasured amount of the year-to-year differences between estimates can be attributed to weather's effect on habitat which in turn affects distribution of birds, these data reflect flyway- and nation-wide long-term trends in populations better than either state-wide or annual changes.

Cygnus columbianus columbianus

Most numerous of the North American swans, *C. c. columbianus* has averaged about 124 000 birds during 10 winter surveys from 1970 to 1979. The Atlantic and Pacific Populations constitute 58% and 42% respectively of the nation's population, with only fractional percentages wintering in Alaska (Fig 1). Canada, primarily British Columbia and secondarily those provinces bordering the Great Lakes, may winter 1% or 2% of the species' population. Swans are irregularly observed during surveys in Mexico.

Atlantic swans winter mostly in and about Chesapeake Bay in Maryland, North Carolina and Virginia. The primary terminuses of the Pacific Population are in California's Sacramento Valley, the delta of the Sacramento and San Joaquin Rivers and San Francisco Bay, with the lower Columbia River in Oregon and Washington and the Great Salt Lake marshes in Utah being secondary. A small but distinct and most likely unique population, perhaps fewer than 200 birds, winters on the Alaska Peninsula (John E Sarvis pers. comm.), with 700 miles separating them from the nearest flock. Areas in other states and flyways are indispensable during migration, and some will host above-average numbers of swans throughout mild winters. Wintering areas, migration routes, stopovers and breeding grounds of these swans have been adequately described (eg Bellrose 1978, Palmer 1976).

Numbers of *C. c. columbianus* counted in Midwinter Waterfowl Surveys since the winter of 1937/38 are shown in Fig 2. From 1948 to 1980 (33 winters) the Atlantic Population averaged about 54 000 swans with an average annual increase of about 1100 birds, and the Pacific Population averaged about 43 000 swans with an average annual increase of about 1200 birds. Erratic counts in the Pacific Flyway, particularly in the early 1970s and in the Atlantic Flyway during much of the 1950s, cannot be attributed solely to changes in survival and recruitment rates but in part reflect imperfections of the surveys.

Cygnus cygnus buccinator

C. c. buccinator is segregated into Pacific and Midcontinent Populations. The Pacific Population breeds entirely in Alaska and winters in coastal areas from southeastern Alaska through British Columbia and Washington to Oregon. The Midcontinent Population breeds in that area where Montana, Idaho and Wyoming join boundaries, in southern Saskatchewan, western Alberta and more recently in eastern British Columbia. The Midcontinent Population winters in its entirety in that same tri-State area, primarily Red Rock Lakes, Henry's Fork of the Snake River and Yellowstone National Park. Additionally, there are small but locally important 'refuge flocks' of *C. c. buccinator* breeding in and wintering near National Wildlife Refuges in Washington, Oregon, Nevada, Wyoming and South Dakota. In an effort to prevent the demise of the species, these flocks were established beginning in the 1930s from swans taken from their then only known stronghold, the Red Rock Lakes National Wildlife Refuge.

The Midwinter Waterfowl Surveys tallied an average of 1041 *C. c. buccinator* wintering in the conterminous United States during the period 1971–80 (Fig 1). Average counts in Idaho, Montana and Wyoming were 412, 217 and 54 respectively. Coverage of the Midcontinent Population's wintering area was incomplete because the densities of other waterfowl did not warrant the additional costs and efforts to achieve the needed coverage. Washington and Oregon averaged 178 and 34 respectively during the 10 years; but intermingling of the Pacific Population with those of refuge flocks confounded differentiation between the groups. Increases in Washington's *C. c. buccinator* from about 100 to nearly 400 during this period more likely reflects an increasing awareness and recognition of Pacific Population *C. c. buccinator* amongst the *C. c. columbianus* than an actual increase in population. Nevada's Ruby Lake National Wildlife Refuge flock averaged 25 *C. c. buccinator,* with a high of 38 recorded in 1971. The flock at LaCreek National Wildlife Refuge in South Dakota has averaged 121 swans, with a high of 201 swans in 1979.

The Midwinter Waterfowl Survey as it has been conducted does not adequately provide the information needed to monitor the status of the small (about 1000 birds) and potentially precarious Midcontinent Population of *C. c. buccinator.* A few will most likely be found outside traditional wintering areas once observers can better distinguish them from *C. c. columbianus,* eg in Utah (Bartonek 1966) and North Dakota (Cowardin and Bartonek 1968). The Pacific Population is best counted during late summer on its breeding grounds in Alaska rather than during winter when foul weather in coastal areas would preclude most surveys. The five-year interval between current surveys in Alaska seems adequate to monitor the status of this more abundant (nearly 5000 birds) and widely dispersed population.

Cygnus cygnus cygnus

This swan winters in the western and central Aleutian Islands of Alaska. Although there has been no comprehensive survey, this population is estimated to number about 300 or 400 birds. The habitat is remote, seldom visited by man, and secure in that it is entirely within the Aleutian Islands National Wildlife Refuge. The specific breeding ground and migration route of this small population are not known. While *C. c. cygnus* are sighted in western Alaska at other times and elsewhere in North America, these other occurrences are of greater interest than significance.

Cygnus olor

C. olor escaping and being released from ornamental and avicultural flocks has become established in the wild in many states and poses threats to wintering and in some cases breeding native swans. Because *C. olor* is not hunted and mostly non-migratory, it has been largely ignored or misidentified during Midwinter Waterfowl Surveys. Although the populations of *C. olor* are poorly defined by these surveys, other evidence suggests that they are increasing in size and range.

In the Atlantic Flyway, during 1975–79 when absolute rather than rounded numbers of waterfowl were reported, midwinter surveys tallied an average of 2424 *C. olor* (Fig 1).

C. olor in the Mississippi Flyway is irregularly reported in Midwinter Waterfowl Surveys but, nonetheless, constitutes possibly the majority of the flyway's wintering swans. Michigan, particularly the northern part of the Lower Peninsula in Traverse Bay, wintered 1080 in January 1979 (Gerald F Martz pers. comm.). Wintering *C. olor* has been identified in Minnesota, Wisconsin and Indiana, with many other states possibly having the species but not distinguishing it from *C. c. columbianus* and possibly *C. c. buccinator. C. olor* was introduced and has become established in reclaimed coal fields of Illinois (John W Ellis pers. comm.) but is not inventoried.

C. olor has not been reported in the Central Flyway but is becoming established in the Pacific Flyway. As many as 30 feral swans, possibly originating from birds near Livingston, Montana, are expanding their range into already crowded breeding and wintering habitats of *C. c. buccinator* in the tri-state area (Ruth E Shea pers. comm.). If any of these *C. olor* were identified during Midwinter Waterfowl Surveys they went unreported. Richard C Parker (pers. comm.) reports that *C. olor* escaping from captive flocks is irregularly observed wintering in the Puget Sound area of Washington. He also observed a male *C. olor* with its *C. c. columbianus* mate and their progeny wintering near Skagit Flats. The pair had apparently nested somewhere in Alaska. The hybrid swans but not the parent *C. olor* were observed during the following winter. During the 1978 survey, two and three *C. olor* were counted in Idaho and Oregon respectively.

In states of the Mississippi and Atlantic Flyways numbers of waterfowl estimated during Midwinter Waterfowl Surveys are rounded to the nearest 100 birds or called 'trace' when the number is 50 or less. While this procedure may be both practical for reporting the more abundant species and appropriate when considering the impreciseness of the survey and estimates, it nevertheless obscures changes in status of the less abundant species such as *C. c. buccinator* and *C. olor* at both state and flyway levels. We recommend that absolute values, rather than rounded or trace, be reported for these less common species. Also those waterfowl species that are lumped into a 'miscellaneous' category because they are uncommon should be identified so that potentially important information on zoogeographic changes, as with that on *C. olor,* will not be sacrificed for convenience.

Acknowledgements

We acknowledge the efforts by the many state and federal biologists and volunteers throughout the United States who conducted the Midwinter Waterfowl Surveys over the past 45 years.

Henry M Reeves provided useful suggestions in improving early drafts of this manuscript.

Summary

Numbers of native *Cygnus columbianus columbianus* and *Cygnus cygnus buccinator* and feral *Cygnus olor* as measured during nation-wide January surveys are reported by state and by flyway for each year from 1948 to 1980. Additional data, beginning in 1936, are available for certain states in the Pacific Flyway. Trends in numbers and distribution of these wintering swans are discussed. The status of wintering *C. c. cygnus* and the irregular occurrence of other species are also discussed.

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A CORRELATION BETWEEN *CYGNUS COLUMBIANUS COLUMBIANUS* TERRITORIES AND WATER BODIES IN WESTERN ALASKA

J G KING and J I HODGES

Introduction

The purpose of this paper is to show the relationship of swan data gathered on routine waterfowl surveys to habitat features shown on topographic maps in Alaska. There is a possibility that knowledge of the biology and ecology of swans on their northern breeding habitat will be helpful in understanding factors that affect less highly visible waterfowl species. Intensive study of swans will be needed to develop and test their use as an 'indicator species'. This study is perhaps an early step toward that goal.

The systematic North American waterfowl breeding population surveys were begun some 35 years ago and have been standardized since 1955. This paper deals with just one of the 49 strata included in the Continental Survey or about 2% of the annual North American survey sample. Methods and biasses regarding swan data acquired on this survey in western Alaska were discussed by King (1973).

Methods

C. c. columbianus nests in Alaska on the western and northern tundras (Fig 1). Most of the habitat except the most northerly is covered by the annual waterfowl breeding pair surveys in late May or early June. The highest density of territorial swans is observed on the 6 734 208 ha of lowland tundra habitat on the Yukon Delta. The swans here are best described by Lensink (1973). A wealth of geese and ducks also nest in this area (King and Lensink 1971).

Eight survey transects have been laid out across the Yukon Delta habitat which are further subdivided into 65 segments each 25.7 km long (Fig 2). These lines are marked on detailed topographic maps for navigation by the pilot. Survey is immediately after the ice on the lakes is gone, about 1 June. Swans at this time are beginning incubation; thus the breeding population is distributed on nesting territories. A single-engine, high-wing aeroplane is flown at 30 m elevation and 160 km/hr along each transect. Thus it takes about 10 minutes for each of the 65 segments. The pilot on the left and an observer on the right record all waterfowl sightings within 200 m of each side of the aeroplane. This results in an actual sample of 1037 ha for each segment flown (USDI 1977). Swans are recorded as singles, pairs or flocks of three or more. Forty-nine segments have been flown every year from 1956 to 1977, and the remaining 16 were added in 1964. Segment averages used in the calculations are based on either 14 or 22 years of data. Trend is shown

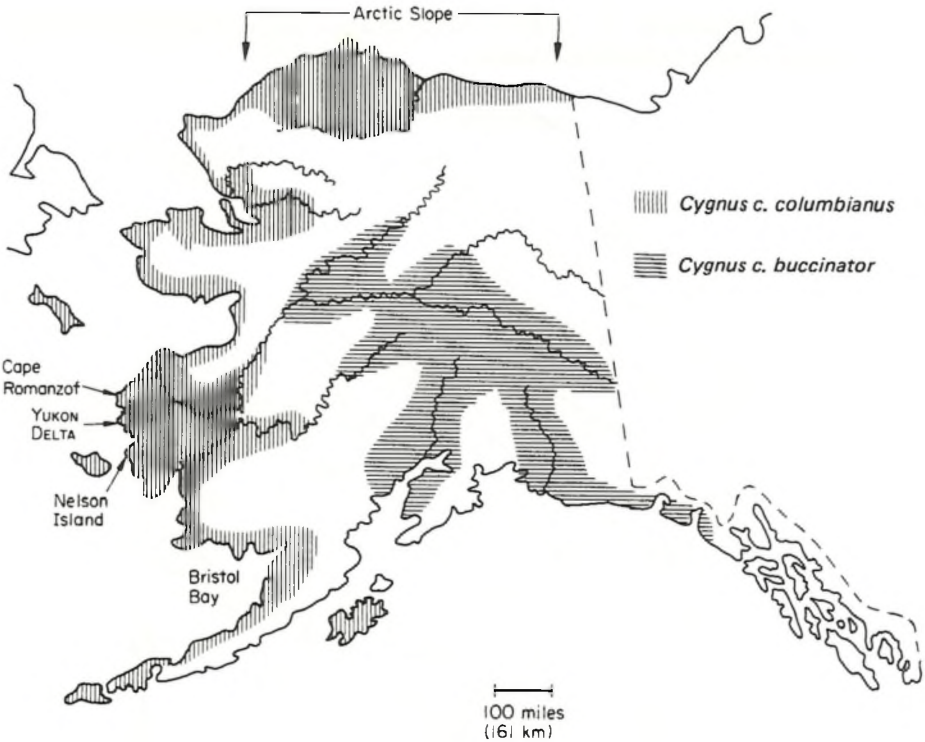

Fig 1. Approximate swan breeding range in Alaska (from King 1973).

using only the 49 segments flown in each of the 22 years.

The data for the ten variables listed in Table 1 were calculated from US Geological Survey topographic maps, scale 1:63 360. These maps were made from aerial photographs taken in the early 1950s. Swans are seldom seen on a water area too small to show on the map. Area values were calculated using an 'area graph' dot card with 100 randomly distributed dots per 6.45 sq cm and lake shoreline was calculated using a Numonics electronic digitizer.

Flocked swans in June represent non-breeding birds and are not included in our calculations. Birds seen as pairs appear to be defending territories, are often seen associated with nests and are well spaced. Single birds are sometimes seen associated with a nest and, if not, may represent one half of a nesting pair. For our calculations here we add single and paired birds on the assumption that they represent the breeding population.

Fig 2. A correlation of *Cygnus columbianus columbianus* territories and water bodies in Western Alaska.

Fig 2. The Yukon Delta showing location of each of the 65 line transect survey segments, each 25.7 km long. The number below each segment is the 22 year average number of swans seen there that appear to be on territory. The dotted lines group areas according to density, low averaging from trace (t)–3, medium 4–8 and high 9–18. (Adapted from King 1973).

Results

Correlations with environmental variables

The correlations between average swans per segment and ten environmental variables are summarized in Table 1. These long-term averages are an excellent measure of the value to swans of habitat crossed by these segments. Swan density

Table 1. Correlation coefficients between swan density and ten environmental variables

Independent variables	Correlation coefficient with swan density	Significance
1. Lake area per segment	0.230	$p < 0.10$
2. Linear miles of lake shoreline/sq mile	0.673	$p < 0.001$
3. Number of lakes/sq mile	0.703	$p < 0.001$
4. Number of small islands/sq mile	0.464	$p < 0.001$
5. River area per segment	–0.207	$p < 0.11$
6. Linear miles of river shoreline per segment	–0.088	Not significant
7. Linear miles of stream per segment	–0.076	Not significant
8. Altitude	–0.203	$p < 0.11$
9. Miles to nearest village	0.020	Not significant
10. Population of nearest village	0.122	Not significant

correlated best with the variables related to lakes, numbers 1–4. The highest correlation is for linear miles of shoreline and for total number of lakes with the latter being slightly higher. These two variables are highly dependent with respect to each other ($R = 0.83$) and usually represent the same water conditions. A scatter diagram by segment of swans versus lakes (Fig 3) demonstrates the linear relationship between the two.

$y = 0.984 + 0.0672x$ or
swans/segment = 0.984 + 0.0672 lakes/square mile

Some of the outliers can be partially explained by the varying quality of the maps used to determine numbers of lakes. The precision with which swan density can be predicted with this equation will increase with the size of the area to which it is applied.

The other two items (numbers 5 and 8) that show some significance are the area of river water and altitude above sea level. As expected, both show a slight negative correlation with swan densities.

Swans are seldom seen on the murky waters of the Yukon and other rivers. The mean elevation for all segments is 10 m above sea level with a range of 2 to 43 m, sufficient to show that higher elevations generally have fewer swans and are quite likely drier.

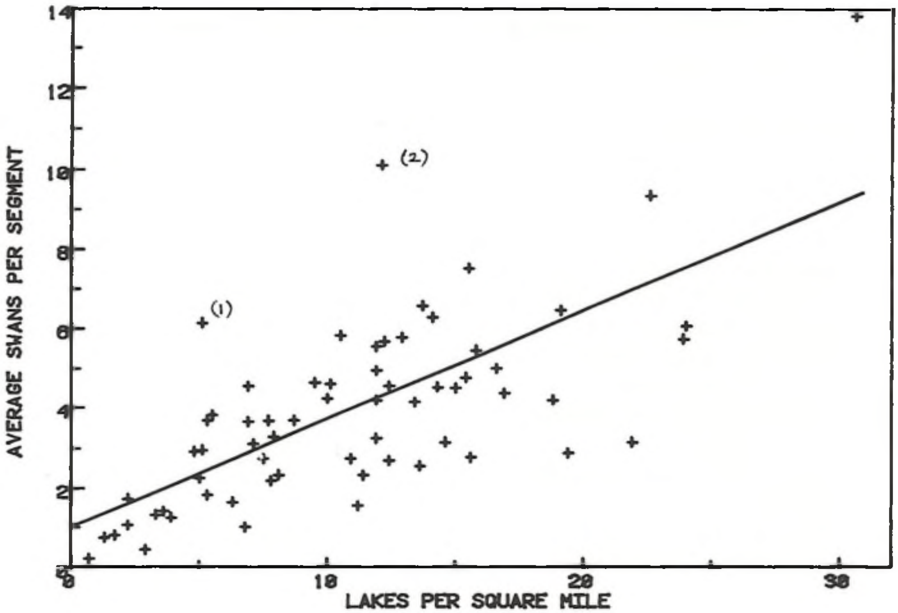

Fig 3. Scatter diagram of breeding swans versus lakes for 64 segments. Least squares fitted line has a correlation coefficient of R = 0.703. Outliers: (1) segment lies on Kashunuk River; (2) suspected map detail problem, habitat has swamps not showing as lakes.

The length of shoreline of running water in streams and rivers does not indicate any attraction for swans. The lack of correlation of any sort with the distribution and density of people may reflect that hunting pressure in summer relates to boat access rather than direct distance from communities.

A multiple linear regression analysis with these variables showed little gain over the simple linear regression.

Population trends

The ratio of singles to pairs varies considerably over the 22 year period (Fig 4). This may reflect that the proportion of swans nesting varies from year to year depending on weather conditions, number of first-year breeders, etc. Some separation of nesting pairs during this period is inherent as one bird sits on the nest and the other defends the territory. Lensink (1973) found that more than 50% of pairs evidently defending territories do not raise broods and probably do not attempt to nest. After the hatch in late June pairs are seldom separated. Thus early July surveys would provide a neater picture of annual numbers of pairs on territory. In spite of this difficulty we find no grounds in our data to indicate a long-term trend either up or down in the swan breeding population of the Yukon Delta.

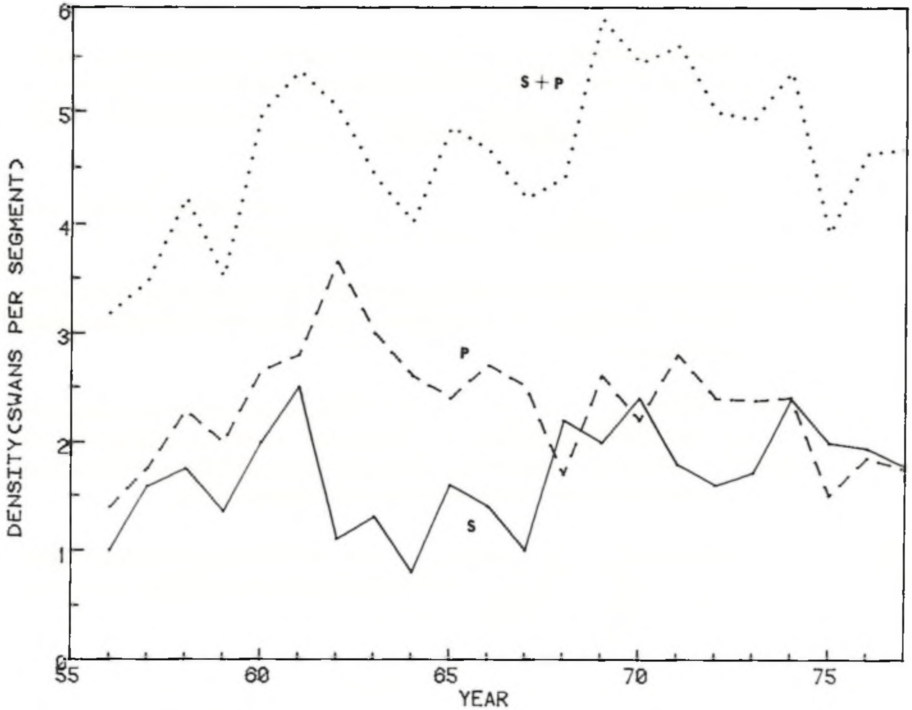

Fig 4. Average swans per segment. Singles (S): solid line. Pairs (P): dashes. Singles plus pairs (S + P): dots.

Stratification of habitat

We have stratified the swan nesting habitat of the Yukon Delta on the basis of average swan sightings per segment (Fig 2). We now know that the distribution of lakes correlates rather well with average swan distribution. A stratification of the habitat based on the distribution and density of lakes would be similar in shape but more refined. We find that there is no need to embark on the time-consuming process of calculating total edge effect on the margins of lakes as a simple count of lakes per unit area serves as well.

Discussion

No one familiar with northern swan habitats will be particularly surprised at the findings reported here. However, now that we have demonstrated these things factually we can use the knowledge to reorient and improve our ability to monitor waterfowl populations in the north where water areas remain relatively stable from year to year.

1. A more precise population estimate for the Yukon Delta swans could be obtained by using maps to stratify the area according to distribution of lakes and then designing a survey based on optimum allocation of sampling effort. Higher quality per unit costs of surveys would be achieved this way.

2. The same procedure could be used for all *C. c. columbianus* habitat and perhaps other tundra nesting swans wherever suitable quality maps exist.

3. The facts demonstrated here should be equally valid for ducks. Correlations between average duck numbers and distribution of water along standard survey transects could be calculated.

4. We could now draw a transect on a Yukon Delta map, count the lakes and predict a probable breeding population of swans that would be affected by a man-made project in the area. In this way 22 years of data could be utilized instead of the one or two which are usually obtained from pre-project studies.

Perhaps a final conclusion from this exercise is that if we keep our eye on these noble birds we can learn things that may ultimately improve our ability to conserve their smaller, less visible relatives nesting with them.

Summary

From 1956 to 1977 eight aerial survey transects consisting of 65 segments have been flown annually across the 6 734 208 hectares of the Yukon Delta tundra habitats on about 1 June. Swans and other waterfowl have been tallied within 0.2 km on each side of these 25.7 km long segments, providing an actual count of birds on 67 342 hectares or 1% of the entire Yukon Delta habitats. The transect lines have been plotted on US Geological Survey maps of scale 1:63 360. There is a mean of 43.9 lakes per segment with 29 km of lake shoreline. *C. c. columbianus* at the survey time are seen as singles or pairs evidently on breeding territories and as flocks of 3 or more non-breeding birds. The 22 year mean of singles and paired swans is 4.12 swans per segment. The correlation coefficient between swans and lakes is $R = 0.703$ ($p < 0.001$) and between swans and length of shoreline $R = 0.673$ ($p < 0.001$). Other physical factors such as length of streams and area of water showed little or no significant correlation. It is concluded that density of nesting swans within units of their breeding range can be estimated using numbers of lakes present on detailed maps. The more time-consuming process of determining length of lake shoreline yields little additional information. The annual averages show no significant population trend for swans observed on Yukon Delta territories during the 22 year period. The habitat is stratified according to average swan densities. Management implications are discussed.

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THE STATUS AND FUTURE OF THE ALASKA POPULATION OF *CYGNUS CYGNUS BUCCINATOR*

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Introduction

The Alaska population of *Cygnus cygnus buccinator* is distributed along the coastal plain from Yakutat to Cook Inlet, in the forested Interior valleys of the Copper and Susitna Rivers and in the Yukon River system east of the tundra and south of the Arctic Circle. Some of the highest mountains of North America occur in this region, including Mount Mckinley (6187 m). Extensive ranges of lesser peaks and the largest ice fields of the continent are also features of the area. Interspersed are temperate lowlands interconnected by large river valleys. Most of the 70 000 km^2 of *C. c. buccinator* habitat is below the 300 m contour. The tree line is generally about 825 m and no swans are seen above this elevation. Because of the low passes interconnecting all areas it is now assumed that the Alaska *C. c. buccinator* is one population. For census purposes the area is divided into eight units (Fig 1). A detailed description of the swan habitat and the historical record is provided by Hansen *et al* 1971.

In 1975 we conducted an intensive aerial search of all the known *C. c. buccinator* habitat except for three tundra areas where there are isolated reports of *C. c. buccinator* within the nesting range of *Cygnus columbianus columbianus.* The results are compared with counts in the previous 20 years and especially the intensive 1968 survey.

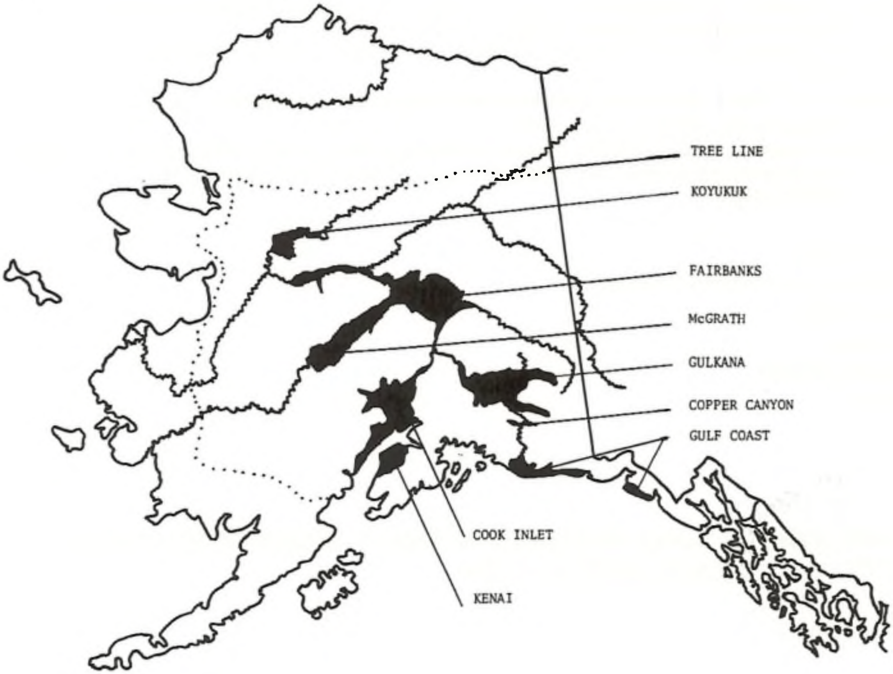

Fig 1. Habitat units of *Cygnus c. buccinator* in Alaska.

Survey method

A Cessna 185 amphibian, a high-wing single-engine four-place aeroplane, was used. USGS maps of a scale 1:63 360 were used to navigate and to record all data precisely. The survey was conducted between 7 August and 15 September, at the time when broods were large enough to be easily seen and before fledging, giving a record of swans on territory. This survey required 186 hours of flight time for a total of some 31 423 km.

Swans were recorded as single birds, pairs, flocks of three or more and a number of young birds in broods. A comparison of birds in pairs that appear to be on territory, whether accompanied by young or not, seems to offer the best indication of population trends. Production seems to have been better in 1968 when 32% of the population were young-of-the-year compared with only 28% in 1975.

Results

The actual counts of *C. c. buccinator* were 2847 in 1968 and 4170 in 1975 for an increase of 46% in observations (Table 1). Paired bird observations increased from

1320 to 2102. A direct comparison is not possible as the 1975 survey included four habitat units not covered in 1968 and required 81% more air miles and covered 64% more habitat. A map by map comparison of areas covered in both years indicates a 24% increase of paired birds since 1968 which works out to a compounded annual increase of 3.1%.

Table 1. Total swans 1968 and 1975 and percent composition

		Single adults		Paired birds		Flocked adults		Young in broods		Totals	
		no.	%	no.	%	no.	%	no.	%	no.	%
Gulf Coast	68	29	3	442	43	191	19	363	35	1025	100
	75	32	4	442	52	190	22	193	23	857	101
Copper Canyon	68	5	3	56	35	53	34	44	28	158	100
	75	2	1	56	31	72	40	49	27	179	99
Gulkana	68	31	5	288	49	81	14	191	32	590	100
	75	43	4	556	54	155	15	284	27	1038	100
Kenai	68	3	2	86	48	27	15	65	36	181	101
	75	5	3	72	50	29	20	39	27	145	100
Cook Inlet	68	19	5	224	54	50	12	124	30	417	101
	75	36	6	340	55	60	10	181	29	617	100
Fairbanks	68	21	4	224	47	94	20	137	29	476	100
	75	21	2	518	47	185	17	388	35	1112	101
McGrath	68	—		—		—		—		—	
	75	6	16	20	54	4	11	7	19	37	100
Koyukuk	68	—		—		—		—		—	
	75	6	3	94	52	45	25	35	19	180	99
Fort Yukon	68	—		—		—		—		—	
	75	0		2	67	0		1	33	3	100
Haines	68	—		—		—		—		—	
	75	0		2	100	0		0		2	100
Totals	1968	108	4	1320	46	496	17	923	32	2847	99
	1975	151	4	2102	50	740	18	1177	28	4170	100

Gulf Coast There are 504 144 ha of coastal lowland habitat along the Gulf of Alaska coast. The area had 1025 swans in 1968 and 857 in 1975, an apparent decrease; however, birds seen in pairs remained exactly the same at 442. The land is largely in US Forest Service ownership with perhaps 20% in State of Alaska ownership and a smaller portion eligible for native selection as private lands. The habitat is pristine except for an oil-field and mining venture abandoned before World War II, a few fishermen's cabins along the coast and a short road. There is a potential for oil development both onshore and offshore, for strip coal-mining and for recreational cabins. Helicopters and low-flying light planes involved with prospecting are a daily feature. Several swan territories along the road occupied in 1968 were vacant in 1975 and hearsay information suggests they were shot by vandals.

Copper Canyon There are only 12 701 ha of habitat here. Total swans increased from 158 to 179 but paired birds here, too, remained the same at 56 birds. The habitat is in narrow river bottoms surrounded by high mountains. The land is federal property with proposals for refuge status as well as native ownership pending. The area is pristine except for a railroad right-of-way abandoned in the 1930s. A state project for conversion of the railroad grade to a highway seems a likely possibility.

Gulkana Basin This area contains 1 293 408 ha of habitat in an intermountain basin with swan habitat at elevations from 488 to 823 m. Swan totals increased 76% from 590 to 1038 between the two surveys with a 96% increase of paired birds from 288 to 566. It seems likely that surplus birds from the saturated habitat on the Gulf Coast and Copper Canyon units are moving into this contiguous area. The trans-Alaska pipeline corridor bisects this area as well as several roads. About half the area, including the best habitat, is state land with the other subject to native ownership. There are several hundred recreational cabins on major lakes within the state lands and further cabin building seems likely for this famous hunting and fishing area midway between the population centres of Anchorage and Fairbanks.

Kenai Peninsula The Kenai habitat with 402 278 ha is really part of the Cook Inlet area but as it is entirely within the Kenai National Moose Range it has been censused separately. Total birds dropped from 181 to 145 with a drop from 86 to 72 paired birds. Long-term records indicate this may be a natural fluctuation and the population is relatively static. The Moose Range has an active oil-field and a popular recreational canoe system within the swan habitat. An intensive, largely successful effort has been made to prevent swan disturbance.

Cook Inlet In this coastal valley of 1 399 420 ha total swans increased 48% from 417 to 617. Paired birds increased 52% from 224 to 340 indicating a substantial increase. Virtually all habitat in the area is state and private land. It is the site of Alaska's major population centre, largest agricultural development and has the greatest concentration of float planes in the world. Since 1968, recreational cabins have been built on every lake suitable for float plane landing. Many lakes adjacent to the highway network are ringed with cabins. An active oil-field, power lines, roads, railroads and airfields are features of the region. The future promises more of the same plus the possible relocation of the state capital to a wilderness site and strip mining for coal. There is a pending proposal for protected swan management areas covering some 20 250 ha of the best swan habitat.

Fairbanks There are 1 893 715 ha of habitat in the broad valleys of the Interior. Observed birds increased from 476 to 1112 in this unit with paired birds increasing from 224 to 518 for an increase of 131%. The 1975 survey was more extensive; thus the true increase, though substantial, is less than indicated. The habitat is two thirds in state ownership with native selection and National Interest lands making up the other third. Disturbance by subsistence hunters and the urban Fairbanks population may affect swan numbers. Recreational cabins are increasing. Expansion of agriculture and oil development are possibilities.

McGrath The 646 185 ha of habitat were not surveyed in 1968. Only 37 swans were seen in 1975. Subsistence hunting may be a factor as the best habitat is along the Kuskokwim River near Indian villages in areas destined for native ownership.

Koyukuk The 1 034 208 ha of habitat had a total of 180 swans observed in 1975. This area, too, is a subsistence hunting area destined largely for native selection. A refuge proposal largely misses the best swan habitat.

Other areas There are isolated *C. c. buccinator* breeding records from the Haines area in southeast Alaska, the Stoney River, the Yukon Flats and the Yukon Delta. A possible nesting record from Prince of Wales Island in southeast Alaska was reported in summer 1976. There are three summer observations from the northeast coast of Alaska. Whether these records indicate pioneering by an expanding population or are isolated occurrences in the marginal fringe of habitat is not known at present.

Discussion

It appears that Alaska's *C. c. buccinator* has been increasing steadily for three or more decades. Just why Alaska's relatively pristine habitat should have become depopulated is not clear. Glacial retreat and thermal records from permafrost indicate a warming during the past 100 years. On the Gulf Coast some glaciers have retreated as much as 100 km (Pewe 1975). It seems likely that in the southern half of the *C. c. buccinator* range much or most of the present habitat was ice-covered 100 years ago. A remnant population may have survived in the never glaciated valleys of the Interior. After the gold rushes at the turn of the century trappers were hunting muskrat *Ondatra zibethicus.* Swans in pairs settling into nesting territories were extremely vulnerable to these undisciplined subsistence hunters. The fur boom peaked in the 1930s and has been declining ever since. Likewise, Alaskan swans may have been persecuted by hunters in winter, particularly in the early occupied portion of the lower Columbia River and Puget Sound.

In 1968, the Alaska *C. c. buccinator* was almost entirely on federal lands and the habitat appeared to be relatively safe from encroachment. Since then, the infant oil industry has already more than doubled the human population within the swan range. Float planes, helicopters, roads, powerlines and pipelines are increasing.

Perhaps the most dramatic change in Alaska, however, has been the yet to be completed change in land ownership. Major portions of the swan habitat have been selected by the state under terms of the Alaska Statehood Act. State lands have been made easily available to those interested in recreational cabin building. Timm and Wojeck (1978) point out there has been a 257% increase in the number of recreation cabins in the Cook Inlet area over the past ten years and that swans fail to return to traditional territories on lakes when the number of actively used cabins exceeds two. The Native Claims Settlement Act of 1971 will convey some 16 million ha of public lands into private native-owned corporations. Most will be in lowlands adjacent to their villages which naturally enough were located in the best wildlife habitats available. Major portions of the best swan habitat will therefore become private lands. Virtually none of the swan habitat is included in new National Park and National Wildlife Refuge proposals pending before Congress.

It seems unlikely that the net result of the changing land status and development in Alaska will result in a complete disaster for *C. c. buccinator.* The 4500-odd individuals are scattered over an enormous area. They utilize some large lakes but also beaver *Castor canadensis* ponds and marshy lakes. Much of the preferred habitat will be unaffected by further development. Experience at Red Rock Lakes and perhaps the Gulf Coast, Copper Canyon and Kenai habitat indicates that populations saturate their nesting areas at rather low densities, thereafter remaining static.

Exclusion from major blocks of habitat means an earlier peak in numbers of this presently expanding population. It seems doubtful that the 3.1% rate of expansion can be sustained and that we will achieve an 8000 bird population by 2000 AD.

At present the US Fish and Wildlife Service is budgeting for a complete *C. c. buccinator* census every fifth year. It is in everyone's best interest to avoid the administrative problems that are the inevitable consequence of allowing the species to decline to the point where they come under the restrictive provisions of the Endangered Species Act. Armed with good information, the public, the native corporations, the State and the Federal Government will wish to co-operate in efforts to perpetuate a healthy population of this noble species.

Summary

An extensive aerial survey of *Cygnus cygnus buccinator* in Alaska in 1975 disclosed a total of 4170 birds. An adjusted comparison with a somewhat less complete survey in 1968 indicates a 24% increase or a compounded annual increase of 3.1%. Changes in land status and economic activity may limit continuing increase.

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STATUS OF *CYGNUS OLOR* IN THE EASTERN UNITED STATES

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Since its introduction early in the 20th century, *Cygnus olor* has become established in the eastern United States and is now expanding its range up and down the coast. In Chesapeake Bay, the southern limit of its range, *C. olor* is being seen farther south each year. Swans are moving north from Massachusetts into New Hampshire and are established in Ontario, Canada. Other North American populations are stable or expanding in Michigan, Montana and British Columbia. Populations are increasing in many coastal areas though actual numbers are difficult to determine because of the species' increasingly migratory habits and lack of cooperation between states making surveys.

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THE NUMERICAL DISTRIBUTION AND THE CONSERVATION REQUIREMENTS OF SWANS IN NORTHWEST EUROPE

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The International Waterfowl Censuses

This paper provides an example of the ways in which the results of the International Waterfowl Censuses are being used to examine the conservation requirements of individual species.

The censuses began in 1967 and are conducted annually over a period of two weeks in the middle of January. The field work is undertaken almost entirely by volunteer observers. Fig 1 shows the location within northwest Europe of the 10 km grid squares in which counts were made in one or more of the seasons between 1967 and 1976. Counts were also made in many parts of northern and central Africa and southwest Asia. In Europe alone, more than 54 000 records were received from a total of 13 380 sites during the course of the ten-year period.

These data are currently being used to compile maps showing the numerical distribution of the species, to estimate the total numbers wintering in each region, to locate and identify the main centres of population, and to look for trends in the levels of population of selected species. These studies provide the information on which to base a sound international programme for the conservation of both wetlands and waterfowl and to demonstrate to governments the extent of their responsibilities.

Waterfowl conservation requirements

During the course of each year the migratory populations of waterfowl pass through many different countries, each of which must take appropriate measures to safeguard the stocks. In the countries bordering the Atlantic and the North Sea the main period of responsibility extends from October until March, when the migrants from the Soviet Union, Scandinavia and Iceland are present in strength. With a few notable exceptions, the breeding populations are small and unimportant. In some places there are large concentrations of moulting ducks, but these are special cases deserving individual attention.

During the autumn and winter months the populations of all waterfowl are confronted by a wide range of hazards; food is often in short supply and the impact of human activities is probably greater than at any other time of year. The greatest single threat is the loss or denial of the wetland habitats on which the birds depend, whether through drainage or development, or disturbance or pollution. In recent years the rate of these losses has increased alarmingly.

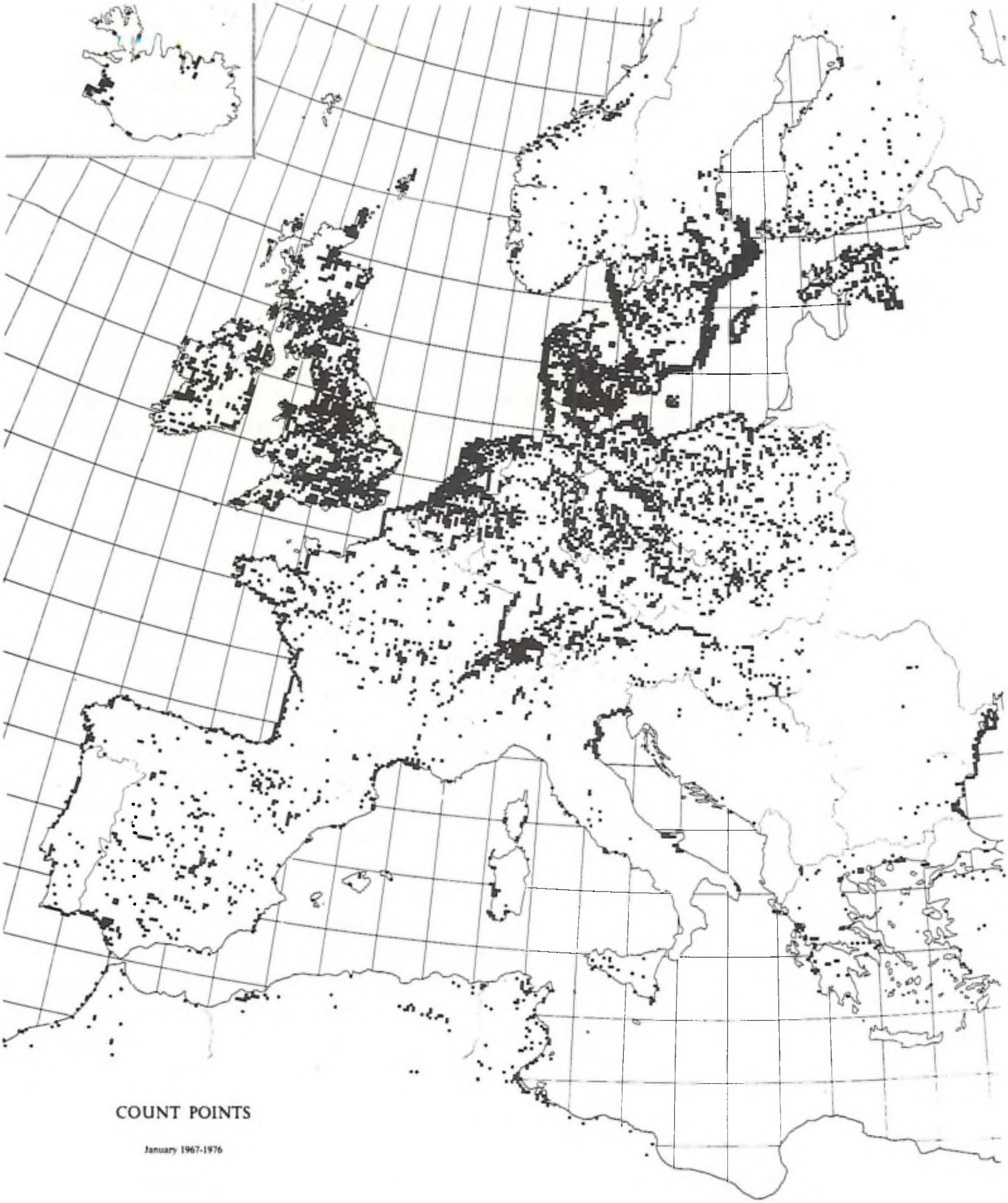


Fig 1. 10-km grid squares in which International Waterfowl Censuses were carried out in January in one or more years between 1967 and 1976.

The primary task of the conservation bodies must be to ensure that the remaining major wetlands are safeguarded from destruction. This can be achieved by advertising their value to wildlife, by insisting that this be taken into account in the planning of new developments and, more especially, by establishing a comprehensive network of reserves. The latter is undoubtedly the most flexible and the most immediately effective form of action.

The censuses show that some waterfowl are much more threatened by loss of habitat than others. The ones most affected are those whose specialized requirements force them to concentrate onto a few traditional resorts. Such species need to be given especial consideration in the planning of reserves, because their requirements can be met at so few places. In some cases the loss of even one major centre might prove disastrous. Some other species have very large populations and are sufficiently adaptable to take advantage of a wide range of coastal and inland habitats. In their case the numbers at any one site are likely to represent only a very small proportion of the population and the provision of specific reserves is seldom warranted. If further protection were needed, the most effective and certainly the most economical action would be to modify the shooting season.

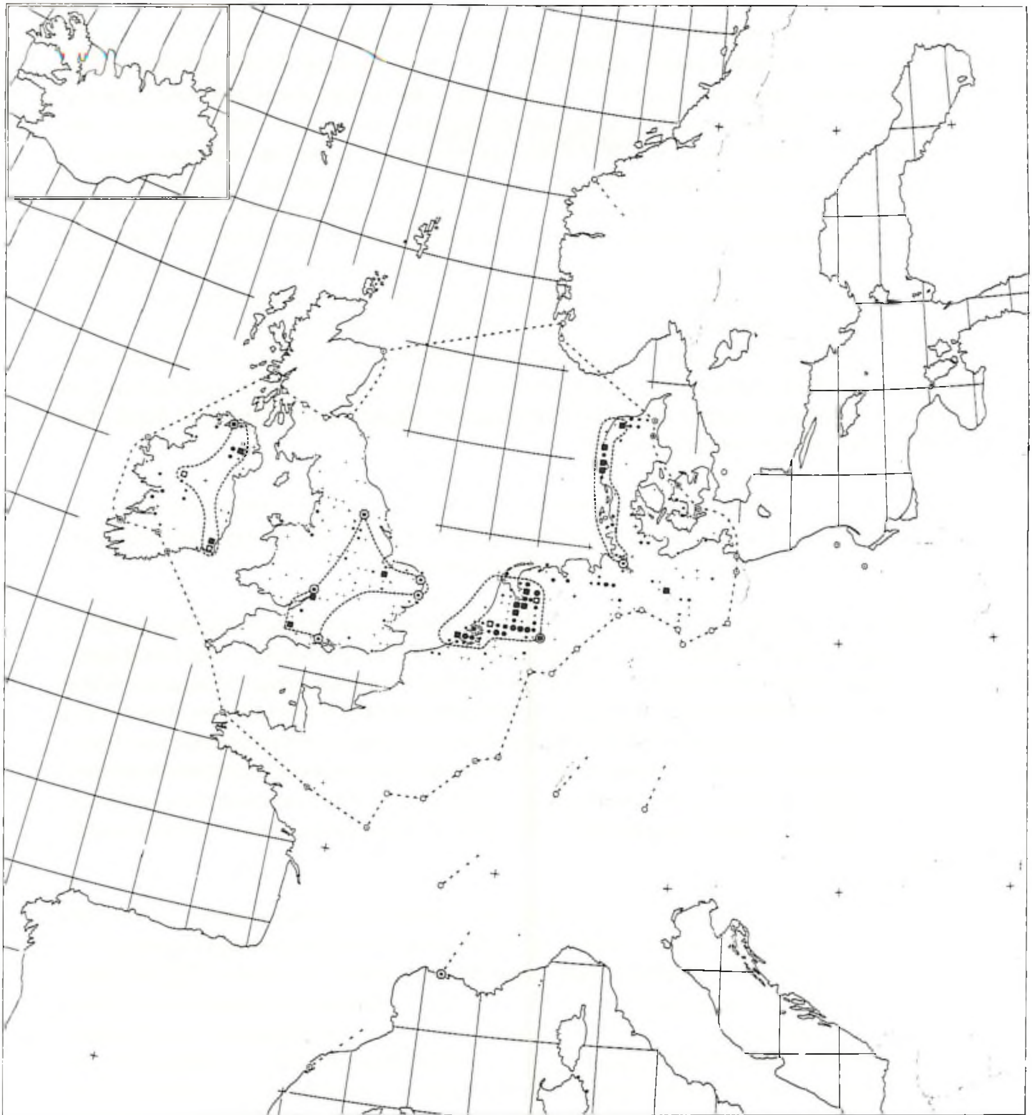
The maps in Figs 2, 3 and 4 are designed to show the numerical distribution of the species, to identify the areas of especial value and to demonstrate the need for conservation. It is now widely accepted that any site which regularly supports more than 1% of a population of a species should be regarded as internationally important. The sites concerned are marked on the maps by squares, the less important areas by dots of varying sizes to indicate the scatter of the population. In the aggregate, the numbers on these smaller centres often represent a sizeable proportion of the total population and many of the sites are likely to be of substantial interest in the national or local context. At least some of them should be safeguarded on this account in addition to the main centres.

The frequency with which a species occurs in a given area is a further aid to the correct siting of reserves. Except in special circumstances, a place which holds substantial numbers every year is a better choice than one which holds very large concentrations in two years out of ten but next to none in the other eight. The maps attempt, therefore, to define the areas within which the species were recorded regularly on most of their main resorts. To qualify as 'regular' a species must have been present at a site on at least 75% of the occasions on which counts were made.

Numerical distribution of swans in northwest Europe

The three species of palearctic swans each present quite different problems in conservation.

Fig 2. January distribution of *Cygnus columbianus bewickii* (right).



Assembled by:
Population and Distribution Division,
International Waterfowl Research Bureau

1978

JANUARY RANGE

O----O	Boundary of the areas within which the population wintered regularly
O	Outlying resorts at which the species was recorded regularly
o- - -o	Probable extent of the normal winter range in western Europe (as shown by the January counts)
o	Casual outlying records

ABUNDANCE

Average counts per 20 km grid square
January 1967-1976

1-4	· ·	5-9
10-19	• •	20-39
40-59	• •	60-79
80-99	●	
100+	◘	- dispersed
	■	- at one site
Concentrations of international importance	■	

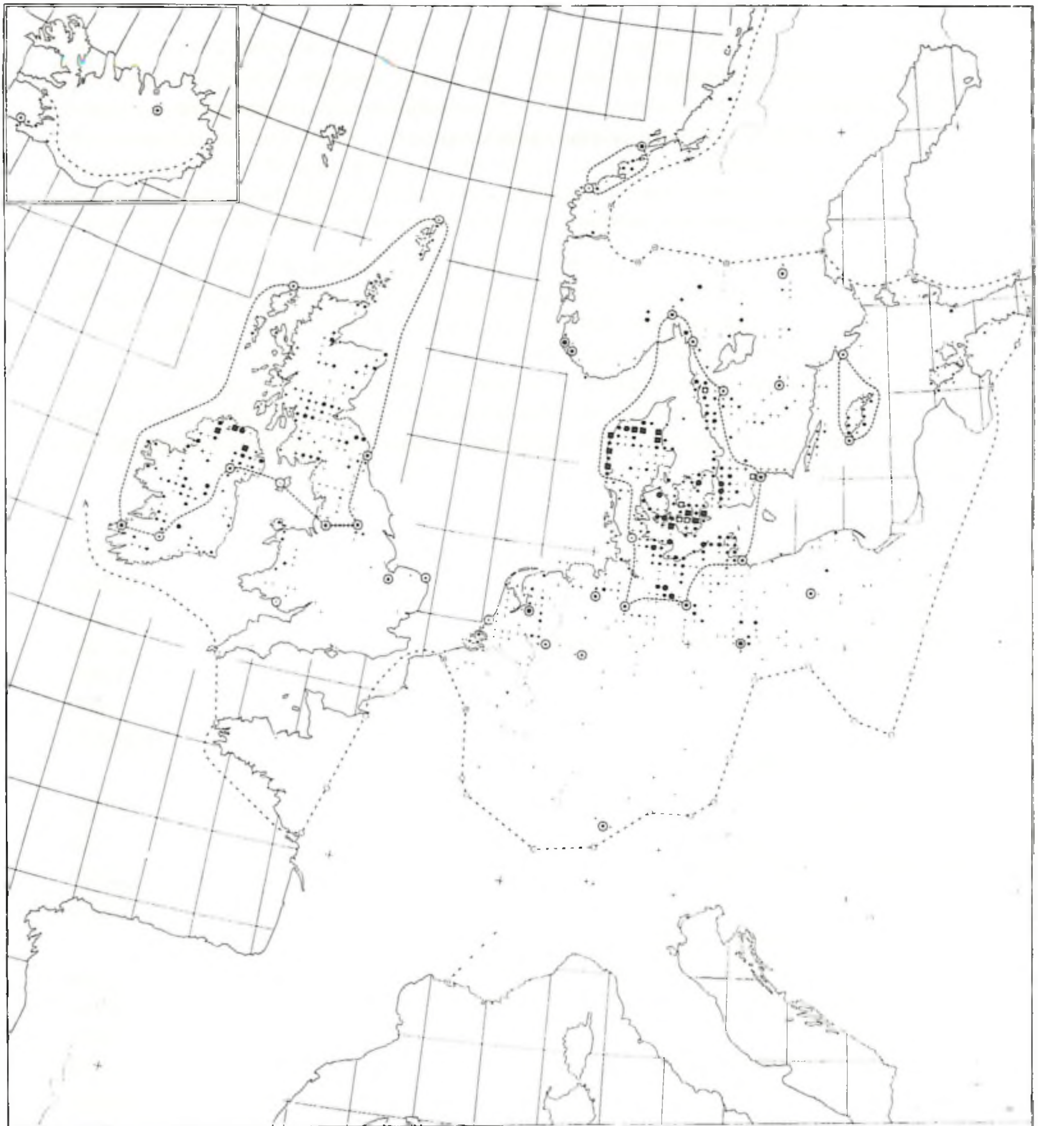
Cygnus columbianus bewickii, with a European population of about 10 000, has by far the most restricted winter range (Fig 2). During January of the ten years 1967 to 1976 it was recorded regularly in five small areas only: along the west coast of Jutland, in the Netherlands, in southern England, in eastern Ireland and in the Camargue. It feeds traditionally on wet pastureland, a type of habitat which is becoming increasingly scarce. Several major changes in the winter distribution have occurred over the past 20 years, only some of which are directly attributable to the loss or deterioration of former resorts. The most striking examples have been the advent of large numbers in several areas of England during the 1950s and 1960s, the virtual abandonment of the meadows along the lower Rhine and Waal in the 1970s and a corresponding increase around the IJsselmeer and in southern Ireland. This adaptability to changing conditions has enabled the species to maintain and even increase its population. There must, however, be a limit to the number of places, at present unused, to which the species could turn in time of need. The present resorts may well be the last.

Cygnus cygnus cygnus has an estimated northwest European population of about 20 000 (Fig 3). Another group of at least 25 000 winters around the Black Sea and eastwards into Turkestan, but these are quite separate.

In northwest Europe more than half the population winters in Denmark and the adjoining areas of Sweden, Schleswig-Holstein and Mecklenburg. The birds here, and elsewhere on the mainland of Europe, belong to a population of about 14 000 individuals, which breeds in Scandinavia and the western Soviet Union. Their main resorts are on the coastal bays and shallows of the western Baltic and on the fjords of north Jutland. Many of these areas are also used extensively by other waterfowl and are obvious targets for conservation. The rest of the population is scattered over a variety of inland habitats, the distribution depending largely on the severity of the winter.

Cygnus c. cygnus wintering in Scotland and Ireland is predominantly, if not exclusively, of Icelandic origin, and is quite distinct from the previous group. The population to which it belongs totals some 5000 to 6000, of which 1000 to 1500 remain in Iceland throughout the winter. The major centres in Ireland are of prime importance and there are a number of other resorts in both Scotland and Ireland, whose value is substantially greater than the map suggests. This is because, in the present study, the northwest European population is considered as a whole: if the Icelandic element were treated separately, several more of the Scottish and Irish sites would qualify as internationally important. The same problem arises with several other species of waterfowl; on balance it seems better to start by looking at the general distribution of the wintering flocks, regardless of their origin, and to discuss the special cases individually in the light of additional information.

Fig 3. January distribution of *Cygnus cygnus cygnus* (right).



Assembled by:
Population and Distribution Division,
International Waterfowl Research Bureau

JANUARY RANGE

- O----O Boundary of the areas within which the populations wintered regularly
- O Outlying resorts at which the species was recorded regularly
- o- - -o Probable extent of the normal winter range in western Europe (as shown by the January counts)
- ∘ Casual outlying records

ABUNDANCE

Average counts per 20 km grid square
January 1967 - 1976

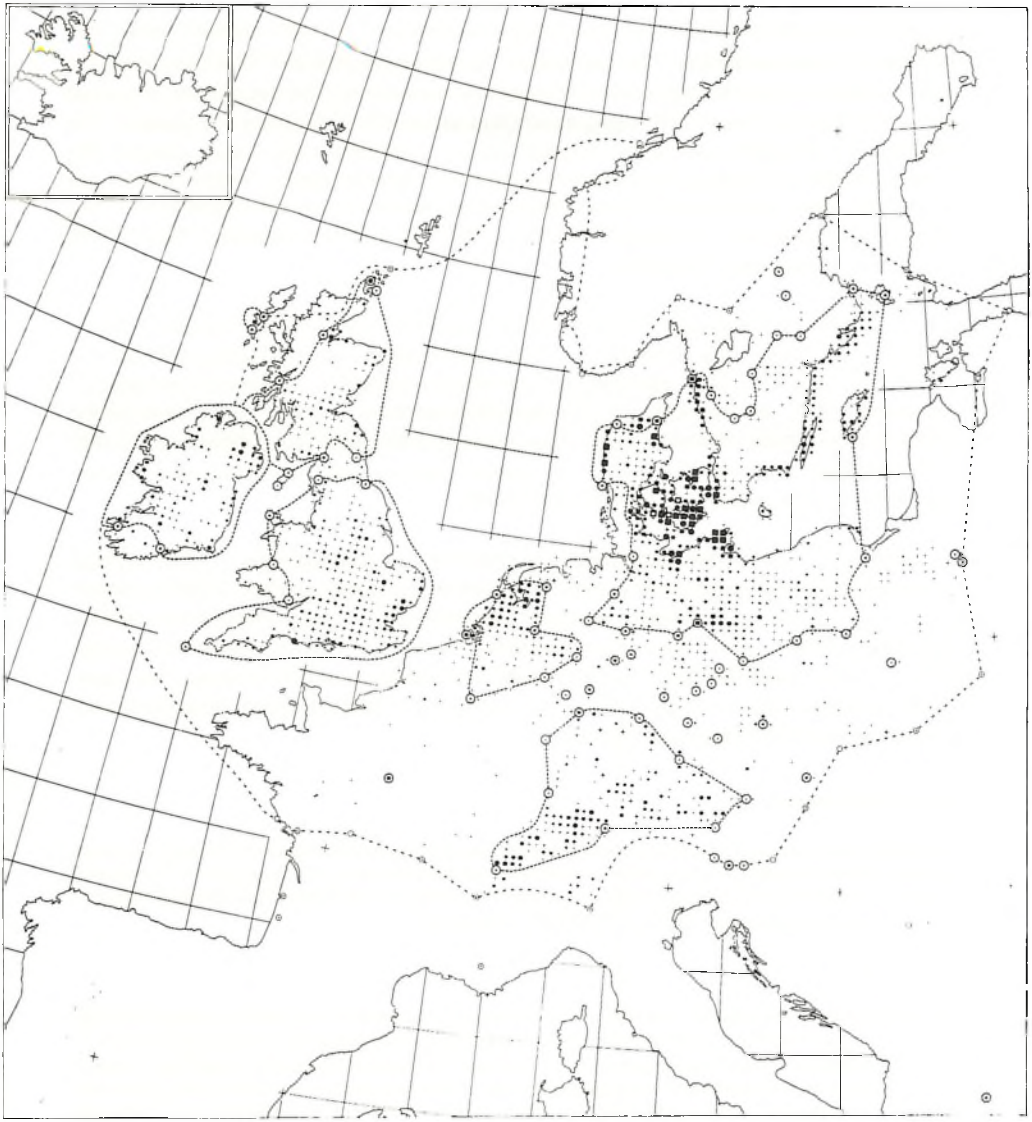
1 - 4	·	+	5 - 9
10 - 20	•	•	20 - 50
50 - 100	•	•	100 - 150
150 - 200	●		
over 200	□		- dispersed
	■		- at one site
Concentrations of international importance	■		

1978

Cygnus olor, unlike most other species of waterfowl, is either sedentary or moves only short distances between its summer and winter quarters (Fig 4). It is the only swan breeding in the area under review. In consequence its conservation is largely a matter of national rather than international concern. Being highly adaptable and tolerant of most human activities, it is able to take advantage of an unusually wide range of urban, rural and coastal wetlands and so is not much threatened by loss of habitat. In several areas the numbers have increased remarkably in recent decades.

The total number of *C. olor* in northern and central Europe is currently estimated at 140 000. From the ringing data and various national studies, it seems that the population can be divided into seven groups, each of which is more or less independent. This is reflected in the distribution map, which shows that the areas of high density are interspersed with zones in which the species is scarce and has relatively few regular resorts. The numbers in each group are made up as follows, the totals for the various countries being the estimated January populations under normal weather conditions:

(1) *Scandinavian-Baltic Group*	
Finland, Baltic republics, Poland	2 000
Sweden	10 000
GDR, West Berlin	15 000
FRG: Schleswig-Holstein, Niedersachsen	3 000
Denmark	70 000
Norway	300
	100 300
(2) *Netherlands Group*	
Netherlands	4 500
FRG: Nordrhein-Westfalen	800
Belgium, northwest France	600
	5 900
(3) *Central European Group*	
Czechoslovakia, Austria	1 250
FRG: central and south	4 000
Switzerland	4 200
Southeast France, north Italy	650
	10 100
(4) England and Wales	14 700
(5) Scotland: mainland and Orkney	2 600
(6) Scotland: Hebrides	900
(7) Ireland	5 000
GRAND TOTAL	139 500
Highest total actually counted in any one census	103 440



Assembled by:
Population and Distribution Division,
International Waterfowl Research Bureau

JANUARY RANGE

- Boundary of the areas within which the population(s) wintered regularly
- Outlying resorts at which the species was recorded regularly
- Probable extent of the normal winter range in western Europe (as shown by the January counts)
- Casual outlying records

ABUNDANCE

Average counts per 20 km grid square
January 1967-1976

1 - 10			10 - 20
20 - 50			50 - 100
100 - 200			200 - 500
500 - 1000			
over 1000			- dispersed
			- at one site
Concentrations of international importance			

Fig 4. January distribution of *Cygnus olor* (right).

The Scandinavian-Baltic group has increased greatly in recent decades and now comprises three-quarters of the northwest European population. The birds here are more migratory than those in other groups and in summer the population is spread over a wide area around the Baltic, extending eastwards to Estonia. By January the majority of the birds are concentrated into a relatively small area around the Danish islands and along the Swedish and East German coast. These resorts are clearly of great importance to the group and ought to be safeguarded on that account. Oil pollution is a major hazard in this area and is probably a much more serious threat than loss of habitat.

The groups in the Netherlands and central Europe have both shown recent signs of increase. The safeguards afforded by the wide dispersal of the flocks, and by the reserves set up for other species, are probably sufficient. It should perhaps be mentioned that the numbers in the Netherlands have not yet been determined satisfactorily: several recent books have quoted and requoted a figure of 15 000 to 20 000 but there is no evidence to support this in any of the winter censuses, the highest count amounting to less than 5000.

The population in Britain and Ireland is divisible into four groups. The recoveries of several thousand ringed birds show that the population is almost entirely sedentary; very few of the movements recorded within the country have amounted to more than 50 km, and there is no migration to or from the mainland of Europe, except in very cold winters. As in the Netherlands and central Europe, the population is spread over a large number of resorts, very few of which hold sufficient numbers to warrant especial attention.

Acknowledgements

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Summary

The International Waterfowl Censuses held annually in January since 1967 produced 54 000 records from 13 380 sites in Europe in their first ten years and are used to compile maps showing the distribution of wintering waterfowl. The maps illustrate distribution of species, areas of especial value and the need for conservation, as well as the frequency of a species at a given site. Figures are given for the current size of the northwest European populations of *Cygnus columbianus bewickii, Cygnus c. cygnus* and *Cygnus olor.*

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CYGNUS COLUMBIANUS BEWICKII IN THE BORDER LAKES OF THE IJSSELMEER POLDERS

E P R POORTER

Introduction

The shallow coast of the IJsselmeer and the border lakes of the IJsselmeer polders (Fig 1) have always been an important area to the western palearctic population of *Cygnus columbianus bewickii,* which winters in northwest Europe. Regular counts of the swans present during the winter have been carried out since the end of the 1950s.

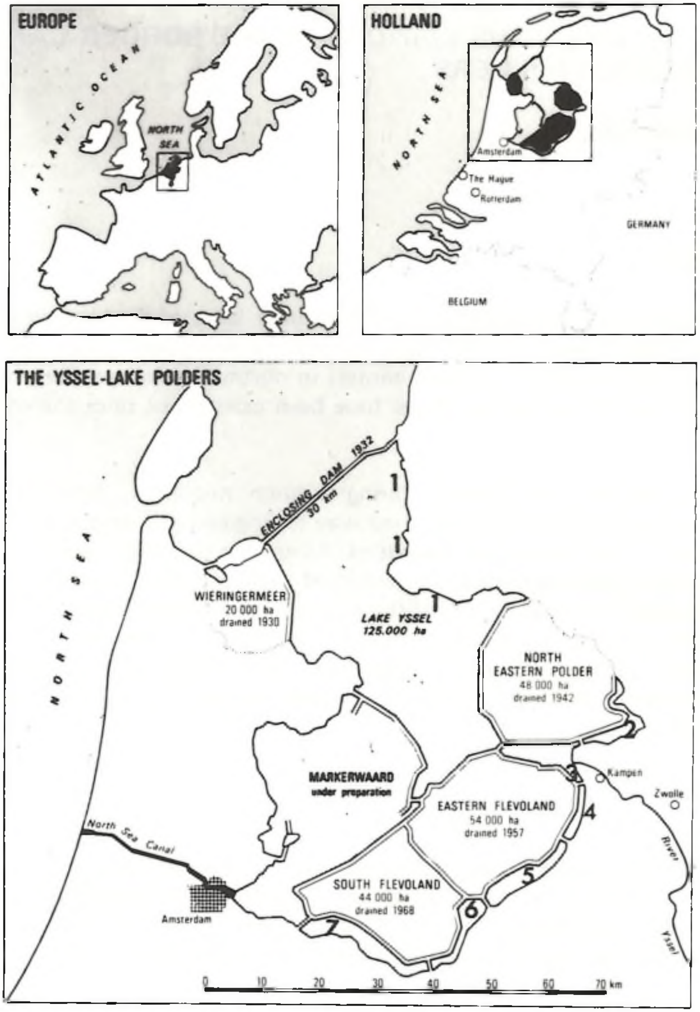
The highest numbers are present during autumn migration, from October to December, when birds that stop on their way to England and Ireland and the birds that will stay for the winter are assembled. As arrivals and departures of transient birds take place before and after the period of peak numbers, the total number of birds that exploit the food supply of the area is greater than indicated by the maximum number present.The maximum numbers (4203 on 18 November 1976; 2790 on 21 October 1977; 2561 on 7 November 1978; 2649 on 25 October 1979) amount to between 20% and 30% of the western palearctic population, assessed at about 13 000.

Food

The food of the swans in the IJsselmeer and its border lakes consists of the nutritious perennial organs of pondweeds, ie tubers of *Potamogeton pectinatus* and stolons of *P. perfoliatus.* When the water level is lowered in the autumn for hydrological reasons, new food supplies come within reach of the swans.

During the late 1960s the water quality in the area deteriorated quickly, hypertrophication causing the pondweeds and other submerged vegetation to vanish from most of their former area. The swans, having lost much of their rich food-stock, became field-feeders on pastures, grass-ley, winter-wheat, waste potatoes and sugar-beet leaves and tops. Some parts of the border lakes where the vegetation of pondweeds remained or where it recovered after being nearly exterminated are still of importance to the swans.

Measures are in operation or planned to improve the water quality of some lakes, including phosphate-retainment at the purification plants and at the sources. These can be expected to end the permanent bloom of blue algae *Oscillatoria agardhii,* enabling the pondweeds to grow again in extensive zones and high biomass.



1 FRISIAN COAST
2 ZWARTE MEER
3 VOSSEMEER
4 DRONTERMEER
5 VELUWEMEER
6 WOLDERWIJD
7 GOOIMEER

Fig 1. Europe, the Netherlands and the IJsselmeer border lakes. 1 Frisian coast; 2 Zwartemeer; 3 Vossemeer; 4 Drontermeer; 5 Veluwemeer; 6 Wolderwijd; 7 Gooimeer.

Water quality

Other shallow waters where extensive fields of *P. pectinatus* grew in the past and where large numbers of swans used to stay, ie the Frisian coast (4000 to 7000 at peak), Zwartemeer and Vossemeer (Fig 2), are all in open connection with the outlet of the River IJssel (a tributary of the River Rhine) and will remain hypertrophicated and polluted. The swans will therefore be entirely dependent on the purified lakes, Veluwemeer, Wolderwijd (including Nuldernauw) and the Gooimeer. None of these is protected by law and apart from one or two small islands there are no reserves. All these lakes are used for recreation and no restrictions have been made on behalf of the birds. Indeed, sailing, boating and wind-surfing show increasing tendencies to extend far into the waterfowl winter season. All the lakes are State-owned and their main function is hydrological.

Conditions in individual border lakes

VELUWEMEER (Gelderland and IJsselmeer district)

2880 ha. 52°25'N 5°45'E. Shallow eutrophic freshwater lake (depth: 0.1 to 2.5 m; salinity: 100 mg/l).

Main habitats: Reedbeds on the shallow side, on average 20 m wide; local sandbanks with clumps of *Scirpus maritimus;* zone of submerged waterplants, notably *Potamogeton pectinatus,* extending from 0.3 to 1.0 m below summer level; zone of deeper water with patchy distribution of *P. perfoliatus.*

Avifauna: Birds of reed-land and marsh, waders, dabbling and diving ducks, swans and roosting geese.

The lake is of international importance for the western palearctic population of *C. c. bewickii* (Fig 3) and *Anas clypeata* (average 1250).

Before hypertrophication the area was also of international importance to: *Anas acuta* (average 15 000), *Mergus albellus* (average 350), *Bucephala clangula* (average 5000), *Aythya ferina* (average 3000).

The lake has been of outstanding importance to migrating and wintering *C. c. bewickii* since 1935. Submerged waterplants, notably *Potamogeton pectinatus,* became more abundant when the area was separated from the IJsselmeer in 1956. Regular counts have been carried out since 1957. Fig 3 shows that the swans occurred in large numbers in winter as well as in autumn.

The summer water level was raised by 30 to 40 cm in 1959, 1960 and 1961, result-

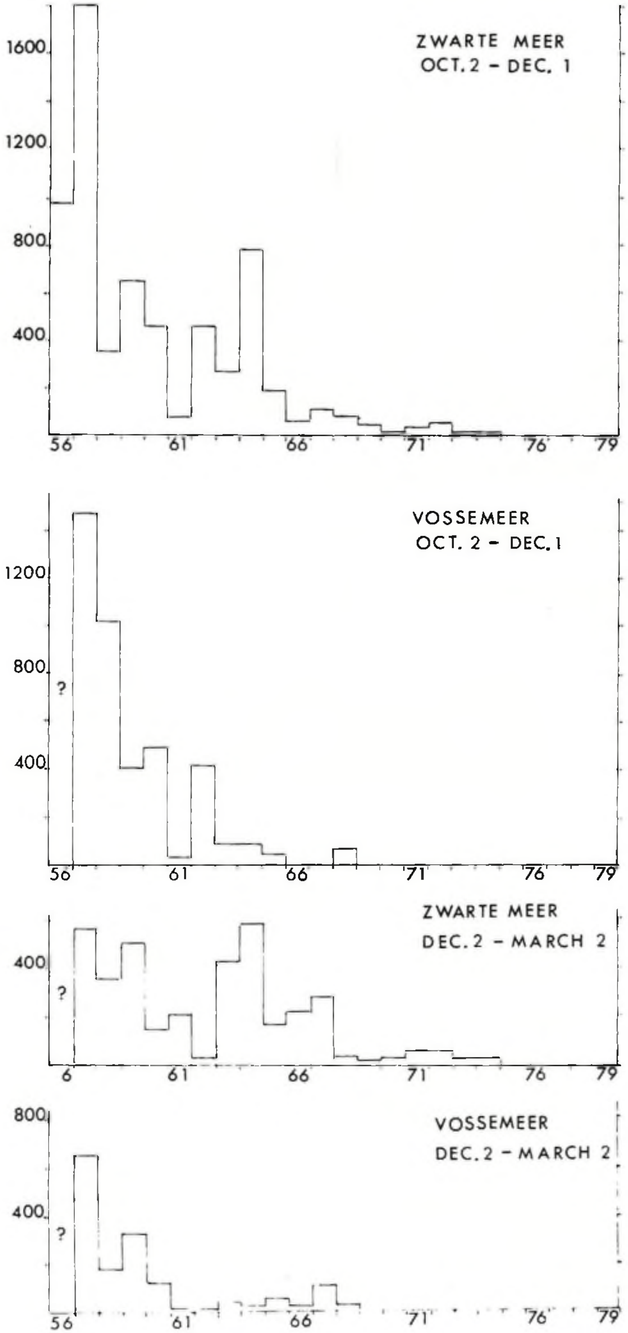


Fig 2. Average numbers of *Cygnus columbianus bewickii* at Zwartemeer and Vossemeer.

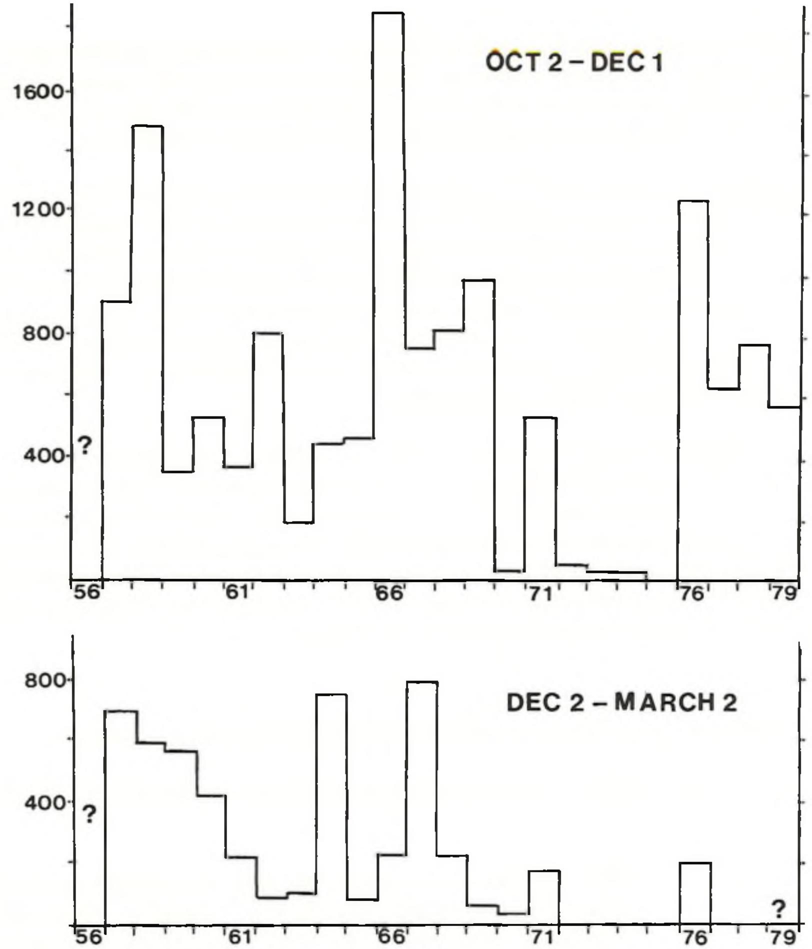


Fig 3. Average numbers of *Cygnus columbianus bewickii* at Veluwemeer.

ing in almost complete replacement of *P. pectinatus* by *P. perfoliatus;* the winter level was high in 1960/1961 and 1961/1962. These factors made the area less suitable for feeding swans from 1959 to 1961. During the following years *P. pectinatus* was again dominant, with the exception of 1965 when the water level in summer was again raised. During the 1960s the water quality gradually deteriorated through eutrophication. In 1969 the submerged vegetation was still in rather good condition. In 1970 the biomass suddenly dropped to less than 30% of that in 1969. In 1971 the submerged vegetation largely recovered but during 1972 to 1975 it was almost absent. Hardly any *C. c. bewickii* visited the lake for feeding during this period, either in autumn or in winter.

Since 1976 the water quality has been improved to some extent and the vegetation of *P. pectinatus* has partly recovered, especially in places where water percolates from the higher sandy soils of the Veluwe which borders the lake on its shallow side. The swans immediately took possession of the lake again that year.

In the autumn of 1978 and 1979 counts were carried out daily, resulting in 32 000 and 20 000 'swan days' respectively. The carrying capacity of the vegetation is still too low to supply a large number of swans with food as in former years, but can be increased to perhaps five times that of 1978 when further measures to repel eutrophication have been effected. Water quality improvement in the Veluwemeer has much greater potentiality than in other parts of the IJsselmeer area because of the relatively high quantities of water percolating into it. Phosphate is precipitated by the iron in this water in aerobic conditions.

Nearly half of the area of the lake (1375 out of 2880 ha) has a depth of 70 cm in the winter. This enables the swans to dig out tubers and stolons of pondweeds over large stretches. During the summer of 1978 the total area of *P. pectinatus* was 351 ha. Dry weight of stems and leaves was 23 718 kg (mid-July). This total biomass corresponds with 40 083 kg of tubers (sampling between 23 September and 8 November). From sampling in March 1979 it appeared that 17 500 kg of the tubers of *P. pectinatus* were consumed by the swans.

WOLDERWIJD, including Nuldernauw (Gelderland and IJsselmeer district)

2400 ha. 52°20'N 8°35'E. Shallow eutrophic freshwater lake (depth: 0.1 to 2.5 m; salinity: 100 mg/i).

Main habitats: Small reedbeds on the shallow side, on average 10 m wide; zone of submerged waterplants, notably *Potamogeton pectinatus,* extending from 0.3 to 1.0 m below summer level; zone of deeper water with patchy distribution of *P. perfoliatus.*

Avifauna: Waders, dabbling and diving ducks, swans.

The lake is of international importance for *C. c. bewickii* (Fig 4) and *Anas clypeata* (average 300).

Before hypertrophication the area was of international importance to: *Anas strepera* (average 100), *Anas crecca* (average 3000), *Anas acuta* (average 5000), *Aythya ferina* (average 3000), *Mergus albellus* (average 300), *Mergus merganser* (average 900).

The area has been of outstanding importance to migrating *C. c. bewickii* in autumn

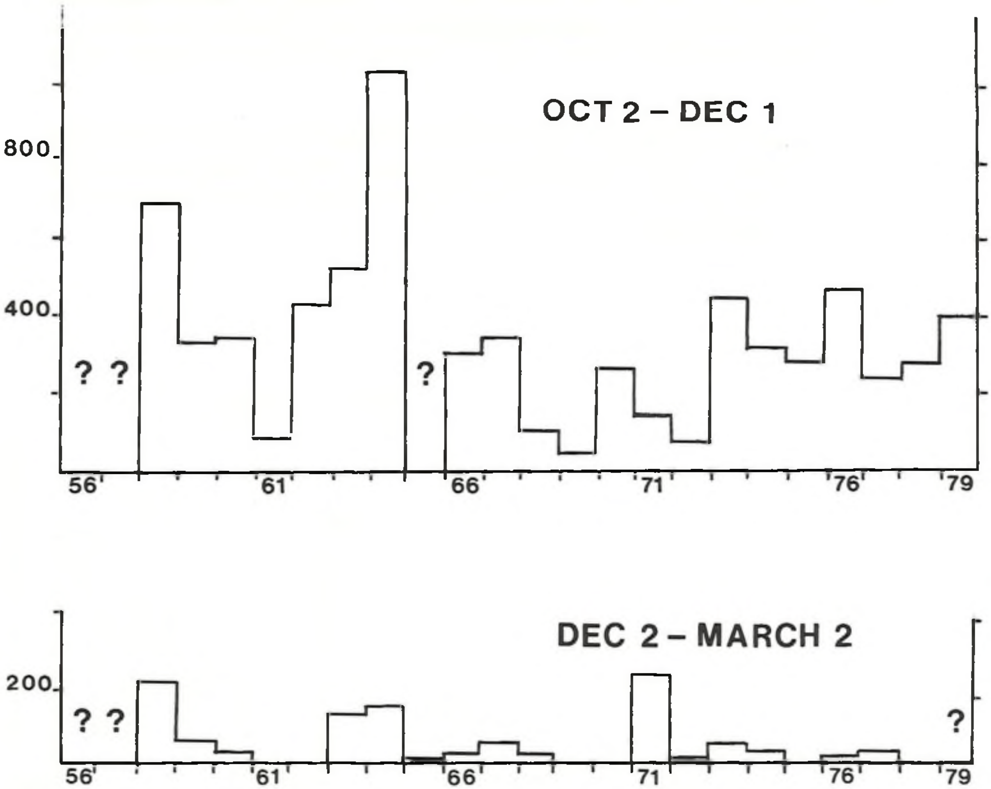


Fig 4. Average numbers of *Cygnus columbianus bewickii* at Wolderwijd.

since 1935. The vegetation of submerged waterplants did not become more abundant when the area was separated in 1967 from the IJsselmeer as it did in the border lakes Veluwemeer, Drontermeer, Vossemeer and Zwartemeer, because the water quality caused severe limitations as soon as dike-building for the new polder of South Flevoland was finished.

Regular counts have been carried out since 1958, but before 1969 most counts did not cover the whole area. Average numbers prior to 1969 are therefore too low in Fig 4. Contrary to most of the other areas where *C. c. bewickii* used to stay in the IJsselmeer area, the Wolderwijd (and Nuldernauw) did not usually hold (and still does not hold) large numbers of swans during winter: the carrying capacity of the vegetation was obviously too low. An explanation could be that before enclosure the water was too broken for extensive and high biomass pondweed vegetation, while after the enclosure the water quality was limiting because the effluent of duck-farms and purification plants was no longer diluted by the water of the IJsselmeer.

When water quality improvement measures have been taken it can be expected that the carrying capacity for *P. pectinatus* will increase. About 1000 ha of shallow water have a potential for carrying a high biomass of vegetation in water where the bottom is accessible to swans.

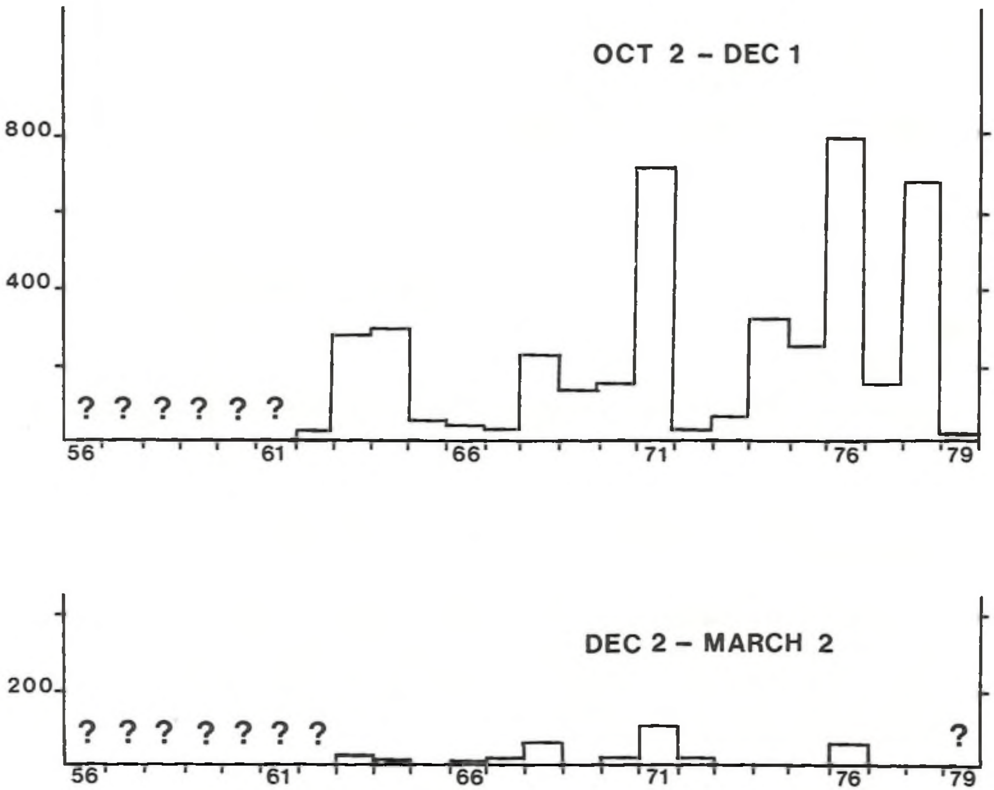


Fig 5. Average numbers of *Cygnus columbianus bewickii* at Gooimeer.

GOOIMEER (Province of Noord-Holland and IJsselmeer district)

2200 ha. 52°20'N 5°10'E. Shallow eutrophic freshwater lake (depth: 0.1 to 2.5 m; salinity: 125 mg/l).

Main habitats: Reedbeds on the shallow side, on average 20 m wide; zone of submerged waterplants, notably *P. pectinatus,* extending from 0.3 to 1.0 m below summer level; zone of deeper water where *P. perfoliatus* has disappeared.

Avifauna: Birds of reed-land and marsh, dabbling and diving ducks, swans, cormorant.

International importance to western palearctic population of *C. c. bewickii* (Fig 5), *Anas clypeata* (average 300) and *Phalacrocorax carbo sinensis* (feeding area for some hundreds of birds from the breeding colony in the Naardermeer).

Before hypertrophication the area was of international importance to: *Aythya fuligula, Aythya ferina, Bucephala clangula, Mergus merganser* and *Mergus albellus.*

The lake has been of outstanding importance to migrating *C. c. bewickii* since 1935. As in the Wolderwijd, the submerged vegetation of the Gooimeer did not become more abundant when the area was enclosed. It does not hold large numbers of swans during winter.

The carrying capacity of the lake for feeding swans may increase when measures to improve the water quality of the River Eem, which flows into the eastern part of the lake, come into full operation. As in the Veluwemeer, water from the higher sandy soils of the Gooi percolates into the lake. About 500 ha of shallow water is suited for high biomass pondweed vegetation in water where the bottom is within reach of feeding swans.

Summary

The paper reviews the numbers of *Cygnus columbianus bewickii* occurring in the border lakes of the IJsselmeer and their food. Because of hypertrophication and pollution on other waters in the Netherlands, the swans are dependent on these lakes. Conditions in individual lakes are reviewed.

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Migration

ON THE MIGRATION ROUTE OF SWANS IN HOKKAIDO, JAPAN

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Introduction

It is well known that more than several thousand *Cygnus cygnus cygnus* and about a thousand *Cygnus columbianus bewickii* winter in Japan. Recently a few *Cygnus columbianus columbianus* have been reported. There is general agreement on the migratory routes of *C. c. cygnus* along the northern coast of Hokkaido, the Sea of Okhotsk and the Pacific coast of Honshu. On the other hand, there is no established theory on the migration route of *C. c. bewickii* and it is not clear whether it reaches Honshu after coming down to the Gulf of Aniva from Sakhalin or goes back by the same route.

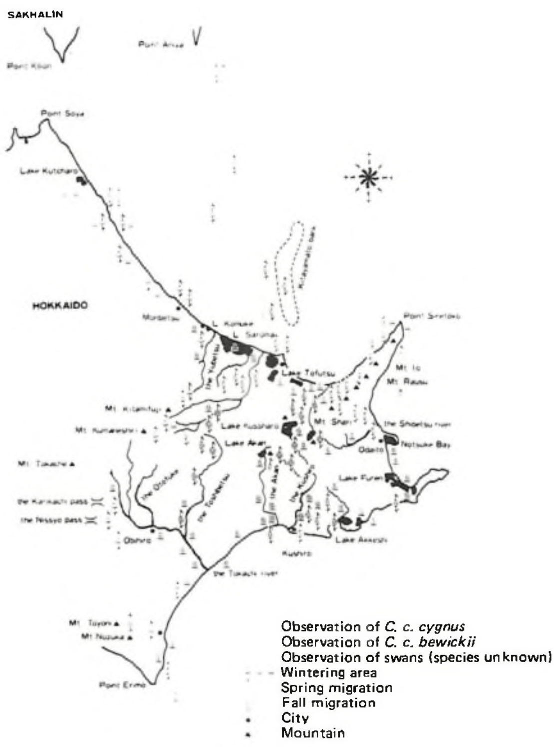

Fig 1. Observations of migrating swans in eastern Hokkaido.

One of the authors observed thousands of swans at Lake Kutcharo near the coast of the Sea of Okhotsk during the spring and autumn migration periods.

As the result of many observations we found the migration route of *C. c. bewickii* follows a line joining the Teshio River, the Ishikari River, Lake Utonai in Tomakomai City and the Shimokita Peninsula in the northernmost tip of Honshu. Sighting points of migratory swans, temporary resting areas and wintering grounds of swans in Hokkaido are plotted in Figs 1 and 2. We concluded that there were three main migration routes in Hokkaido and each route was across the sea and along the coast line.

The migration routes of the swans

Okhotsk–Pacific route

Most swans wintering in Japan come from Point Aniva on Sakhalin to Lake

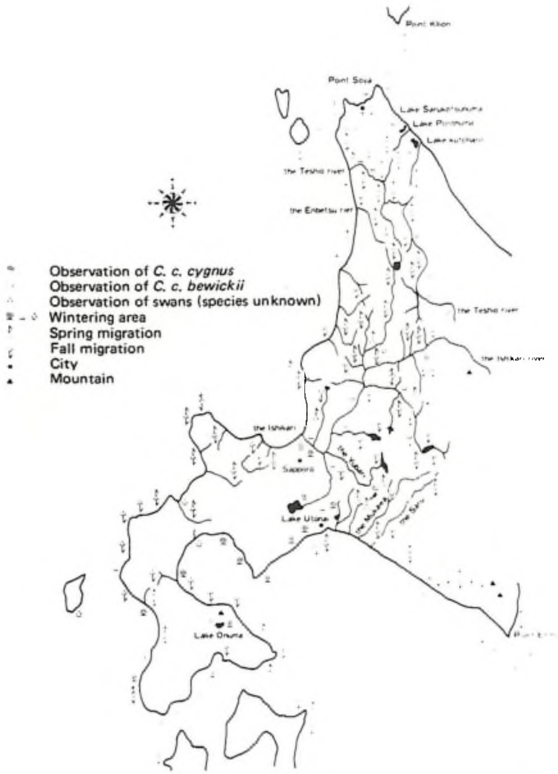

Fig 2. Observations of migrating swans in central and western Hokkaido.

Komuke in Monbetsu City, Lake Tofutsu in Abashiri City and Point Shiretoko in Shiretoko Peninsula. They then move down to Shimokita Peninsula, Aomori Prefecture, via Point Erimo along the coast line of the Okhotsk (Figs 1 and 3).

Some of the migrants arrive at the Plain of Tokachi after crossing the Kitami range and the Ishikari range.

They move continuously southward across near the Karikachi Pass, Nissho Pass, the Hidaka range between Mt Nozuka and Mt Toyoni and reach Lake Utonai on the Pacific coast (Figs 1 and 3). Almost all flocks winter in Lake Utonai but the remainder continue down to the Shimokita Peninsula. The wintering swans in Japan return north on the same route in spring. This course is used mainly by the flocks of *C. c. cygnus* but also by a few *C. c. bewickii.*

Fig 3. Presumed swan migration routes in Hokkaido.

Central axis route

Large flocks of swans arrive at Wakkanai district, northern tip of Hokkaido from Point Klilion in Sakhalin. Most stay at Sarukotsu marsh facing the Sea of Okhotsk, Poro-numa marsh and Lake Kutcharo for a while, then move down to the Teshio River which is situated southwest of these areas. A few move to the mouth of the Teshio River. Most move along the main stream and tributaries of the Teshio River, or the Ishikari River, and reach Lake Utonai. After staying for a short period, they fly over to Shimokita Peninsula (Figs 2 and 3).

Most of the *C. c. bewickii* pass along this route, but *C. c. cygnus* is rare. Most of the *C. c. cygnus* that reach Lake Utonai by Route 1 stay there during the winter. Most of the *C. c. bewickii* go south and in spring, on their way back to their breeding ground, they stay in this area for a while. No wintering *C. c. bewickii* are reported here. Most of the flocks which go south from Lake Utonai set course for Shimokita Peninsula. In autumn some of them go south, and in spring, north, along the coast of the Pacific Ocean (Figs 2 and 3).

C. c. cygnus is usually observed on this coastal route. However, just a small number of *C. c. bewickii* that fly down or stay on this route are observed at Lake Onuma in the southern part of Hokkaido (Fig 2), so it is presumed that *C. c. bewickii* passes along the route on the Pacific Ocean.

Sea of Japan route

The third route starts downstream of the Teshio River and terminates at Tsugaru Peninsula on Honshu along the coast of the Sea of Japan. Among these, some reach the plain of Ishikari via the Teshio range, others from Ishikari Bay. After that they go to the Shimokita Peninsula from Lake Utonai. On the other hand, some flocks go farther south from Suttsu Bay to Tsugaru Peninsula across the central region of Oshima Peninsula and Funka Bay of southern Hokkaido. In spring they go back north along the same course (Figs 2 and 3). Both *C. c. cygnus* and *C. c. bewickii* migrate along this route but the exact ratio is still not known.

Short cuts

In these three migration routes some swans go round the Peninsula, others take short cuts. On Route 1 there are several short cuts, one over the col of the Shiretoko Peninsula and three over the cols of the Hidaka range. On Route 3 they cross at two points at the base of Shyakotan Peninsula and some reach Funka Bay across the base of Oshima Peninsula from Suttsu Bay. Some also fly over the Kariba range from Funka Bay to the Sea of Japan.

Temporary resting on the sea

Several hundred swans on Route 1 were observed at rest on the sea near Point

Shiretoko in spring and some flocks on the floating pack ice in the Sea of Okhotsk. On Route 3 there are some flocks of *C. c. cygnus* and of *C. c. bewickii* every spring on the water 3 to 5 km off Ishikari Bay. From this it can be supposed that not all flocks fly over the Sea of Okhotsk or the Sea of Japan in one stretch.

Flying speed on migration

We used automobiles to follow flocks of swans that move round during the migratory season and we could catch up with them at a speed of 100 km/h. At this time it was windless. In a fair wind, they would fly faster.

Movement of neck-banded swans

A *C. c. cygnus,* IC22, banded at Kominato, Aomori Prefecture, in March 1977 appeared at Lake Akkeshi on 12 March 1977 and at Lake Tofutsu on 14 March

Fig 4. Resightings in Japan of *C. c. cygnus* neck-banded IC22.

1977; it returned to Kominato Bay on 29 December 1977 and to Lake Tofutsu in March 1978 (Fig 4, Table 1). IC05, banded at Kominato Bay on 23 March 1975, appeared at Notsuke Bay on 4 January 1976 and at Kominato Bay on 27 January 1976. IC45, banded at Kominato Bay on 8 March 1978, was at Lake Utonai on 16 March 1978, at Ominato Bay on 10 February 1979 and at Lake Utonai on 4 March 1979 (Fig 5). IC60, banded at Lake Utonai on 1 March 1978, appeared at Lake Tofutsu on 7 December 1978 and at Lake Utonai on 10 December 1978. It stayed there till 4 March 1979. The following winter it was at Lake Utonai till 28 March 1980 and on 29 March 1980 it appeared at Lake Tofutsu (Fig 5). These sightings prove the presence of Route 1, ie the route connects Lake Tofutsu, the Pacific Ocean and Shimokita Peninsula.

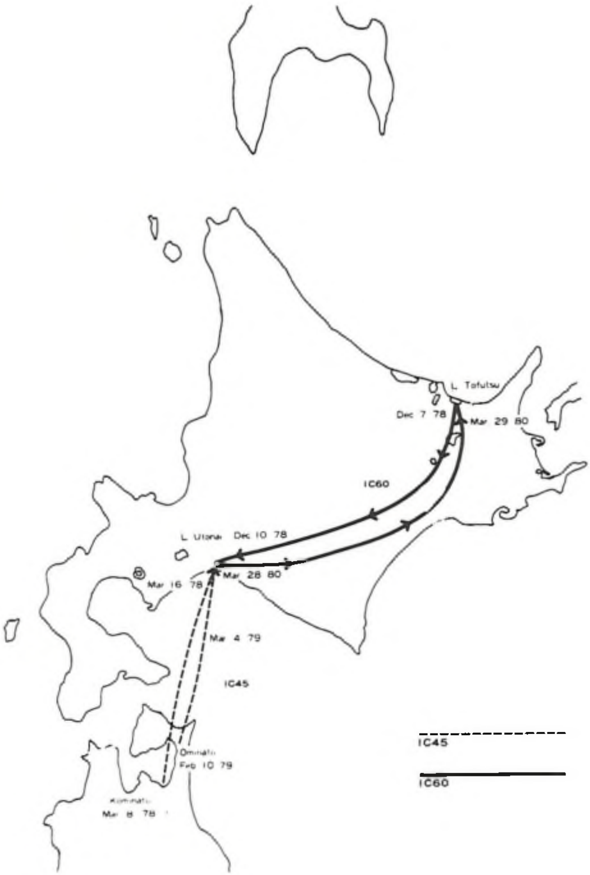

Fig 5. Resightings in Japan of neck-banded *C. c. cygnus.*

Ring no \ Year	1976	1977					1978	
IC02	★Mar 15 L. Tofutsu	Mar 13 L. Tofutsu			Nov 16 L. Kussyaro		Mar 13 Apr 2 L. Tofutsu	
IC11	Dec 2 L. Tofutsu	Jan 3 L. Tofutsu	Mar 27 Notsuke B	Mar 31 Apr 8 L. Tofutsu			Jan 4 Mar 26 Notsuke B	Apr 1 27 L. Tofutsu
IC22		★Feb 13 Mar 1 Kominato	Mar 12 L. Akkeshi	Mar 14 Apr 7 L. Tofutsu	Nov 12 Dec 24 L. Tofutsu	Dec 29 Kominato	Mar 25 Apr 22 L. Tofutsu	
IC26		★Feb 13 Mar 28 Kominato		Apr 4 L. Toro				
IC27		★Feb 13 Mar 1 Kominato	Mar 14 Apr 5 L. Tofutsu					

★ ringing date

Ring no \ Year	1975	1976		1978			1979	
IC05	★Mar 23 Kominato	Jan 4 Notsuke B	Jan 27 Kominato					
IC45				★Mar 8 Kominato			Feb 3 Ominato B	Mar 4 L. Utonai
IC96				★Mar 11 L. Utonai	Dec 7 L. Tofutsu	Dec 10 L. Utonai	★Mar 8 Notsuke B	Jan 14 L. Tofutsu

Table 1. Resightings in Japan of neck-banded *C. c. cygnus*

Ring no \ Year	1978			1979		
006C	Nov. 1 L. Utonai	Nov. 4 L. Izunuma	Nov. 11 L.Toyanogata	Jan. 24 Abukuma r.	April. 23 L. Utonai	
014C	Oct. 31 L. Izunuma	Nov. 22 Abukuma r.		Jan7~Mar.20 L. Izunuma		Apr. 3 L. Kutcharo
015C	Nov. 1 L. Utonai	Nov. 3 L. Toyanogata				
023C	Nov. 4 L. Sarukotsu		Dec. 26 L. Fukushimagata	Mar. 10 L. Hyoko	Apr. 1 L. Utonai	Apr. 23 L. Kutcharo
030C	Nov. 8 L. Izunuma	Nov. 11 L. Toyanogata			Mar. 25 L. Utonai	
034C	Nov. 8 L. Izunuma	Nov. 11 L. Toyanogata			Mar. 25 L. Utonai	Apr. 8 L. Kutcharo
037C	Nov. 4 L. Hyoko	Nov. 7 Dec. 29 L. Izunuma		Jan. 7~ Mar. 20 L. Izunuma	Apr. 1 L. Utonai	
051C	Nov. 3 L. Sarukotsu	Nov. 12 L. Kutcharo	Nov. 18 L. Hyoko	Feb. 18 L. Hachirogata		
052C	Nov. 3 L. Sarukotsu	Nov. 12 L. Kutcharo	Nov. 18 L. Hyoko	Feb. 18 L. Hachirogata		
053C	Nov. 3 L. Sarukotsu	Nov. 12 L. Kutcharo	Nov. 18 L. Hyoko	Feb. 18 L. Hachirogata		

Table 2. Resightings in Japan of neck-banded *C. c. bewickii*

A *C. c. bewickii,* 023C, was observed at Lake Sarukotsu in November 1978, at Fukushimagata on 26 December 1978, and at Hyoko on 10 March 1979, at Lake Utonai on 1 April 1979 and at Lake Kutcharo on 23 April 1979 (Table 2). 006C was observed at Lake Utonai on 1 November 1978, at Izunuma on 4 November 1978, at Toyanogata on 11 November 1978, at Lake Inawashiro from 24 January to 2 February in 1979 and at Lake Utonai on 24 April 1979 (Table 2, Fig 6).

These two examples prove the existence of the central axis route through Lake Sarukotsu, north Hokkaido, and Lake Kutcharo and Lake Utonai.

The movement of 006C in Fig 6 shows that there is a route between the Pacific Ocean and the Sea of Japan and all of these facts have been proved by banding research for the first time. As far as Route 3, along the coast of the Sea of Japan in Hokkaido, is concerned, no banded individual has been discovered. But we can assume the existence of the route because of many reports by many observers, by dead bodies and by photographs of individuals sheltering. The ratio of the two

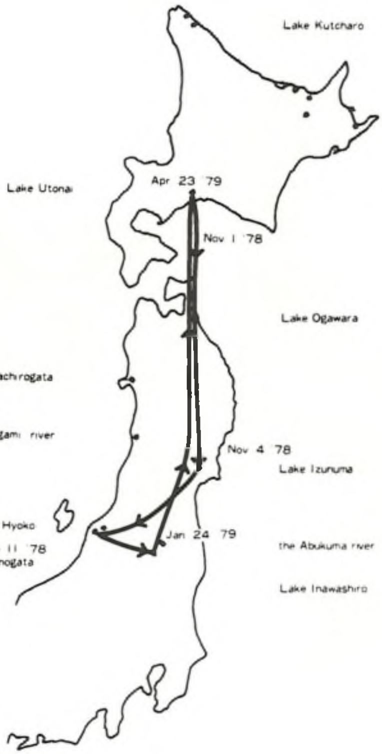

Fig 6. Resightings in Japan of *C. c. bewickii* neck-banded 006C.

species should be investigated in the near future. As for the route between the Sea of Okhotsk and the Pacific Ocean and the central axis route, there are few reports of banded individuals, so much more observation will be required.

Paleogeographical considerations

It is considered that the migration routes of waterfowl are along the shoreline. How is it applied to the three routes of swans we suggest?

Many bird species which live in the world of today appeared in the Pliocene about 1.3 to 2 million years ago. We therefore superimposed the paleogeographical map of Hokkaido upon our migration routes (Fig 7) to find out whether these migratory

Fig 7. Presumed swan migration routes in Hokkaido superimposed on paleographic map of Hokkaido.

routes coincided with the shoreline in the Pliocene. We might well think that the route lies across the ancient sea or shoreline. Judging from the movement of shoreline, the route is assumed to be wide.

Consideration from literature

Much has been reported on migratory routes of swans since 1924 (Fig 8). Most of them concern *C. c. cygnus.* Dr Udagawa suggested in 1967 by pictures that *C. c. bewickii* migrates along the shoreline course or the Sea of Okhotsk and the Pacific Ocean in Hokkaido, but in relation to the *C. c. bewickii* in north Hokkaido, it has been proved that just a small number of them can be seen among the flocks of *C. c. cygnus* (Hatta 1924). The route suggested by Dr Udagawa has not been proved yet. The shoreline routes suggested by lots of experts are in accordance with the results of our research. The route between Shimokita Peninsula and Point Erimo suggested by Dr Mikami has been backed up with the observations of swans at sea along the route (Figs 1 and 2). But in relation to the route between Lake Saroma and Sakhalin, there are no observations which afford proof.

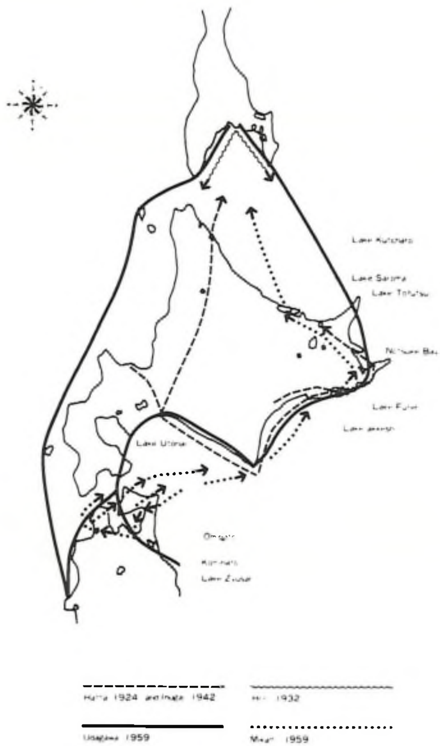

Fig 8. Swan migration routes presumed by earlier observers.

Dr Hatta stated in 1924 that *C. c. cygnus* moving from Lake Utonai to Lake Kutcharo at Hamatonbetsu were the ones that came from Lake Furen and he insisted that they flew to Lake Kutcharo instead of going back to Lake Furen. However, this is the route along which *C. c. bewickii* is mainly moving in spring and autumn, so *C. c. cygnus* is rare. Besides, no banded *C. c. cygnus* has been observed in Lake Kutcharo. Furthermore, no banded individuals that come to Lake Utonai from Lake Tofutsu, located in the south of the Sea of Okhotsk, fly to Lake Kutcharo. Judging from this, flocks of *C. c. cygnus* that came to Lake Utonai from the Okhotsk side of east Hokkaido in autumn cannot be assumed to fly to Kutcharo along the central axis.

Conclusion

We have proved three migration routes of swans — tne route between the Sea of Okhotsk and the Pacific Ocean, the route of the central axis and the coastal route by the Sea of Japan — by getting information from many people, from observations of banded individuals and from literature. Finally, the proof of these routes is not complete and we are going to continue our research and observations.

Summary

The paper reviews observations of migrating swans in Hokkaido and defines three routes used by *Cygnus columbianus bewickii.* Observations of neck-banded swans confirm the use of the routes and possible relationship of the routes to paleogeographical conditions is suggested.

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THE COLD AIR CURRENT IN THE KHABAROVSK AREA AND THE CORRELATION WITH SWAN NUMBERS AT LAKE HYOKO, JAPAN

A NAKANISHI

Introduction

Every winter Lake Hyoko, which is the birthplace of swan protection and is designated as a Natural Monument, is visited by hundreds of migrating swans. The maximum number of swans at Lake Hyoko occurs in the last third of February. In 1950, when swans first migrated to the lake, only 146 swans came, but in 1963, when there was a very heavy snowfall in the area, 315 swans came. In 1970, when the temperature had been low since the autumn, as many as 1019 swans were found there. This was the largest number ever recorded.

The winter of 1979 has been the warmest since the Meteorological Agency was founded in Japan, with the exception of Okinawa and Hokkaido where they had their eighth warmest winter. The largest number of swans (950) was at Lake Hyoko on 3 February. This was the second largest number in 29 years. We feel they came south because they were driven away by the cold air current in the Siberia and Sakhalin areas. Consequently, we tried to find out what kind of relationships there are between the average temperature in January and the number of swans at 12 points which are estimated to be on the courses of both swans and the cold air current.

Data and their processing

The data we used were obtained by Mr Shigeo Yoshikawa. The temperature in northern Japan, Siberia and Korea was the average temperature obtained from weather maps at 0900 in January from 1960 to 1979.

Fig 1 shows the correlation coefficient between the average temperature in January at Khabarovsk and the maximum number of swans at Lake Hyoko and its regression line. The confidence limit at $p = 0.01$ is –0.56, so the value $r = -0.59$ is significant. The linear regression showing the relationship between the two is: X (number of swans) = –3109.3 – 156.2 T (°C).

The correlation coefficient between the average temperature in January in the areas other than Khabarovsk and the maximum number of swans at Lake Hyoko is low. Okhotsk (+0.11), Seoul (+0.12) and Sendai (+0.05) show insignificant plus coefficients. On the other hand, Niigata (–0.06), Aomori (–0.19), Vladivostok (–0.14), Irkutsk (–0.23) and Yakutsk (–0.33) show small minus coefficients. However, in Alexandrovsk the value is –0.47, which is significant at $p = 0.05$ level. In Sapporo (–0.43) and Nemuro (–0.39) the values are also significant. The correlation coefficient in Khabarovsk is the largest of the 12 points.

The characteristics of the weather in January 1962 when the number of swans at Lake Hyoko was small were:

(1) there was a prominent pressure peak over the west coast of Canada and a small number of areas of low atmospheric pressure moving toward the Aleutian Islands;

(2) because the high pressure area near Lake Baikal developed to some extent and

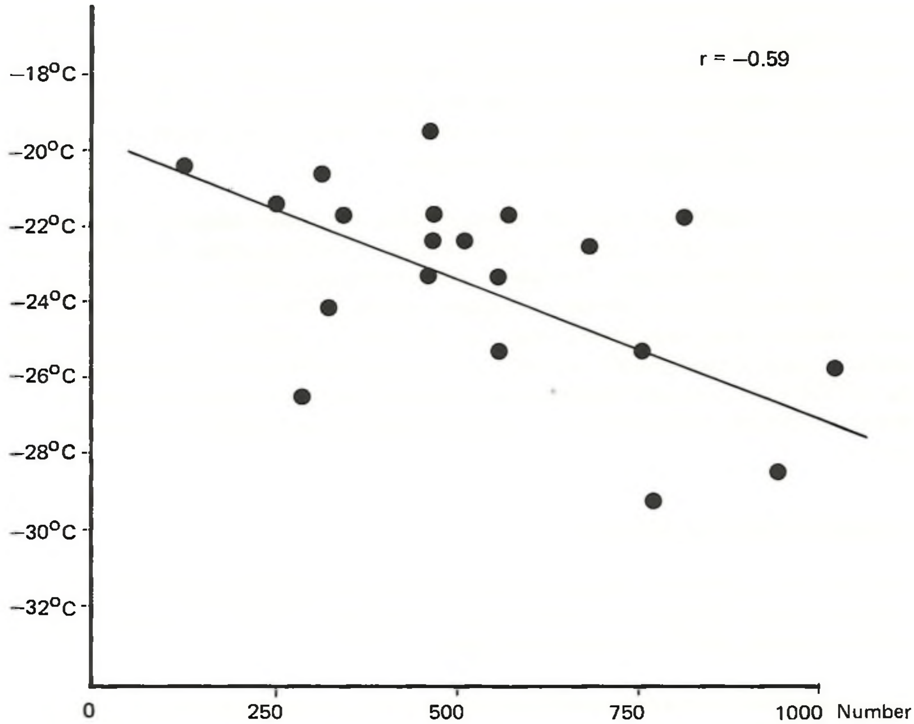

Fig 1. The correlation coefficient between the average temperature in January at Khabarovsk and the maximum number of swans at Lake Hyoko.

a trough of low pressure arose over the eastern Sea of Japan, the cold air current came down to the western part of Japan;

(3) the unusually high temperature over the whole of Siberia continued from the previous month, with its centre located near Lake Baikal. The temperature on the eastern Siberian peninsula registered +11°C. The low temperature area extending from South China to the southern Sea of Japan was the most prominent since the war. In northern Japan the temperature was 11.2°C higher than the average of past years, while it was low in Shikoku and Kyushu and about the same as average in the area from Kanto to Kinki and San-in.

The characteristics of the weather in January 1970 when the number of swans was large at Lake Hyoko were:

(1) the cold air current nucleus coming south from Manchuria reached the Sea of Japan on the night of 16 January, and the temperature at 500 millibars above Wajima registered –44.5°C. As a result, the temperature stood –6.2°C at Matsue

and $-8.0^{o}C$ at Maizuru on 20 January, each of which was the lowest January temperature registered;

(2) various places in northern Japan were hit by the lowest atmospheric pressure area and great damage was done to a wide region. In Tokyo 58.5 mm of rain were registered, the heaviest single rainfall that year;

(3) the ridge of the pressure developed in Siberia in the first ten days of January and a cold air mass from the North Pole moved over the Sea of Okhotsk. In the area of the Pacific Ocean, the altitude of 500 millibars was generally low and a great deal of the polar air of Siberia came south. The temperature in Kinki and the western part of Todaido was the same as the average of past years, while it was low in Hokkaido and its vicinity.

Conclusion

It is obvious that the number of swans coming to Lake Hyoko increases as the temperature at Khabarovsk, Alexandrovsk, Sapporo and Nemuro goes down. The fact that individual swans at Lake Hyoko come from Hokkaido has been confirmed by observing their neck-bands.

Acknowledgements

For comments and suggestions we would like to thank Dr Hisano Hatakeyama, Dr Koichiro Takahashi, Prof Masatoshi Yoshino and Mr Masao Ouchi.

Summary

The routes of cold air currents and average temperatures in January since 1960 were examined to show that high numbers of swans at Lake Hyoko coincide with low temperatures in Khabarovsk (correlation coefficient –0.59), Alexandrovsk (–0.47) and Sapporo (–0.43).

Editorial note

The paper presented to the Symposium had originally been published with many meteorological maps which could not be reproduced in these Proceedings. The full text can be obtained from the author.

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THE WILD SWANS AT LAKE INAWASHIRO, JAPAN: SOME ASPECTS OF THEIR MIGRATION

T OHMORI

Introduction

The greater part of wild swans passing through Lake Inawashiro is *Cygnus columbianus bewickii,* there being a very small number of *Cygnus cygnus cygnus.* For the first time in Japan, a *Cygnus columbianus columbianus* was found and identified in 1968. By 1978, arrival in Japan of eleven *C. c. columbianus* had been confirmed (Table 1).

Table 1. Observation records of *Cygnus columbianus columbianus*

No	Year	First date	Number	Wintering area	Last date
1	1968	Mar 29	1	Lake Inawashiro	Apr ?
2	1973	Jan 21	1	Lake Izunuma	Feb ?
3	1973	Dec 16	1	Lake Izunuma	Feb 17
4	1974	Feb 5	1	Lake Hyoko	Mar 20
5	1974	Feb 6	1	Lake Inawashiro	Apr 12
6	1974	Nov 5	1	Lake Inawashiro	Apr 17
7	1974	Nov 24	1	Lake Ogawara	Dec ?
8	1975	Dec 24	1	Lake Izunuma	Mar ?
9	1975	Apr 14	1 immature	Lake Kutcharo	Apr 14
10	1978	Nov 10	1	Lake Obuchi	Mar ?
11	1978	Dec 16	1	Ominato Bay	Mar 4

Located in the northwestern part of Honshu, Lake Inawashiro region rises highest above sea level among other wintering regions in Japan, forming an inland plateau at 514 m. The lake is up 49 km in circumference. The wintering place, located on the northern bank of the lake, is 13 km in length. There, water plants grow. The remainder of the coast surrounding the lake consists of sand and pebbles with scanty vegetation, and is by no means fit for the wintering of many wild swans. Inawashiro is thought to be a caldera lake born of volcanic activity about a million years ago.

Although little is known as to when migratory birds first saw Japan, the oldest extant record is 'Aizu Fudoki' (Topography of Aizu Region), which Masauki Hoshina ordered his 'Kerai' (retainer) to compile. Masauki Hoshina was the leader of the Aizu clan who lived in what is now Aizu Region, Fukushima Prefecture. The record covers a period of 11 years from 1661 to 1672, and records that wild swans were actually seen swimming.

During the subsequent period of 307 years, wild swans, for the first time in 256 years, were specified as 'protected birds' in 1926, after many years of hunting. Subsequently, we have gone through a period of indiscriminate hunting by the US Occupation Forces. In 1948, when the writer started observing wildfowl, only seven wild swans were found. Later, after a period of very slow increase, since 1965, when the author started protecting and feeding wild swans, there has been a marked increase until at last the 'paradise of wild swans' has been realized (Table 2).

Table 2. Maximum number of the swan species at Lake Inawashiro

	1973	1974	1975	1976	1977
Cygnus columbianus bewickii	600	678	448	404	523
Cygnus cygnus cygnus	33	22	12	13	2
Cygnus columbianus columbianus	1	1	0	0	0

Conservation

We have been trying not to cause the swans to lose their genuine quality as wildfowl, while helping to support their lives and removing threats to their existence. Nevertheless, as they increased in number, we realized there was a want of naturally provided food. Besides, when winter comes, the field on the shores of the lake is completely closed with snow and the swamps buried up to a depth of 80 cm. Confederates, gathered in 1965 to form the 'Lake Inawashiro Wild Swans Conservation Association', therefore started planned feeding in earnest.

Arrival of the swans begins in the middle of October and departure ends in the middle of April. Here autumn comes early and spring late. Thus, migrants stay here longer than in other regions in Japan. From January to February, some wild swans arrive from other wintering regions, but only a very few move away. Thus, a clear line may be drawn between periods of migration, movement and departure (Fig 1).

Aspects of migration

As the winter season arrives, barograms on weather charts assume the 'high in the west and low in the east' character. When the centre of low pressure is near Lake Baikal a strong southeasterly seasonal wind blows all over Hokkaido and northern Honshu.

This low pressure passes through quickly. Subsequently, when the lake enters the high pressure behind the low pressure, the sky over the lake suddenly clears. Then, wild swans make their appearance, increasing in number.

A clear line could be drawn between those swans whose passage courses are obviously related to those of mobile high pressure zones and those whose courses

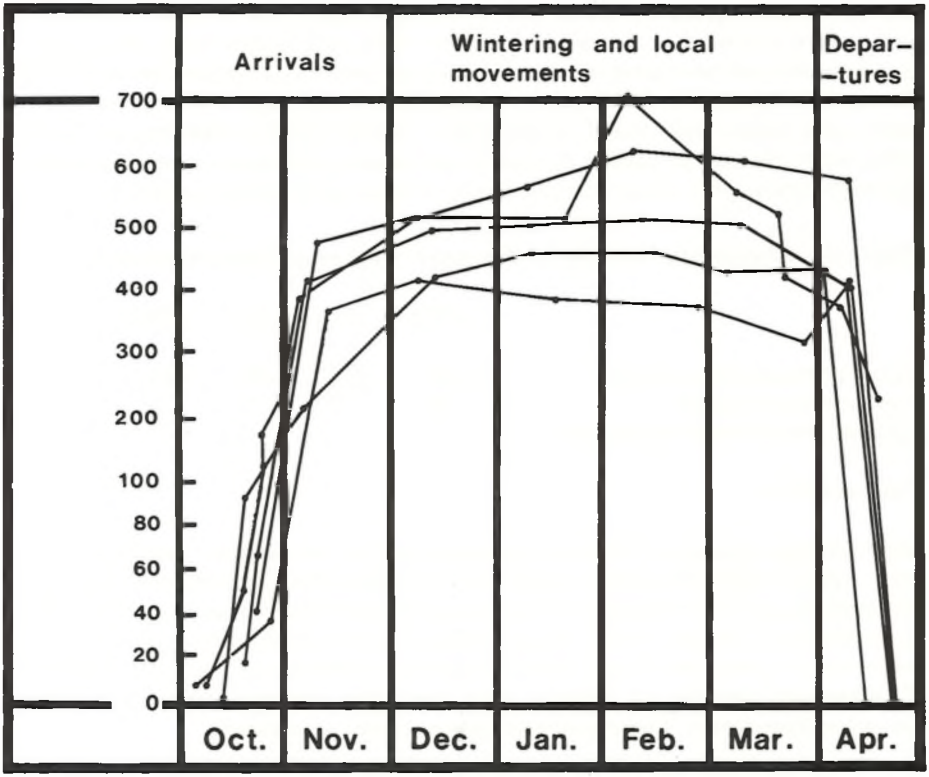

Fig 1. Total swan numbers at Inawashiro in relation to the seasons.

are not so related.

Relation of 'migration' to high pressure centre courses

Wintering period

a) 'A' course

The centre of a high atmospheric pressure zone passes through Lake Baikal, thence in a southeasterly direction. Taking a turn to the east at around 40^{o}N, it proceeds in a northeasterly direction along the Primorski coast, thence passing into Kamchatka. This course is taken mostly in warm years when migrants are few in number.

b) 'B' and 'C' courses

High pressure centres passing through Lake Baikal take either a 'B' or 'C' course. In the former case, the centres proceed in a southeasterly direction. Then, in northern China, turning eastward to the southern part of Korea, they pass into the Sea of Japan. In the latter case, high pressure centres proceed eastward over the whole span of Japanese islands from the western extremity to Hokkaido. At this time, high pressure centres pass through Hokkaido, and sometimes near Sakhalin. Under these favourable conditions, many wild swans winter.

c) 'D' course

Passing through the central part of China, a high pressure centre proceeds northeastwards along the Pacific coast of Japan. Although the sky is clear throughout Japan, warm south winds blow in the opposite direction to the flight course of wild swans. At this time, no swan will arrive to winter.

Departure period

In spring, under conditions of 'high in the south and low in the north', seasonal winds will come over Japan by way of Siberia. An isobaric line surrounding a high pressure zone takes the shape of an oblong band. As it proceeds eastward, it increases in power extending to an oblong area embracing Primorski, the Amur River and Sakhalin. The centre of this high pressure zone passes through Lake Inawashiro. When the after-edge of the high pressure zone reaches the lake, wild swans suddenly take their leave. The next day, as soon as the trough of low pressure passes through, it begins to rain.

a) 'E' course

A high pressure centre will pass through the northern part of China, cross South Korea and then enter the Sea of Japan.

b) 'F' course

A high pressure zone will pass through Shanghai as a Yangtse airmass. After affecting the western part of Japan proper, it will proceed northeastwards.

c) 'G' course

Crossing the East China Sea, a high pressure zone proceeds either along the coast of the Pacific Ocean or northeast over the ocean.

Although wild swans will leave in any of the above-mentioned cases, more take flight in the last two.

Meteorology and migratory conditions

1. An instance from the wintering period, 7 November 1973

When a seasonal wind began to blow, the atmosphere, with the North Pole Crown as the centre, rotated clockwise at a very high speed, attended with a continued jellyfish movement of an isobar. Simultaneously, as if to baffle this movement, a cold air mass nurtured in the western part of the northern polar region moved southward.

The cold snap takes its rise in the orbit motion and rotation of the earth, the temperature of the northern hemisphere drops; stimulated by this, cold snaps or high pressures grow and move southward. These air-currents, as jet currents in the upper air and seasonal winds at ground level, blow from the north into Japan proper.

At an altitude of 3000 m, winds blew constantly, stretching out to the whole of Japan proper and even to Sakhalin. As for the phenomena at ground level, a high pressure centre was moving south-southeastwards at a speed of 45 km/m. The previous day, a 1024 mb high pressure centre was located near Tsingtao, and a cyclone located off the eastern coast of Hokkaido was moving northeastwards. When this Siberian air mass passed Lake Inawashiro, followed by a low pressure area, the lake was enveloped in markedly dense fog assuming an extraordinary aspect of rough weather in the upper air. A northwesterly wind blew all day; there were snowfalls on high mountain tops and rainfall in lowlands. At midnight, the after-edge of the air mass passed over the lake region. On the morning of the same day, the high pressure centre just referred to was located in South Korea. It was reported to be 1021 mb. At that time, the low pressure centre was counted at 984 mb, showing some development. Thus, at 0600 on the same day, 194 *C. c. bewickii* had arrived. Invariably, wintering has occurred and will occur under these conditions. Obviously, the migrants had taken the 'Sea of Japan' course, because it is quite unthinkable that any had migrated at that time from Sakhalin or Kamchatka, which were within the sphere of low pressure. No wild swans would dare to pass through rough weather attended with adverse and cross winds.

2. An instance from the departure period, 13 April 1974

Unlike those in autumn, seasonal winds in spring come from the west as a Yangtse air mass (polar continental air mass). Early in April at Lake Inawashiro, the mild season of spring advances with rapid strides; wild swans start brisk flight training early in April. As a zonal anticyclone approaches, northwest winds gradually turn into west winds. Soon a southwest wind begins to blow, when the after-edge comes in. At this time, the front edge of the high pressure zone expands like a round fan covering a wide arc extending from Primorski to the Amur River. Already, in the west of Primorski, a second high pressure zone makes its appearance. Such a pattern of high pressure is often observed in the departure season. On their flyway, wild swans may smoothly change to a second high pressure, which is thought to facilitate their northward advance. Hence the departure of 514 swans!

The following day was one of nationwide observation by the Japan Wild Swan

Conference. It was found that 580 swans were missing. We feel that these swans had probably flown in the direction of Primorski, the Amur River, and Khabarovsk regions.

Table 3. Meteorological conditions at time of migration

	Wintering	Leaving
Distribution of pressure	West High, East Low, (Winter type)	South High, North Low, (Spring type)
Course of anticyclone	B or C course	F or G course
Wind direction	NW or N	SE or S
Section of anticyclone	Front edge	After-edge

The state of migration under different meteorological conditions is summarized in Table 3.

By looking at the map in Fig 2 and tracing back the wind directions along arrival

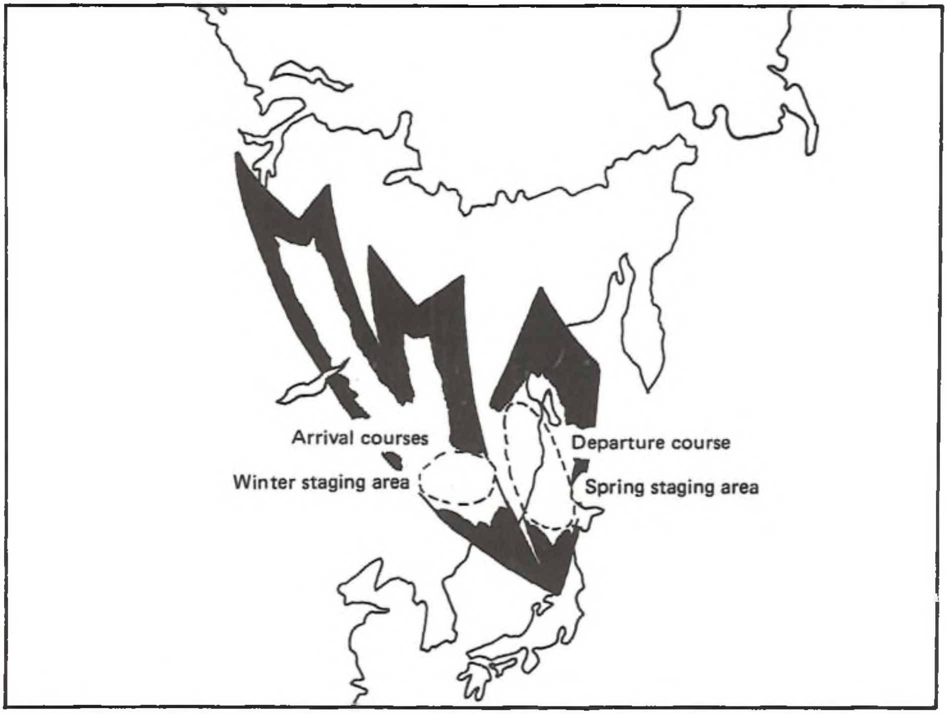

Fig 2. Breeding areas and places of transit on migration courses.

routes in autumn, we are led to think that the *C. c. bewickii* passing through Lake Inawashiro are probably none other than those which had been bred along the coast of the Arctic Ocean. But it never migrates straight from there to wintering regions in Japan.

There are seasonal differences on the long routes from the Arctic Ocean and there are resting places on the way to control and modulate these differences. On the wintering routes, there are resting places such as the Ob, Yenisei, Lena, Sungari and other rivers, and marshes in northern Manchuria; and, on departure routes, marshes and the Amur and Ussuri Rivers.

In many breeding places, wild swans are seen to establish separate territories, yet we feel it strange that at Lake Inawashiro two separate groups are observed never to join one another. Probably congregation of western and of eastern *C. c. bewickii* causes this separation.

Summary

Wild swans have increased rapidly in the last ten years at Lake Inawashiro, a site where conditions are different from those in other wintering regions. The author reports on the current situation and the relationship between meteorology and migratory behaviour of swans wintering at Lake Inawashiro.

Editorial note

The paper presented to the Symposium had originally been published in 1978 and contained many meteorological maps which cannot be published in the Proceedings. Full texts can be obtained from the author.

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NECK-BANDING OF SWANS IN JAPAN

M YOSHII

In the years 1975 to 1979 inclusive, 91 *Cygnus cygnus cygnus* and 19 *Cygnus columbianus bewickii* were marked in Japan with neck-bands. These included 23 and 10 juveniles respectively. *C. c. cygnus* was marked at six locations in Hokkaido and Honshu, *C. c. bewickii* at Lake Kutcharo. Soviet scientists also marked 43 birds of this species near Tchaun Bay, USSR. The neck-bands of 16 *C. c. cygnus* dropped off and 11 birds were found dead. For *C. c. bewickii* these figures were 1 and 8.

Resightings were made of 43 *C. c. cygnus* (47%), 7 Japanese-banded *C. c. bewickii* (37%) and 12 Soviet-banded *C. c. bewickii* (28%). Some individuals were resighted in several successive winters.

Editorial note

The paper presented at the Symposium included a number of tables and maps, full texts of which can be obtained from the author.

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TRADITIONAL RETURN OF *CYGNUS COLUMBIANUS COLUMBIANUS* TO WINTERING AREAS IN MARYLAND'S CHESAPEAKE BAY

R E MUNRO

Introduction

The continental population of *Cygnus columbianus columbianus* has averaged about 105 000 birds during the 1955 to 1977 period (unpubl data, US Fish and Wildlife Service (USFWS) Migratory Bird Management Office (MBMO), Laurel, Maryland), including about 56 000 swans in the Atlantic Flyway. Other than limited hunting seasons in some western states and subsistence hunting by natives in northern Canada and Alaska, swans have been completely protected from legal hunting for over 60 years.

Wintering waterfowl in the United States are surveyed each January by the USFWS in co-operation with the states. Survey procedure and documentation of results varied during the 1940s. Beginning in 1953, survey results have been summarized annually in the 'Special Scientific Report — Wildlife' series. The survey provides the only annual population estimate for *C. c. columbianus.*

From 1955 to 1977 more than 99% of Atlantic Flyway *C. c. columbianus* wintered in Maryland, Virginia, or North Carolina. Because of their stable or increasing numbers during this period, swan populations have received little attention. There is almost as much literature on populations of feral *Cygnus olor* in the eastern United States as there is on native *C. c. columbianus.* Similarly, studies on the previously endangered *Cygnus cygnus buccinator* are numerous.

Strong tradition in waterfowl movements, migrations and wintering area locations is usually assumed to be fact and has been generally demonstrated in a number of banding studies. Based on banding evidence, Hochbaum (1955: 111) suggested that '. . . not only do they (waterfowl) start and end the annual cycle of travel at a familiar home range, but the adults visit familiar stopping places along the routes of migration'. Specificity of food habits certainly has a marked effect on the distribution of eg *Branta bernicla nigricans* (Einarsen 1965). Reduced food availability, adverse weather or shortage of suitable water areas have been shown to alter winter distributions of, for example, *Anas platyrhynchos* and *Anas rubripes* (Bellrose and Crompton 1970), *Branta canadensis* (Rutherford 1970), *Anser rossii* (Dzubin 1965) and *Cygnus columbianus bewickii* (Ogilvie 1969).

Waterfowl return rates to specific wintering areas have also been examined over a wide array of species and locations. Examples include *A. platyrhynchos* (Anderson and Henny 1972), *A. rubripes* (Geis *et al* 1971), *Aythya valisineria* (Geis 1974), *Aythya americana* (Weller 1964), and *Anser anser* and *Anser brachyrhynchus* (Newton *et al* 1973). In general, most investigators found that at least 50% of the birds returned to the same wintering areas during subsequent seasons. However, few of these studies addressed the extent of return of individuals to wintering areas over a number of years.

Description of the Atlantic Flyway, the Chesapeake Bay and specific study areas

The Atlantic Flyway (Fig 1), easternmost of the four US flyways, is bounded by the Atlantic Ocean and encompasses states from Maine to Florida. One of the most important wintering areas in the Flyway is the Chesapeake Bay, the largest estuarine system along the eastern coast of North America. Shared by Maryland and Virginia, the Bay and coastal North Carolina are the winter range for almost all eastern *C. c. columbianus.*

With more than 13 000 km of shoreline (Lippson 1973), the Bay offers a great diversity of habitats for up to 30 species of wintering waterfowl (Stewart 1962). Salinities in the upper or Maryland portion of the Bay range from 0 to 15 parts per thousand. Waterfowl survey strata used by the Maryland Wildlife Administration were combined into five broad survey areas (Fig 2).

Five study areas (Fig 2) were selected. The Rhode/West River area, located south of

Fig 1. The Atlantic Flyway of the United States

Annapolis in Anne Arundel County on Maryland's western shore, annually wintered a small but relatively constant population of *C. c. columbianus.* The remaining study areas were located on Maryland's eastern shore. Claiborne, near the mouth of the Miles River in Talbot County, also wintered a small but stable population of swans. Blackwater National Wildlife Refuge (NWR) in Dorchester County was selected due to the relative ease of capturing swans there during late winter. Brackish impoundments on the Refuge had recently become attractive to swans. Eastern Neck NWR, an island between the lower Chester River and the Bay proper in Kent County, had long been known to be a major staging area for waterfowl. Although wintering swan populations were usually less than 1200 birds, many

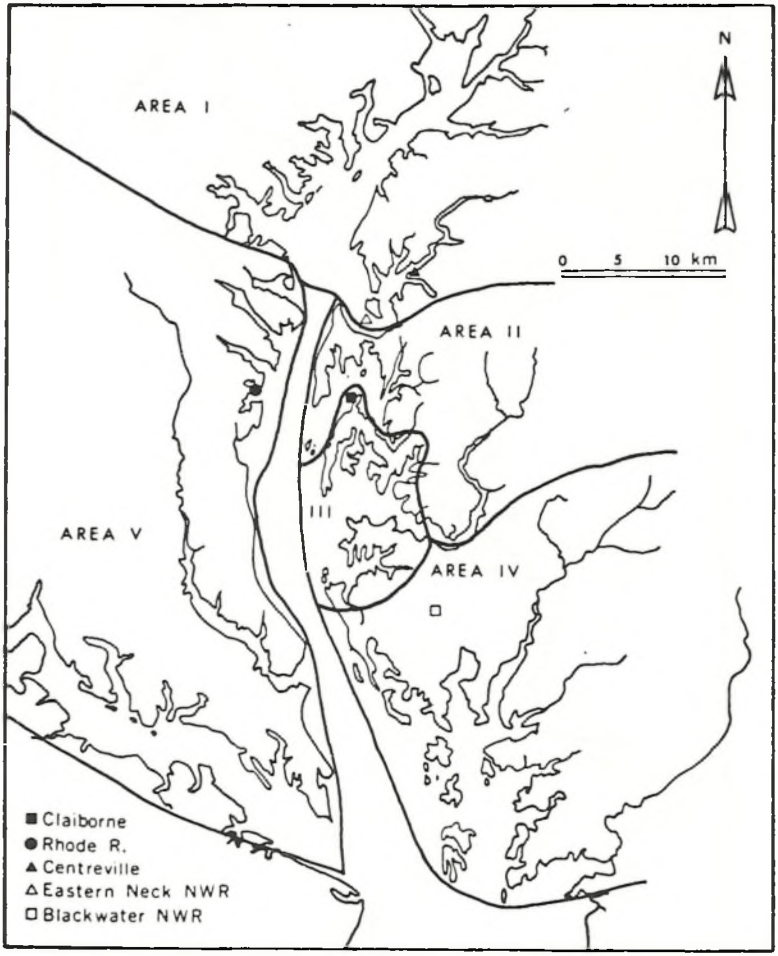

Fig 2. Locations of study areas in the upper Chesapeake Bay of Maryland, and waterfowl survey areas I—V

thousands of ducks, geese and swans frequented the shallow water areas surrounding the Refuge each fall and spring. An area near Centreville in Queen Anne's County was included because of the availability of a small number of swans captured in agricultural fields by the Maryland Wildlife Administration.

Methods and materials

Original tabulations of winter survey data from MBMO were used rather than transcribed data from over 20 publications. Since the January 1954 survey in the

Atlantic Flyway was severely hampered by inclement weather (Crissey 1954), January 1955 is the first year in the analysis. The years 1955 to 1971 were taken to represent the previous long-term distribution, and 1972 to 1977 to represent the current distribution of birds. The latter period corresponds to one during which submerged aquatic vegetation in Maryland's Chesapeake Bay became less abundant (Kerwin *et al* 1976). New long-term distributions based on all years (1955 to 1977) were also determined. Since most Flyway swans winter in Maryland, Virginia and North Carolina, survey results from 'other' areas were combined.

Laminated plastic neck-bands (Sladen 1973) 77 mm wide and 55 mm in diameter were used as the principal marker. Standard USFWS bands and plastic tarsus-bands were also used. All plastic bands were engraved with a letter prefix and three digit suffix for individual recognition.

Three hundred and forty swans were marked during the winter of 1969/70. Most swans were captured at Blackwater NWR in early March. Much of this report is based on about 3500 observations of these birds that accumulated during the next six years.

Birds were observed with 15-60x spotting scopes which enabled positive identification up to 150 m under ideal conditions. Although many observations of marked birds were collected at or near study areas, many were contributed by volunteers from all parts of the Bay. Observer effort was therefore opportunistic rather than random or systematic.

A computer algorithm was coded to approximate distances (km) between any two points or observations, based on latitude-longitude co-ordinates. A constant of 1.36 km per minute of longitude was used for the Chesapeake Bay area; the constant for latitude was 1.85 km per minute.

Analysis of variance (ANOVA) and linear regression used in this study followed the Statistical Analysis System user's guide (Barr *et al* 1976). ANOVA assumes, among other factors, sample independence. This assumption was not always met because observations of the same animals were represented a number of times across a six-year period. In spite of this difficulty, I concur with Myers (1974), who concluded, 'Although statistical rigor may be lost, the value of the additional insight into populations that can be gained from sequential samples seems more important.'

Analyses of percentages were based on arcsine-transformed data, as suggested by Snedecor and Cochran (1967), followed by a duplicate analysis on the untransformed data. Where no differences were indicated between results of the duplicate analyses, untransformed results were used. Indicator variables, discussed in detail by Neter and Wasserman (1974), were used to represent categories of a variable such as sex.

Distances (km) at which birds were observed from their banding sites were not normally distributed because of a disproportionate number of zero values. A log transformation to stabilize variance (Snedecor and Cochran 1967) of distance measurements resulted in no improvement; untransformed distances were therefore used.

Table 1. Numbers and linear regression analyses of percent distributions of Atlantic Flyway *Cygnus columbianus columbianus* over three time periods

Species, period and parameter		US total	Atlantic Flyway	Maryland	Virginia	North Carolina	Other
			Number and % of Atlantic Flyway				
1955 to 1971							
Mean number		97 976	52 712	35 018	3 741	13 868	85
Percent	mean		53.8	65.4	7.6	26.9	0.2
	S.E.		2.5	2.7	1.6	2.1	0.0
	C.V.		19.3	16.8	86.9	32.7	74.0
	F value		0.0	0.1	1.7	1.6	1.0
	p>F		0.898	0.779	0.208	0.229	0.342
	slope estimate (%)		–	–	–	–	–
1972 to 1977							
Mean number		124 284	67 583	33 167	4 083	28 833	1 500
Percent	mean		55.1	50.2	5.9	41.6	2.3
	S.E.		3.3	4.8	0.9	4.7	0.6
	C.V.		14.7	23.2	35.4	27.4	63.8
	F value		2.5	25.5	0.3	108.3	2.7
	p>F		0.189	0.007	0.609	0.001	0.175
	slope estimate (%)		–	–5.8	–	+6.0	–
1955 to 1977							
Mean number		104 839	56 591	34 535	3 830	17 772	454
Percent	mean		54.1	61.4	7.2	30.7	0.7
	S.E.		2.0	2.7	1.2	2.4	0.2
	C.V.		17.9	20.9	80.5	37.0	167.2
	F value		0.2	6.2	1.0	13.5	18.1
	p>F		0.656	0.021	0.334	0.001	0.000
	slope estimate (%)		–	–0.9	–	+1.1	+0.1

Since cygnets (hatch-year swans) could be distinguished from adult-plumaged birds throughout their first winter, they will be referred to as 'young', even though after January they would be in their second calendar year of life. These birds of known age, if observed during their second winter, would be considered 'subadults'. However, they would be indistinguishable from adults of unknown age on the basis of plumage alone.

The term 'winter', unless otherwise specified, will refer to the period 1 November to 30 March. The term 'upper Bay' means 'Maryland's Chesapeake Bay'.

Results

Distribution of Atlantic Flyway C. c. columbianus

For each time period a hypothesis of no consistent, linear change (zero slope) in percent distribution was tested.

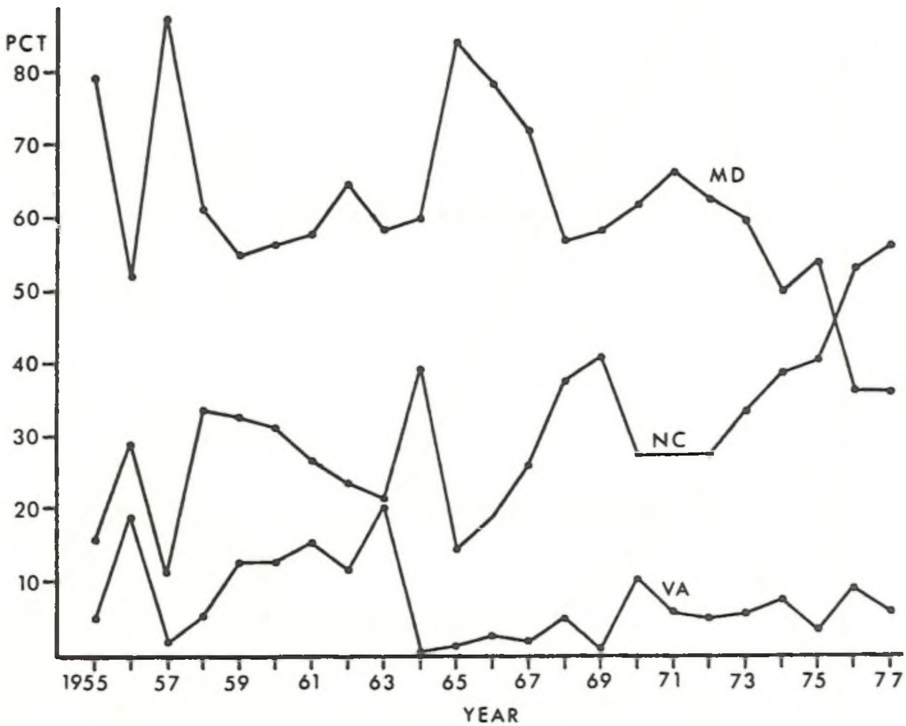

Fig 3. January inventory of *Cygnus columbianus columbianus* in Maryland, North Carolina and Virginia for the years 1955 to 1977. (Unpublished data, Migratory Bird Management Office, Laurel, Maryland).

The Flyway population averaged 53 000 birds or 54% of the US total during the previous long-term period, and about 67 000 birds or 55% of the total during the current period (Table 1). Although numbers of birds were greater during the current period, there was no trend in the proportion of the continental population that wintered in the Flyway during either period. Maryland, Virginia and North Carolina wintered 99.8% of the Flyway total through 1971, and only slightly less through 1977. Percent distribution is therefore illustrated only for these three states (Fig 3).

Within the Flyway there was no change in percent distribution for any area during the 1955 to 1971 period (Table 1). However, highly significant trends were detected for Maryland (−5.8%/year, $p = 0.007$) and North Carolina (+6.0%/year, $p = 0.001$) during the current period. In January 1976, North Carolina wintered

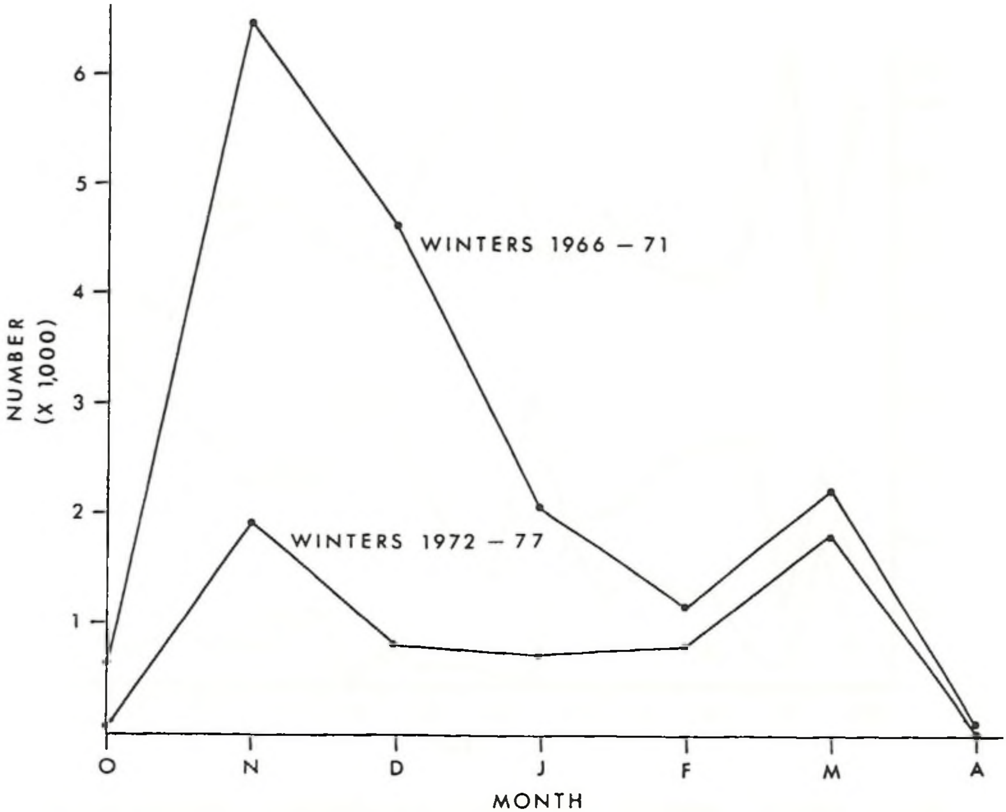

Fig 4. Peak numbers by month of *Cygnus columbianus columbianus* at Eastern Neck NWR averaged over the winters 1966 to 1971 and 1972 to 1977.

more swans than Maryland for the first time in more than 20 years. Trends for the new long-term period (1955 to 1977) were: (1) a gradual decrease in Maryland (–0.9%/year); (2) an increase in North Carolina (+1.1%/year); (3) an increase in 'other' areas (+0.1%/year).

Temporal and geographic distribution of swans in the upper Bay

Numbers of swans observed by Refuge personnel at Eastern Neck NWR during the winters 1966 to 1971 and 1972 to 1977 were examined to determine maximum monthly numbers averaged for each of the two periods (Fig 4). The Refuge, a major staging area for waterfowl, annually received large numbers of swans during November. During both periods, the initial November increase was followed by a sharp decline through December and January to a February low (wintering population), and then an increase during March as swans staged for spring migration. Although curve shapes were similar for the two periods, numbers of swans observed were considerably less during the later period when other surveys (Kerwin *et al* 1976) indicated reduced availability of submerged aquatic vegetation in the Bay.

Surveys of swans from November to January (Table 2) indicate the northern portion of the upper Bay (Area I, Fig 2) decreases in importance from November (35.6%) to December (21.0%). Also, at least 50% of swans during these months are found in the middle eastern shore area (Areas II and III). These areas include Eastern Bay, the Miles and Wye Rivers, as well as the Choptank and Little Choptank Rivers. Together with the Chester River (southeast portion of Area I), these rivers and Eastern Bay represent the main wintering area for about 75% of the upper Chesapeake Bay swan population. Although substantial brackish estuarine bay communities are found in Area V, such as along the lower reaches of the Patuxent and Potomac Rivers on the western shore, and to a more limited extent in Area IV on the lower eastern shore, these areas winter only about 25% of the January population of upper Bay swans.

Table 2. Distribution of *Cygnus columbianus columbianus* by survey area; average numbers during winters 1967 to 1975.

Survey area	November		December		January	
	Number	%	Number	%	Number	%
I	11 000	35.6	8 550	21.0	8 300	20.8
II	9 620	31.1	12 000	29.5	11 250	28.2
III	6 120	19.8	11 400	28.0	9 780	24.5
IV	1 650	5.3	2 280	5.6	3 630	9.1
V	2 530	8.2	6 470	15.9	6 940	17.4
	30 920		40 700		39 900	

Unpublished data, Maryland Wildlife Administration, Annapolis, Maryland. December surveys were not conducted after the 1970 winter. The November 1974 survey was not conducted.

Stewart (1962) also estimated that about 75% of upper Bay swans wintered in the middle eastern shore area during the mid to late 1950s. However, a direct comparison with Stewart's results cannot be made, as he included the Magothy, Severn, South, Rhode and West Rivers of the western shore in his tabulations. Nevertheless, the brackish estuarine bay community is still the preferred habitat of swans wintering in the upper Bay.

Observer effort

All upper Bay observations of 340 neck-banded swans in the original cohort were summarized by 15 day period and year (Table 3). Of 2038 total Bay observations,

Table 3. Numbers of observations of neck-banded *Cygnus columbianus columbianus* during 1970 to 1975 by 15 day period

Delaware is included with Maryland

	State totals			
Period and dates	Maryland		North Carolina	
1 Nov – 15 Nov	80	3.9	0	0.0
16 Nov – 30 Nov	242	11.9	1	2.3
1 Dec – 15 Dec	230	11.3	2	4.6
16 Dec – 30 Dec	97	4.8	3	6.8
31 Dec – 14 Jan	240	11.8	7	15.9
15 Jan – 29 Jan	285	14.0	6	13.6
30 Jan – 13 Feb	196	9.6	7	15.9
14 Feb – 28 Feb	257	12.6	18	40.9
1 Mar – 15 Mar	271	13.3	0	0.0
16 Mar – 30 Mar	140	6.9	0	0.0
	2 038	100.1	44	100.0

about 70% were collected during the first (699) and second (741) winters (1970 and 1971). Subsequent winters provided 365, 124, 59 and 50 observations. Observer effort at first resulted in 5.9 and 5.4 sightings per marked bird, but apparently declined after the 1972 winter to between 2 and 3 observations per marked bird, although effort and availability of marked swans cannot be separated. Both mortality of swans and loss of neck-bands reduced availability of marked birds. Given these limitations, seasonal distribution of observations, other than during the first and last periods when fewer marked birds were available, was fairly uniform and fluctuated around 10% per period except for the last half of December. Only 44 observations of these birds in North Carolina were recorded during six years. The value of these few observations and of even smaller numbers in Pennsylvania and Virginia was realized only when examined on an individual basis.

With the winter divided into 10 periods of 15 days, there were 60 periods for observation of swans during the 1970 to 1975 winters. In actuality, sightings were much less frequent and scattered, as indicated by a sample set out according to banding site in Table 4. There was much variability within and among individuals.

Table 4. Resighting data for a sample (22) of the 224 *Cygnus columbianus columbianus* seen in winters following that of banding (1969/70)

M = Maryland/Delaware, C = North Carolina, P = Pennsylvania, V = Virginia

Banding site/swan	Winter of resighting						Resighted in	
	70/71	71/72	72/73	73/74	74/75	75/76	Years	15 day periods
Rhode River								
C007	M	C	–	M	M	M	5	10
C037	–	M	C	–	–	–	2	4
C040	M	M	C	M	–	–	4	12
C048	M	M	M	M	–	–	4	28
Eastern Neck								
C116	M	C	M	M	–	–	4	16
C119	M	M	M	M	–	–	4	16
C120	M	M	–	–	C	–	3	18
Claiborne								
C129	–	–	M	–	–	C	2	2
C605	–	M	M	C	C	M	5	9
C609	M	–	–	C	P	P	4	6
C622	M	M	M	M	M	–	5	17
C637	M	M	–	–	–	–	2	6
Blackwater								
C176	M	M	M	M	M	M	6	20
C193	M	C	–	C	M	M	5	9
C671	M	–	–	–	–	–	1	1
C689	M	–	–	C	–	–	2	2
C692	M	–	M	V	M	M	5	6
C858	M	M	M	P	–	–	4	3
C886	M	–	C	–	C	–	3	4
C900	–	–	–	M	–	M	2	2
C917	–	C	C	–	–	–	2	2
C940	–	M	–	–	–	–	1	6

For example, C048 was frequently observed in Maryland throughout the 1970 to 1973 winters. C007 was observed early in February 1972, in North Carolina. Not located during the 1972 winter, C007 was then observed in Maryland during the early winter of 1973 and not again until the following winter. A similar pattern was suggested by observations of C037 and C040.

These examples indicate a pattern of seasonal movement and winter residence with which nearly all observations of individually marked swans were consistent. Swans migrated into the upper Bay area during November. Of swans observed in the Bay at any time from early December to mid-February, none was observed outside the Bay area until spring migration. From mid-February on, however, swans moved into the Bay area from wintering areas farther south. Therefore, the period of winter residence in the upper Bay extends from at least the first days of December to mid-February.

Examples of birds banded on other study areas further substantiate this pattern. C116 and C119 were observed together for 20 days during the 1970 winter and always within one-half km of their Eastern Neck banding site of the previous winter. Banded as male and female, their behaviour indicated they were a pair. On 11 and 12 November 1971 both were observed back at Eastern Neck near their band site. C119 was next observed alone for the first time on 16 and 17 November in the usual cove, and then on 19 and 22 November while feeding in corn fields about 8 km from the Refuge. C116, presumed dead at the time, was observed alone later that same winter on 12 February 1972 about 350 km to the south in North Carolina. Fifteen days later C116 and C119 were observed together field feeding on Maryland's eastern shore. Over the next two winters, both were observed only in Maryland and only during mid-winter.

C120 was another winter resident at Eastern Neck, with 40 observations there throughout the 1970 and 1971 winters. This bird was not observed again for over two years and then was found in North Carolina. From Claiborne C605 was observed early or late in Maryland, and during mid-winter in North Carolina. The same pattern was indicated by observations of C193 and by a general lack of observations of Blackwater-banded birds during mid-winter. Since many of these birds were banded during late February and early March, some of them (C689, C886 and C917) were marked while on migration from wintering areas in North Carolina.

Table 5. Number of winters in which *Cygnus columbianus columbianus* neck-banded at various areas of Chesapeake Bay were resighted

Banded in 1969/70 in area	Years subsequently seen 0	1	2	3	4	5	6	Total resighted
Rhode River	11	13	10	5	5	2	2	37
Eastern Neck	10	10	9	8	3	1	1	32
Claiborne	12	23	14	6	5	3	–	51
Blackwater	64	54	21	22	3	2	2	104
Consecutive	–	69	26	21	10	2	5	133
With breaks	–	31	28	20	6	6	–	91

The number of winters, consecutive or with breaks, that swans were subsequently seen are summarized in Table 5.

Availability and survival

All available data on the original neck-banded sample of 340 birds were used to tabulate known survivors for eacn winter to 1975/76 (Table 6). These data include not only direct observations of swans in the various winters, but also those that could be inferred to be alive because they were observed during later years.

Table 6. Minimum numbers (N) of neck-banded *Cygnus columbianus columbianus* known to be available in Chesapeake Bay, expressed as the percentage of the number available the previous year

A = adult, I = immature, U = unidentified, M = male, F = female

Age	Banded	1970/71		1971/72		1972/73		1973/74		1974/75		1975/76	
Sex	1969/70	N	%	N	%	N	%	N	%	N	%	N	%
AM	128	94	73	65	69	39	60	26	67	11	42	7	64
AF	146	117	80	98	84	71	72	51	72	35	69	16	46
IM	26	20	77	16	80	7	44	5	71	2	40	1	50
IF	25	13	52	10	77	8	80	7	87	5	71	3	60
UU	15	13	87	10	77	9	90	3	33	2	67	1	50
All	340	257	75.6	199	77.4	134	67.3	92	68.7	55	59.8	28	50.9

The analysis of variance was designed to detect changes in annual proportions of marked birds (all study areas combined) of each age-sex class that were known to survive from one year to the next. No overall differences in intercept or slope were indicated among age-sex classes. A significant ($p = 0.0047$) downward trend through the years in the combined data was found. One arbitrarily chosen class, adult females (AF), was tested for zero intercept and zero slope, the former being somewhat meaningless. A marginally significant difference (−6.2%, $p = 0.0069$) in slope was detected, ie the percentage of the marked adult female population that remained was estimated to decrease about 6 percentage points per year from 92% (intercept) during the year of banding.

These data provide minimum estimates of annual survival rates that were near 75% for each of the first two years after banding. The 25% lost from the marked population each year include those that 1) died, 2) lost neck-bands, 3) emigrated to other wintering areas and 4) were still marked and alive but not observed. All factors considered, annual survival rates of adult swans probably approach 85% to 90%.

A similar analysis by study area of banding was made with all age-sex classes combined. No differences in intercept or slope were indicated among study areas.

Rates of return to the Bay

Observations of marked swans in Delaware, bordering Maryland on the eastern shore of Chesapeake Bay, were treated as returns to the Bay area, whereas observations in Virginia (south of the Potomac River) and Pennsylvania (north of Maryland's Susquehanna Flats) were excluded. Numbers of neck-banded swans observed each winter were summarized by age-sex class (Table 7) and expressed as a percentage of those known to be available that year (Table 6). For example, 68 neck-banded adult male swans were observed during the 1970/71 winter, of 94 known to be available. Therefore 72.3% of the available marked adult male population were observed in the Bay during the 1970 winter.

Table 7. Numbers (N) of neck-banded *Cygnus columbianus columbianus* which returned to the Chesapeake Bay, expressed as the percentage of the number known to be available that year (see Table 6)

Age	1970/71		1971/72		1972/73		1973/74		1974/75		1975/76	
Sex	N	%	N	%	N	%	N	%	N	%	N	%
AM	68	72	38	58	18	46	13	50	2	18	5	71
AF	83	71	67	68	38	53	23	45	16	46	12	75
IM	11	55	8	50	3	43	0	0	1	50	0	0
IF	9	69	5	50	5	62	3	43	3	60	3	100
UU	10	77	7	70	4	44	1	33	2	100	1	100
All	181	70.4	125	62.8	68	50.7	40	43.5	24	43.6	21	75

Analysis of variance of percent return yielded no differences in intercept, slope or year effect in the combined data or among age-sex classes. Of 340 swans marked during the 1969 winter, only 28 were known to be available for observation after six winters. The fact that 21 (75%) of those individuals were observed six winters after banding had a substantial effect on the analysis and may have obscured an apparent downward trend over the intervening five winters.

A similar analysis by study area of banding also produced no detectable differences or trends in return rates. Since no significant effects were detected in either analysis, the estimated return rate of neck-banded swans to the upper Bay area was between 65% (intercept for adult females) and 75% (Rhode River birds) of the number available each winter.

Return to specific Bay wintering areas

The above analyses examined return rates of marked swans to the Chesapeake Bay wintering area and not their return to specific sites in the Bay. Using the same observations, a more detailed analysis was constructed. Co-ordinates of observation of a marked individual were compared with those of the band site and a return distance (km) determined for each record. Within a winter season, all return distances for an individual were examined to identify the smallest value (nearest to the band site). This resulted in 459 observations of return distance for Bay-marked swans, some of which were represented four or five times (only once per season).

To provide a larger sample as well as a source of comparison, records of swans neck-banded during the summer of 1970 in the Northwest Territories (NWT) were examined to identify individuals that were observed in the Chesapeake Bay area during at least two different winters. The first Bay location of a NWT bird was taken as a 'home base' with which the bird's subsequent return during another winter could be compared. This resulted in 104 observations of return distance for 56 NWT-banded swans.

The analysis of variance examined the effects of age at banding, sex and years since banding on return distance. The most important effect on return distance was an increase with years (6.3 km/year, $p = 0.0001$). Return distances of males and females were similar; those of subadults (marked as young of the previous year) were not significantly different ($p = 0.0656$) from those of adults. Of the between-study area comparisons, only return distances for Blackwater birds were different from those for all other areas. A simplified model, based on significant effects from the full model, yielded very similar parameter estimates; the year effect was 6.2 km/year and the area effect was —0.7 km/year multiplied by an appropriate coefficient.

Swans banded in the Northwest Territories had return distances, similarly measured, which were essentially the same as those for birds banded in the Bay. In effect, these birds represented many more populations, widely dispersed over the Bay area, that showed the same tendency to return to specific areas.

Despite the indicated increase with time in return distance, most swans were observed near their banding areas. Of swans that returned to the Bay within six winters of banding, about 30% were observed within 0.5 km of the band site and about 56% within 10 km. The maximum distances for the same individuals did not exceed 20 km in 50% of cases.

Blackwater birds also differed from others in timing of return. All observations of birds that returned to their band site (same one-half minute block of banding for Maryland-banded swans, or area of observation for NWT-banded swans) were grouped by 15-day periods and categorized as Blackwater birds or 'others'.

Dates of return were not necessarily the first observations during a winter season, but the first dates of return to band sites. By mid-December, more than half of swans from areas other than Blackwater NWR had returned to their band sites (Fig 5). In contrast, Blackwater swans returned mostly during February and March, which provides further evidence that some of these birds wintered farther south of the Bay in Virginia or the Carolinas.

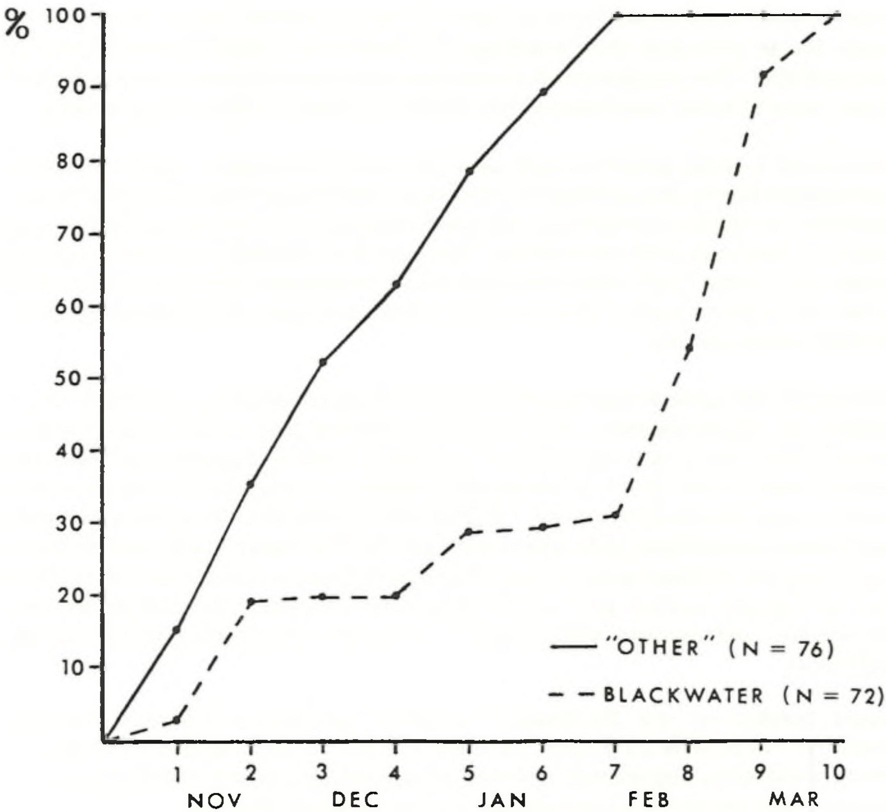

Fig 5. Cumulative percent distribution by time period during which Blackwater and 'other' neck-banded swans were initially observed back at their one-half minute blocks of banding

Conclusions

Traditional use of the Chesapeake Bay by *C. c. columbianus* has been known since the earliest accounts of the Bay were written. Recent winter surveys demonstrated that the middle eastern shore area of Maryland, with its abundance of brackish estuarine bay habitat, continues to be the primary Bay wintering area for swans. Some swans use the Bay during November and after mid-February while on migration to and from wintering areas farther south such as North Carolina. Those that remain until early December comprise the winter residents; most of these birds remain until spring migration.

Based on observations of neck-banded swans, annual survival rates of adults exceed 75% and probably 85% to 90%. Mortality, loss of neck-bands and emigration to other wintering areas account for the remainder.

Annual return rates to Chesapeake Bay wintering or staging areas were estimated at 65% to 75% during the 1970 to 1975 winters. Specifically, about 70% of the number of marked swans known to be available for observation were seen in the upper Bay area at least once each winter. No trend over years or differences between age-sex classes in return rates could be detected. Since January surveys indicated a substantial shift of swans from Maryland to North Carolina during the 1972 to 1977 period, there probably was some reduction in rate of return or use of the Bay by wintering and/or migrating swans.

Swans tended to return to the same locality each winter. Detailed analysis showed a measurable drift of about 5 km per year for all but Blackwater-banded birds. Of more importance, about 56% of all neck-banded swans that returned to the Bay (regardless of year) were observed within 10 km of their banding site.

The most important factor affecting distribution of swans in Maryland and the Atlantic Flyway during the 1970s has been the reduction in aquatic food resources of the Chesapeake Bay. Significant numbers of swans then began feeding in agricultural fields, which they had done perhaps 20 years earlier while on spring migration from the Flyway. The interplay between traditional return to specific Bay wintering areas and adaptation to field feeding will continue for a number of years. New traditions have already formed, as many swans now return to the Bay and feed in the same group of fields each year. It is anticipated that Maryland's Chesapeake Bay will winter an increasing number and proportion of Atlantic Flyway swans, as adaptation becomes tradition for more individuals.

Acknowledgements

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Summary

The paper reviews return of neck-banded *Cygnus columbianus columbianus* to wintering areas in Chesapeake Bay over a number of years. Annual survival rates of adults probably approach 85%; annual return rates were about 70%, and 56% of birds were observed within 10 km of their banding site. Reduction in aquatic food resources has led to agricultural field feeding, and it is suggested that this adaptation will become a tradition for more individuals.

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THE LONG TERM STUDY OF *CYGNUS COLUMBIANUS BEWICKII* AT SLIMBRIDGE

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Introduction

Observations of wintering *Cygnus columbianus bewickii* began at the Wildfowl Trust, Slimbridge, England, in 1964, and the study method has continued almost unchanged to the present day. The purpose of this paper is to summarize the findings to date, most of which have been published or are in press, and to assess both the method of study and its future.

Study area and methods

The swans breed in northwest Siberia and winter mainly in Denmark, the Netherlands, England and Ireland. In February 1964 small numbers from the Severn Estuary, near Slimbridge, were attracted to a lake inside the fox-proof perimeter fence of the Wildfowl Trust by the provision of grain and protection from disturbance. Although Acland (1923) had noted differences between the bill patterns of *C. c. bewickii,* their representation was crude and Scott (1966) was the first to record the bill patterns in such detail that the same bird (second winter or older) could not only be recognized throughout one winter but could also be identified when it returned the following year.

From an initial 24 different swans visiting the lake in winter 1963/64, numbers increased steadily each winter to 439 in 1968/69 (Evans 1979a). Thereafter annual totals fluctuated according to weather conditions (Evans 1979b), peaks of 626 and 721 being recorded in 1970/71 and 1978/79 (Rees 1979) respectively. Every swan was given a name as an 'aide memoire' and, when birds arrived each winter, their names (either those allocated in a previous winter or, if the birds had not been recorded before, new ones) were entered on a register. Every day during the winter the presence on, or absence from, the lake of every swan on the register was checked and new arrivals added. In addition, a printed card was kept for each swan comprising a) basic data: name, age (at first arrival), sex (observed or by cloacal examination), parents, ring numbers, date first caught; and b) annual data: arrival and departure dates, name of mate or other associate(s), number and identity of cygnets, sightings away from Slimbridge, recapture dates and additional notes.

As numbers of swans increased, so too did the problems, not only of recording every bird in one winter but also of recognizing the bill patterns of, and remembering the names of, birds recorded in earlier years. Cygnets (first winter birds) were of particular interest as a group, for both their age and parentage were known. However, when they left in the spring, their bill patterns were still ill-defined. Partly to help solve these problems and partly so that 'Slimbridge' birds might be identified when away from the lake, as many swans as possible were ringed. From 1967/68 onwards large plastic rings, readable with a telescope from up to 300 m, were used (Ogilvie 1972). Most of the swans were caught in a screened channel leading off the lake, into which they were attracted by liberal feeding. When sufficient birds had entered it, a gate was closed by pulley. The whole was netted over, so that ducks and geese were also caught (Evans and Rees 1978). The birds were then driven to a catching area, where the swans were put in individual plastic 'jackets' for processing (Evans and Kear 1975). To date, the largest number of swans caught at once was 145 in December 1978 (Rees 1979).

As well as being ringed, the birds were measured (lengths of bill, head, tarsus and tarsus thickness) and weighed (Evans and Kear 1978). Their bill patterns were photographed. This allowed the reliability of identification by bill pattern by both experienced and inexperienced observers to be assessed (Evans 1977; Brown and Lewis 1977) and a comparison of their bill markings with those of *Cygnus columbianus columbianus* to be made (Evans and Sladen 1980). From 1970/71 to 1972/73 the swans were x-rayed. Over a third of them had lead pellets in their tissue, having been fired at out of range, although they are a protected species (Evans *et al* 1973). During these same winters, the swans' tails and wing tips were dyed yellow to attract the attention of observers at other sites. It was hoped that these dyed birds would not become targets for shooters, and careful monitoring of their returns showed this not to be the case (Evans 1972). During 1976/77 to 1978/79 swans caught were again dyed, because of increased Anglo-Soviet co-operation on migratory species, which enabled a visit to the breeding grounds in 1978 (Scott 1978).

Results

There were four major areas of investigation:

1) The data on the record cards from 1963 to 1978 were analysed to reveal aspects of the swans' life cycle (Evans 1979a). Thus, the average brood size was 2.1 and single cygnets were more often lost on the wintering grounds than those in broods of two or more. Former offspring often associated with their parents; one even did so in its fifth winter; and sibling pairs occurred, although none returned as a breeding pair. Pairing took place between two and four years old with females being more precocious, perhaps because there was an excess of males in the population. The average pair bond lasted 3.6 years. Divorce was unrecorded but 57% of birds losing mates found replacements in the same year; 15 birds found their mate again, after losing them for at least one winter. First breeding was mostly between four and six years but only a third of birds pairing brought young. Some individual pairs were more frequently successful and had larger broods. The annual survival rate for adult birds was not less than 87.1%.

2) The population composition, and returns of different classes of swans, from 1963 to 1976 were investigated (Evans 1979c). The four main classes were: yearlings (second winter birds, recognized by vestiges of grey cygnet plumage on neck and head), singles (unpaired adults), pairs and families. Birds in each class could have been to Slimbridge before and thus be 'Experienced' or 'New'. Up to 1968/69, when annual numbers were increasing, recruitment to the lake was from all the classes but thereafter it was predominantly from single birds. From 1969/70 the number of 'New' families was extremely low (representing 3.6% of total 'New' birds) compared with 'Experienced' families (21.4% of 'Experienced' birds).

There was no difference between the return proportion of males and females. Birds more likely to return were those which had had a long initial visit (Evans 1980). Such birds were more likely to be caught as a result. Significantly more ringed birds returned than unringed. Pairs and families returned in higher proportions than singles, but returning proportions were lower in all classes later in the study (20.5%). Swans with two winters' experience at Slimbridge were more likely to return (54.9%) than those with just one. Returns were not necessarily made in consecutive winters; a third of swans returning missed one or more winters at Slimbridge.

3) The attendance patterns of the swans recorded in the registers of the eight winters 1968/69 to 1975/76 were analysed in detail.

The register clearly showed days of heavy arrivals and departures as well as attendance on, and absence from, the lake. The effects of weather were examined first (Evans 1979b); wind direction was vital. For both arrivals and departures the swans favoured tail winds. Calm, then side winds, were selected next. Head winds were avoided. The proportions of the prevailing winds (south to west) each winter correlated negatively (being head winds) with numbers of swans arriving, and positively with the proportions of swans missing winters. These birds probably stayed on the Continent, for south to west winds are mild and would keep feeding grounds there open. Such winds also correlated positively with how much absence there was during a season by birds visiting Slimbridge; and, finally, correlated negatively with the number of swan-days recorded each year. These results have practical management value. Thus, it was feared that the very low number of swans (259) visiting Slimbridge in 1974/75, their subsequent high amount of absence and the resulting very low number of swan-days resulted from some mismanagement of the lake, eg too much catching in previous years and too little feeding. However, the proportion of south to west winds during that winter was 78%. Thus large numbers of birds were prevented from arriving and those that did come were encouraged to leave early by the abundance of tail winds.

Secondly, the effects of experience and breeding status (ie 'class', as defined earlier) were examined (Evans 1980). 'Experienced' birds arrived proportionally earlier, stayed longer, were absent less and departed later than 'New' birds. The

'Experienced' classes showed few differences in behaviour, except for families, which were absent more and which, in the early part of the winter, left proportionally ahead of the other 'Experienced' classes. New classes showed more differences. Arrivals of yearlings built up most quickly, followed by singles, pairs and families. Pairs had more absence than the other classes. The departures of families were different from those of the other classes and closely paralleled their arrival pattern. This resulted from the number of 'New' families that made only very short visits.

4) An analysis of the sightings of ringed and dyed swans away from Slimbridge from 1961 to 1979 is in progress. Taking only one sighting per swan per site per winter, some 1300 sightings (usually by ring number, occasionally by bill pattern) have been made, in four categories.

a) During the autumn migration: Only 61 sightings made at four places in the Federal Republic of Germany, three in the Netherlands and five in Britain. There were eight examples of birds seen at another Wildfowl Trust reserve (Welney) 200 km to the northeast being recorded at Slimbridge the next day.

b) Between first arrival at and last departure from Slimbridge in one winter: 200 sightings made at three places in Britain and two in the Federal Republic of Germany. The latter resulted from severe weather conditions on the spring migration, which forced the birds back to Britain (Evans 1979b).

c) During the spring migration: 478 sightings made at two places in Ireland, 16 in Britain, ten in the Netherlands, ten in the Federal Republic of Germany, two in Denmark, two in the German Democratic Republic, one in Estonia and two in the USSR. Several swans seen at Slimbridge one day were reported from other places in England the next day and one bird had travelled in that time as far as the Elbe Estuary, Federal Republic of Germany.

d) During a winter when the bird did not come to Slimbridge: 555 sightings at seven places in Ireland, one in France, 18 in Britain, one in Belgium, 18 in the Netherlands, ten in the Federal Republic of Germany, three in Denmark, two in the German Democratic Republic, one in Latvia, six in Estonia and one in the USSR.

There were many additional records of ringed/dyed swans where the bird was not identified, including the Camargue (in southern France), the Shetland Islands (off the northeast of Scotland), in Sweden, Poland and at the mouth of the Pechora River in the USSR, the nearest sighting to the breeding grounds.

Discussion

It would be impossible in this paper to discuss the results in any detail, because they are so many and varied. Precisely for this reason it is perhaps worth evaluating this long-term study.

First of all the study area; it can by no means be called natural. However, it is clear that the swans were well able to exploit the artificial situation. Moreover, the study would not have been possible without a Slimbridge-like situation, for the data depended on the very close observation enabling individual recognition.

There is no doubt that such extensive use of individual identification has produced a wealth of data, but what of the future? Obviously the longer annual records can be kept on the individual birds already on file, especially those of known age, the more valuable they become. However, the bill pattern method of recognition poses many problems in a long-term study and Rees (1981) describes the efforts to computerize the bill pattern data so that a bird may be identified by an observer who has not seen it before. Nearly 4000 different swans have been recorded at Slimbridge.

Instead of recording the bill patterns of further new birds, the study should perhaps concentrate on continuing the records of the birds already on file. A thousand of the swans have been ringed and so are easily recognizable by inexperienced observers. An interesting and important study would be to monitor the effects of feeding the swans, by comparing the detailed behaviour of the Slimbridge birds with that of swans at an unprovisioned site.

Once birds returning to Slimbridge have been recorded, the effort required to monitor their subsequent presence or absence daily will probably produce relatively little new information. Registers now exist for 16 years, so it is likely that nearly every 'idiosyncratic' behaviour (such as a swan staying for only one day in one winter when in a previous winter it stayed over 100 days) is already on record. Existing details from the printed record cards and registers are being put into a computer so that even more detailed analyses than those described above can be made.

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Summary

Cygnus columbianus bewickii wintering at Slimbridge are recognized by bill pattern and some are caught for ringing and closer examination. The four main areas of investigation are: study of life cycle, population composition and return rates, attendance patterns from 1968 to 1975,

and analysis of sightings of marked birds away from Slimbridge. The author discusses future developments emphasizing the need to maintain annual records of known individuals, preferably computerizing descriptions of bill patterns, and to monitor the effects of feeding swans.

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THE RECORDING AND RETRIEVAL OF BILL PATTERN VARIATIONS IN *CYGNUS COLUMBIANUS BEWICKII*

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Introduction

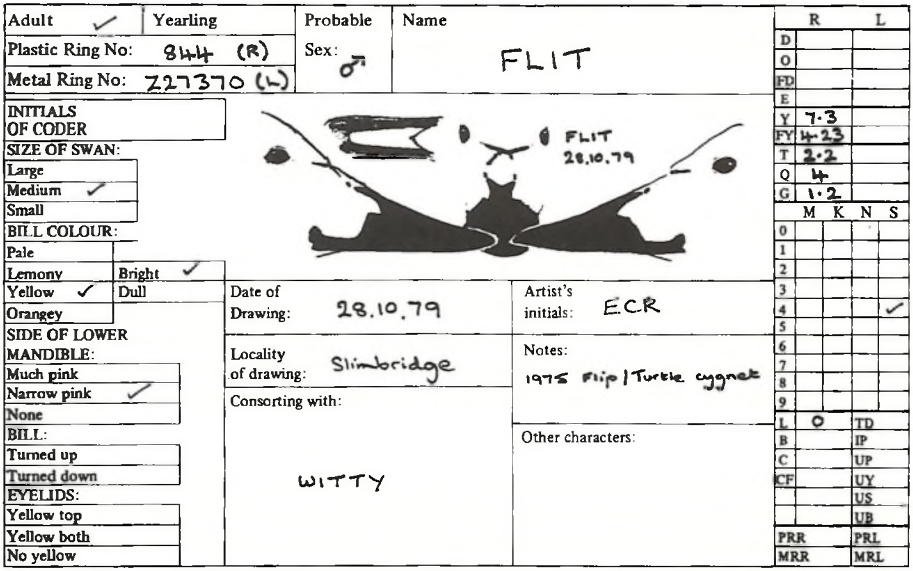
Studies of wild animals are greatly facilitated if individuals of the population can be identified by natural characteristics. It is difficult to catch and artificially mark all individuals, and undue stress can be caused by the process. Differences in features have therefore been used to identify giraffes (Foster 1966), zebras (Petersen 1972), lions (Pennycuick and Rudnai 1970) and red deer (Clutton-Brock and Guiness 1975).

Individual differences in the black and yellow bill patterns of *Cygnus columbianus bewickii* were first reported by Acland (1923). The artist, Tunnicliffe, sketched a few of the variations in 1946 (Tunnicliffe 1979). Géroudet (1962 and 1963) and Sermet (1963) made similar observations in Switzerland. In 1964 when wild *C. c. bewickii* started to winter regularly at the Wildfowl Trust, Slimbridge, Gloucestershire, (P Scott 1966), recognition of individuals by their bill pattern was first used for an extensive study of the population. This proved to be a facile and rapid means of identification, particularly useful in studying behavioural encounters (eg D K Scott 1978a) when instant recognition is necessary.

To assess the accuracy of this identification system, Bateson (1977) asked an experienced swan watcher, D K Scott, to identify swans from slides taken two weeks earlier. She correctly named 29 out of 30 good quality slides and 23 out of 30 less clearly portrayed. Evans (1977) devised a recognition test which showed that swans can be reliably identified over a period of years.

Between the winters of 1963/64 and 1978/79 the number of swans wintering at Slimbridge rose from 24 to 721, with some 3000 adult and second-winter birds being identified by their bill patterns. An accurate recording system had to be constructed so that individuals could be recalled in subsequent years without relying on human memory, particularly since birds may return after spending a number of winters elsewhere (Evans 1978).

The methods used for recording and filing the bill patterns of different swans have already been described in detail (D K Scott 1978b). Every unknown bird is first recorded by drawing its bill pattern on a form (Fig 1). This is kept in a folder with details of the bird's movements, associations and, if possible, head photographs. The folders are filed alphabetically according to the names given to the swans to help memorize pairings and, sometimes, characteristics.



Adult ✓ | Yearling | Probable Sex: ♂ | Name: FLIT

Plastic Ring No: 844 (R)

Metal Ring No: Z27370 (L)

INITIALS OF CODER

SIZE OF SWAN: Large / Medium ✓ / Small

BILL COLOUR: Pale / Lemony / Yellow ✓ / Orangey; Bright ✓ / Dull

SIDE OF LOWER MANDIBLE: Much pink / Narrow pink ✓ / None

BILL: Turned up / Turned down

EYELIDS: Yellow top / Yellow both / No yellow

FLIT 28.10.79

Date of Drawing: 28.10.79

Artist's initials: ECR

Locality of drawing: Slimbridge

Notes: 1975 Flip / Turtle cygnet

Consorting with: WITTY

Other characters:

	R	L
D		
O		
FD		
E		
Y	7·3	
FY	4·23	
T	2·2	
Q	4	
G	1·2	

	M	K	N	S
0				
1				
2				
3				
4				✓
5				
6				
7				
8				
9				

L	O	TD
B		IP
C		UP
CF		UY
		US
		UB
PRR		PRL
MRR		MRL

Fig 1. Form for recording *Cygnus columbianus bewickii* bill markings.

When new observers take up the study, swans which have previously visited the site will probably be unknown to them. Birds with experience of Slimbridge may, to a certain extent, be discerned by their behaviour. They are generally more confident and know the best places in which to look for food, whereas birds new to Slimbridge tend to swim away from the buildings, looking alert and anxious, particularly when the food barrow is brought round. However, only ringed birds, associates of ringed birds and individuals pointed out by experienced observers will be identified. It was therefore important that a method be evolved for systematically ordering bill pattern types. Then, when a new bird arrived, it would be possible to refer to swans with similar markings and see if any matched. Theoretically, this would enable anybody unfamiliar with a bird to discover if it had previously been recorded.

The development of a coding system

P Scott (1966) suggested a formula in which a swan's bill pattern was divided into 11 variable features. Each feature was given a letter code and each variation of a feature was allocated a number. It was therefore possible to describe a swan's bill pattern by a list of letters and figures.

In 1971 this formula was greatly modified and became what is now called the 'Old Code' (P Scott 1971 unpub). All adult and second-winter swans identified at

Slimbridge between 1963/64 and 1977/78 had their bill patterns identified by this system. The 'Old Code' was further revised and simplified by P Harvey (1977 unpub) into a purely digital form, particularly suitable for computerization. D K Scott (1978a) used this clearly defined version in her study of the social behaviour of *C. c. bewickii* at Welney, Norfolk.

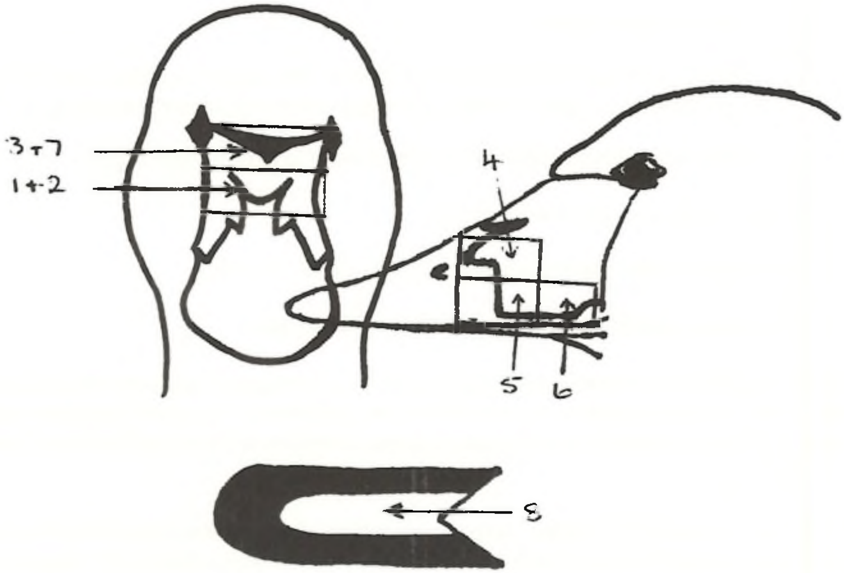


Fig 2. The location of the eight major characters used in coding bill patterns.

In both versions of the code, bill patterns are divided into eight major characteristics, including coloration on the under-bill (see Fig 2). These characteristics are subdivided into the different variations in markings which can occur within each section. A numerical code is allocated to each type of pattern.

The eight major coding items are as follows:

1 The front. Each swan is placed in one of the three major categories: Darkies, Yellownebs or Pennyfaces.

Darkies (code letter D) are swans where the centreline of the upper mandible is black from the feathering of the forehead to the tip of the bill.

Pennyfaces or Off-centreline Darkies (code letter O) are swans where a line other than the centreline can be followed on black from the browline to the tip of the bill.

Yellownebs (code letter Y) are swans where a continuous line of yellow stretches across the bill, linking the yellow patches on either side.

2 The shape of the central black trunk.

3 Markings on the browline.

4 The yellow protrusion towards the nostril in the sector indicated (see Fig 2). This may be absent, vary in shape or be cut off as an isolated yellow spot.

5 The angle of the black edges in the front lower quadrant (see Fig 2).

6 'Gape' (ie the corner of the mouth).

7 The shape of the edge of the feathering between the eyes.

8 Coloration on the underside of the lower mandible.

Possible variations of these characteristics are diagramatically represented on a key sheet. Once the bill pattern of a swan has been sketched, the coder compares each section of the bill pattern with the appropriate diagrams on the key sheet and notes down the code.

As well as the coding of the bill pattern, a number of additional characteristics help to identify a swan. These include size, bill shape, head shape, presence or absence of yellow around the eyes and coloration on the sides of the mandible. The bill colour is usually a cadmium yellow but paler and orangey shades can occur. Such variations may be seen on swans where the yellow was quite normal the previous year (Evans 1977). Therefore this characteristic can aid identification for only one season.

Since 1967/68 all swans caught at Slimbridge have been marked with large plastic leg-rings inscribed with digits or letters, which can be easily read at a distance. Most of the swans caught have their photographs taken from right, left and centre. These photographs are studied when coding bill patterns to augment and verify the drawings. Photographs of unringed swans are taken whilst they are swimming on Swan Lake, enabling observers accurately to code swans which cannot be identified by rings. Cygnets, ringed or unringed, are not generally photographed as bill patterns are often ill-defined until the second winter (Evans 1977).

Ordering the data

In 1972, following the development of the 'Old Code', a number of methods for storing and retrieving the coded information were considered. They included the use of edge-punched cards and 'Peek-a-boo' (pattern-punched) cards (M E Evans pers comm). Punch cards would be based roughly on the formula described, with a drawing of each individual xeroxed onto the card. However, although the card would be coded from the drawing, as the number of variables is so high, inaccuracy in just one section could result in the correct card being missed. Another problem is that punch cards become worn.

'Peek-a-boo' cards would be cheaper and easier to store. However, drawings could not be attached to the cards because the hole patterns would be obscured, so all the results obtained would have to be checked from the original records.

It was eventually decided that a code-book was the most effective method for storing and retrieving bill pattern data. A copy of a swan's code was placed into one of three books according to facial type, Darkies, Yellownebs or Pennyfaces. These books were subdivided into sections representing variations in the shape of the central black trunk (character 2), then again into 'tooth shape' (character 4), markings at the browline (character 3), shaping at the lower forward quadrant (character 5) and 'gape' (character 6). The ordering of the characters was based on their assumed importance in differentiating between individuals.

Limitation of the 'Old Code' and code-book systems

D K Scott (1978b) observed that the accuracy of the bill pattern drawings and therefore the ease and accuracy of recognition depend on a number of factors. These include the skill, practice and patience of the observer, the lighting conditions at the time of drawing and the distance of the swan. Whenever possible, photographs should be used.

The 'Old Code' formula and the code-book storage system also have a number of inherent failings. Although D K Scott (1978) showed that coding is unaffected by personal reliability, problems arise when one observer looks for a bird coded by another. Unless the code is clearly defined, differences in perspective may make it difficult to retrieve the correct pattern. In the case of the 'Old Code' the most subjective area is in defining the central column of black (Fig 2, section 2). This may (1) have parallel edges, (2) be wider at the top, (3) be wider at the bottom, (4) be wider at some intermediate point and (5) be narrower in the middle. However, within these reasonably clear definitions, further categories showing different shapings are represented only diagramatically. Some of these diagrams are very similar and are open to misrepresentation both if the drawing is slightly inaccurate and in the way different observers relate the diagrams to the drawings. Since these central markings are important items in differentiating between individuals and were the first factor to determine a swan's position in the code-book, all the categories have to be made exclusive and clearly defined.

As much information as possible should be used when retrieving a face to help compensate for slight inaccuracies in the drawings and any slight changes in bill patterns over the years. A major failing of the code-book system is that only the right side of the face was used for filing faces. Many of the patterns are asymmetrical so attempts to classify and retrieve the data using both sides would be slow and complicated. Pennycuick (1978) demonstrated that only 29% of the swans have sufficient information in their markings on the right side alone for accurate identification. The 'Old Code' and code-book systems are therefore unreliable. However, by utilizing the left side and features other than bill patterns, the amount of information about each bird would be raised, increasing the proportion which could be reliably identified.

The 'New Code' system

In 1979, P Scott, D K Scott and the author formulated a 'New Code' system (Appendix 1). This version is based on the 'Old Code' and 'Harvey's Code', revising the more subjective areas of the former and utilizing more information than the latter.

The 'Old Code' attempted to cover all possible variations of a character by giving a wide range of choices in the key. As variations in markings shade into each other along a continuum, many of the diagrams presented closely resembled each other. This, and the lack of detailed definitions, led to ambiguity between the divisions and therefore errors in coding. In forming the 'New Code' we limited the variations available, grouped similar characters together and inserted a clear description of each item. For instance, amendments were made to the choice of shapes for the central black column (character 2) in Yellowneb swans. To the broader definitions of the 'Old Code' (see page 2) we added the subdivisions:

(1) No prongs going upwards

(2) Short, thin prongs upwards

(3) Short, thick prongs upwards

(4) Long prongs upwards.

Under these guidelines, similar patterns which were given different code numbers under the old system are grouped together. Variations 2.1 and 2.2, for example, are both 7.1 in the new version (Fig 3).

There does remain the problem of deciding at what point thick becomes thin and short becomes long. It will always be difficult to segregate all the variations, so if a swan does fall between two intermediate patterns, both figures may be entered, divided by a slash.

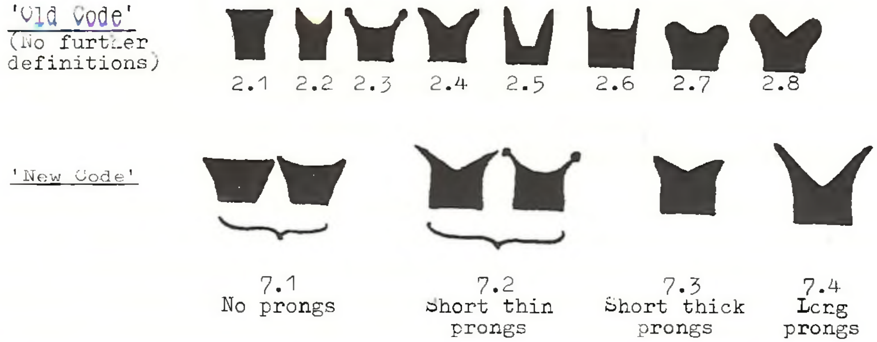


Fig 3. Some variations of the central black column, with trunk widest at top.

To increase the amount of information used to re-identify a bird (recommended by Pennycuick 1978) we made two amendments.

(1) We bisected the three frontal characteristics – basic bill pattern type, shape of trunk on central column of black and forehead markings – by drawing an imaginary line down the centre of the bill. This enabled us to code both sides separately and so fully to describe asymmetrical patterns in numerical terms (Fig 4).

Character	Right	Left
Fr	Y	Y
E	8.2	7.1
F	2.23	2.23

Character	Right	Left
Fr	01	Y
E	4.1	8.3
F	4.20	4.21

Character	Right	Left
Fr	Y	Y
E	8.3	8.3
F	4.1	4.22

Fig 4. *Cygnus columbianus bewickii* with asymmetrical markings and the appropriate codes for the frontal characters.

(2) We added a number of characters to the code other than bill markings. In choosing these we were careful to select ones which are unlikely to change from year to year. Bill colour, however, was included as it is a useful aid for identifying swans within a season.

The computerization of *C. c. bewickii* face patterns

At the end of June 1979, the Wildfowl Trust acquired a 'Research Machines' 380Z micro-computer, with data storage on 8-inch floppy disks. Information is typed in via a keyboard and is displayed on a television screen. Print-outs of stored data can be obtained from a teletype printer.

Computerization of *C. c. bewickii* bill patterns would clearly assist subsequent recognition. When an unknown swan arrives, its code would be typed into the computer and compared with the codes of swans already incorporated into the data bank. The computer would then print out details of three or four swans with codes that approximate closely that of the new bird, enabling the observer to decide if it had been recorded previously. If the swan is not on record its code would be saved for future reference along with any relevant data such as name, arrival date, etc.

Professor R Sibson and his colleagues at Bath University kindly agreed to devise two computer programs:

(1) to enable an observer to retrieve information about swans with bill patterns similar to that of an unknown bird; and

(2) to translate the 'Old Code' into the 'New Code', enabling us to put onto computer some 3000 patterns described by the 'Old Code', without re-coding them manually. Only the 'New Code' will continue to be used.

Bill pattern codes have to be typed onto computer in a set order so that the computer can organize and search the data. The format used is described in Appendix 2.

Opportunities for further study

The computerization of *C. c. bewickii* bill patterns offers more than just an efficient storage and retrieval technique.

An investigation of asymmetries in bill markings would be of particular interest. Pennycuick (1978) points out that correlations may exist between the two sides. As the correlation increases, the markings on one side will predetermine those on the other, so less information is obtained from the second side. If two characters correspond exactly thoughout the population, only one is useful for identifying individuals. It would be useful to see how frequently asymmetry occurs in the population, which characters do correlate and how strong are these correlations.

Similarly, a repeat of Pennycuick's test (1978) but using the new code and all those swans which are fully coded would determine which characters are most useful for reliable identification and which are too common to be used on their own. This would improve the retrieval of birds whose codes are not completely recorded. Swans with rare features may be recalled even if drawings of their markings are incomplete.

Evans (1977), by comparing photographs of 20 adult birds in two successive years, showed that small changes in bill pattern may occur, usually in the upper part of the culmen. Further evidence on changes in markings can be obtained by recoding swans each winter and comparing them with codes of the same birds from previous years. Photographs would be useful in providing an ongoing resource-library.

The question arises of whether certain characters are inherited. Bateson, Lotwick and Scott (1979) investigated similarities between the faces of both parents and offspring in *C. c. bewickii* and also the differences between mates. They concluded, on observing 12 pairs and 20 of their offspring, that the latter resemble both their fathers and mothers more closely than would be expected by chance. They also indicated with less certainty that mates are less similar than would be expected if swans paired at random. Both tests should be re-run for a much larger sample to confirm those characters which are similar in relatives and to test the 'diversity of mates' hypothesis.

D K Scott (1980 submitted) showed that pairs with Darky or Pennyface males are more dominant and aggressive than pairs where the male is a Yellowneb. Female bill pattern type did not relate to the position of the pair in the hierarchy. However, female *C. c. bewickii* seldom enter into physical combat (D K Scott 1978a). If threats are also considered, Darky and Pennyface females may prove to be more aggressive than Yellowneb females.

Summary

Studies of *Cygnus columbianus bewickii* at the Wildfowl Trust, Slimbridge, Gloucestershire, are largely dependent on the identification of individuals by their black and yellow bill markings. Attempts have been made to describe these markings in numerical terms, enabling observers to identify birds which have been previously recorded. The 'Old Code' and code-book systems used to store and retrieve bill pattern information between 1971 and 1979 are shown to be subjective and inefficient. A 'New Code' is proposed which limits these failings. Computerization of the markings is recommended for the effective recall of 'known' birds and for further analyses of swan bill patterns.

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Appendix 1

CODE FOR THE IDENTIFICATION OF INDIVIDUAL BEWICK'S SWANS

The normal starting point for coding a swan is a drawing based on the standard outline on a loose-leaf form. Whenever possible, the swan should be coded as soon as the drawing is complete.

Coding consists of filling in with a number or a tick the appropriate spaces on the right of the drawing form.

NB For all of the first 12 characters (up to and including G), the right and left sides of the bill must be coded separately. Thus for the frontal characters Fr (1 & 2), E (3 & 4) and F (5 & 6), a centreline down the bill may be imagined to help code each side separately. In each case, the right side should be coded first (to correspond with input to computer).

The coder is required to decide which of the definitions with accompanying diagrams most closely resembles the swan's pattern. In the case of intermediate patterns, two figures may be entered on the form, divided by a stroke. At this stage, all black spots surrounded by yellow and all tiny yellow dots on the 'trunks' of darkies should be disregarded altogether, and all 'mushy' areas (confused patches of black dots on yellow or yellow on black) on central culmen should be treated as yellow. They are then later recorded under Sp and M respectively.

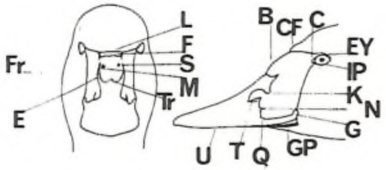
DEFINITION OF CHARACTERS

CHARACTER	VALUES	DEFINITIONS
Fr (I&2) Basic bill pattern types	D = Darky	Centreline of upper mandible is black from feathering of forehead to tip of bill. (Markings of any other colour than yellow orange i.e.red indicating immaturity or white indicating scar, are deemed black for this purpose).
	M = Mo-type . . .	
	M = Mo-type . . .	Same as'D',but with small yellow patches surrounded by black on culmen on either side of centreline. Unless yellow patches are easily visible, this should be coded under Sp (Quad). (Markings of any other colour should be treated as above).

DEFINITION OF CHARACTERS CONTINUED:

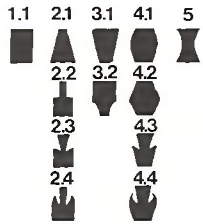
CHARACTER	VALUES	DEFINITIONS
	O = Penny-face	A line other than the centreline can be traced on black from feathering of forehead to tip of bill.
	OI	Central yellow patch rounded
	O2	Central yellow patch shield-shaped
	Y = Yellowneb	A line on yellow can be traced without interruption from the yellow patch on one side of the bill over the culmen to the yellow patch on the other.
E (3&4) Shape of 'trunk' on central column of black	I (For D,M, or O.)	Edge of trunk straight
	2 (For D,M, or O.)	Trunk widest at bottom
	3 (For D,M, or O.)	Trunk widest at top
	4 (For D,M, or O.)	Trunk widest in middle i.e. at some intermediate point between top and bottom
	5 (For D,M, or O.)	Trunk narrowest in middle
	6 (For Y)	Trunk straight or widest at bottom
	7 (For Y)	Trunk widest at top
	8 (For Y)	Trunk widest in middle
	After decimal point .I	No prongs going upwards
	.2	Short protrusions upwards, which are thin
	.3	Short protrusions upwards, which are thick
	.4	Long protrusions upwards (prongs)
F (5 & 6) Forehead markings	1	No black markings on forehead, or single line protruding downwards
	2	Part of forehead has black marking on top of culmen
	3	Broken black markings on forehead
	4	Black markings on forehead are continuous along line of feathering and extend almost to the eyes on either side
	First number after decimal point .1	No intrusion downwards
	.2	Intrusion downwards
	Second number after decimal point .20	For Darkies, Mo-types and Penny-faces
	.21) .22) .23)	For Yellownebs
T (7 & 8) 'Tooth' is a yellow protrusion towards nostril of the pattern in front of the main yellow patch on the side of the bill. It may be absent, or of varying shape or cut off as an isolated yellow spot (Teardrop).	1	No tooth
	2	Tooth with entrance being widest point
	3	Tooth with sides parallel
	4	Tooth with widest point inside entrance
	5	Teardrop
	After decimal point .1	(except 1): Large tooth or teardrop
	.2	(" "): Medium tooth or teardrop
	.3	(" "): Small tooth or teardrop
	.4	Two teardrops
Q (9 & 10) Lower forward quadrant on side of bill	1	Yellow ends with acute angle
	2	Yellow ends with right angle
	3	Yellow ends with arc
	4	Yellow ends with obtuse angle
G (11 & 12) 'Gape' is pattern at corner of mouth	1	Black does not continue beyond corner of mouth up cheek feathering
	2	Black does continue up cheek feathering
	After decimal point .1	No black bump in pattern
	.2	Black bump present
	.3	Black bump with yellow indentation before it

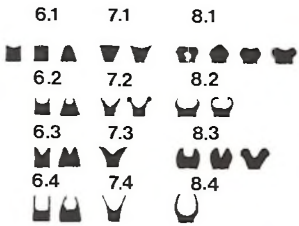
KEY



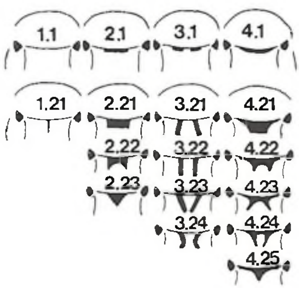
Fr

E





F



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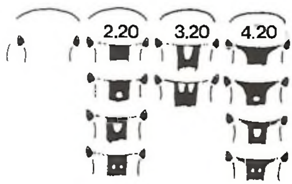
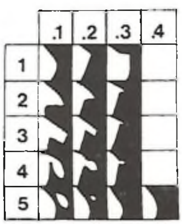
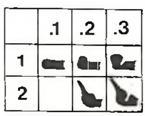


T

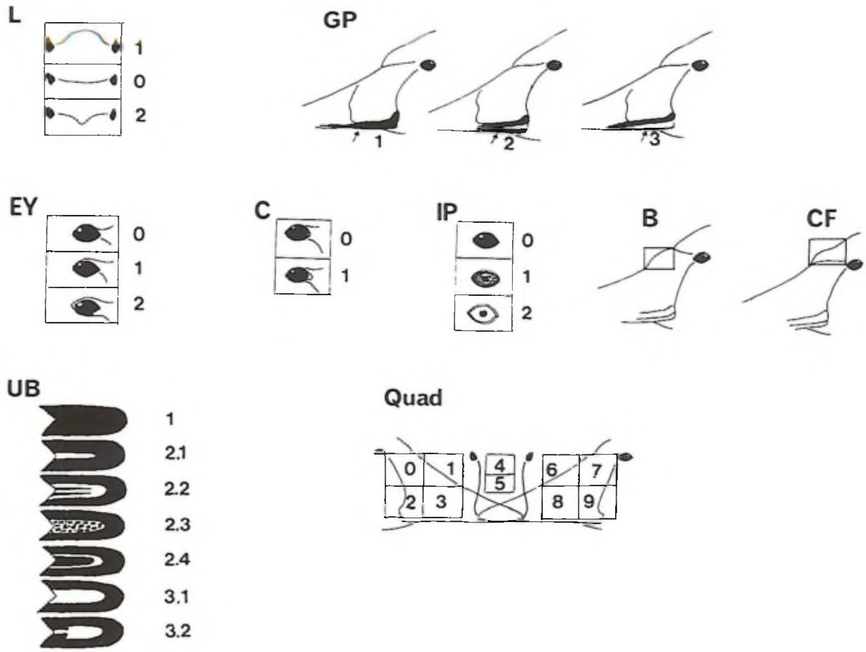


Q

G



Tr



DEFINITION OF CHARACTERS CONTINUED:

CHARACTER	VALUES	DEFINITIONS
L (13) Line of feathering	0.	Medium
	1.	High
	2.	Low
Tr (14) Trident	0.	Black protrusion up central yellow in a Yellowneb or Penny-face
	1.	Black protrusion absent
EY (15) Eyelid colour	0.	No yellow
	1.	Yellow top eyelid
	2.	Yellow both eyelids
C (16) Canalicula (red triangle in front corner of eye)	0.	Canaliculi not prominent (Before coding this, the observer should establish that the canaliculi are more prominent than on neighbouring swans).
	1.	Canaliculi prominent
IP (17) Iris colour	0.	Dark
	1.	Slightly pale
	2.	Very pale
ES (18) Eye size	0.	Medium
	1.	Large
	2.	Small
GP (I9) Pink visible in gape when bill is closed	I	No pink
	2	Narrow pink
	3	Much pink
UB (20) Underbill	I	Black
	2	Some pink or yellow in spots or stripes (.I-.4 : different patterns)
	3	All or almost all pink or yellow

DEFINITION OF CHARACTERS

CHARACTER	VALUES	DEFINITIONS
BD (2I) Bill depth (A-A')	0	Medium
	I	Deep
	2	Shallow
BH (22) Bill shape	0	Straight
	I	Turned down
	2	Turned up
BL (23) Bill length	0	Normal
	I	Long
	2	Short
HS (24) Head size	0	Medium
	I	Large
	2	Small
HH (25) Head shape	I	Domed
	2	Flattened
CF (26) Cat-faced	I	Cat-faced
	0	Not cat-faced
B (27) Bulgy	I	Bulgy
	0	Not bulgy
NE (28) Neck length	0	Medium
	I	Long
	2	Short
NT (29) Neck thickness	0	Medium
	I	Thick
	2	Thin
BP (30) Body posture	0	Medium
	I	Tail turned up
	2	Tail turned down
HC (3I) Head carriage	0	Normal
	I	Head-in-air
	2	Sleepy-head
BS (32) Body size	0	Medium
	I	Large
	2	Small
CY (33) Colour of yellow	0	Normal
	I	Lemony or pale
	2	Orangey
	3	Blotchy
CB (34) Brightness of yellow	0	Normal
	I	Very bright
	2	Dull

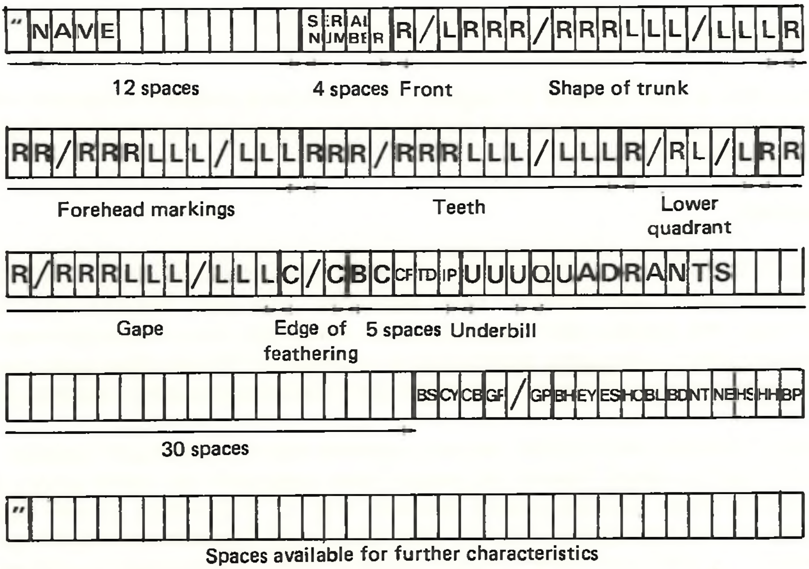
QUAD (35)
Quadrants: The following characteristics can occur on different parts of the bill. The correct letter(s) should be written against the appropriate sector (see diagram). If more than one of these characteristics is present, the letters should be written in the same order as below, in each sector.

- M Mush . . . . a confused patch of black dots on yellow or yellow dots on black in the sector indicated. All such patches should be regarded as yellow while coding above.
- Sp Spots . . . . black spot or spots surrounded by yellow, or tiny yellow spots surrounded by black on the centre of the culmen on darkies (does not include 'teardrops'). Spots touching forehead should be coded under F.
- K Knob . . . . a rounded protrusion of black into yellow not already coded under above characters (e.g. in E for yellownebs)
- N Nick . . . . a pointed protrusion of black into yellow, not already coded above.
- D Dent . . . . a dent in the bill
- R Recent damage . . . . . obviously recent injury on bill
- Sc Scar . . . . scar, or whitened area indicating trauma

Appendix 2

ORDER IN WHICH BILL PATTERN INFORMATION IS PUT ONTO COMPUTER

(Each box is equivalent to 1 space)



R ≡ code for the right side of the face

L ≡ code for the left side of the face

C ≡ code for the centre where the bill remains undivided

/ precedes an alternative code where the pattern falls between 2 values. If there is no alternative value, fill the spaces allocated with *S

U ≡ underbill

If the left side is symmetrical to the right, fill the left hand spaces with *S

When a value is unknown, insert ?

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MIGRATION OF *CYGNUS OLOR* RINGED IN DENMARK IN WINTER AND DURING MOULT

P ANDERSEN-HARILD

Introduction

Since 1963 a great number of *Cygnus olor* have been ringed in Denmark. Large-scale ringing has been carried out on the wintering population and on the flightless moulting swans in summer.

Materials

Some 17 000 *C. olor* have been ringed, 9000 when moulting, the rest in winter. They have so far given about 13 500 recoveries. This total includes birds found dead and, the greater part, those resighted while still alive. All resightings of a particular swan at the same locality within a period of 30 days have been counted as one recovery only. Thus the 13 500 do not include these multiple resightings.

Ringing localities with similar recovery patterns have been grouped together. The swans ringed in winter have in this respect been separated into seven groups, each comprising three to seven ringing localities (Fig 1). This allows a more detailed analysis within each group. Most of the swans were ringed in the eastern part of Denmark. In 1970 and 1979 a small number of swans were ringed in Jutland and on Funen, but the number of recoveries of these birds is insignificant.

Moulting localities have been analysed separately.

The recoveries have been recorded on magnetic tape and analysed using a computer. In this paper a grid with 1^{o} latitude by $\frac{1}{2}^{o}$ longitude is used, the area of each block decreasing to the north. The differences are, however, small and thought to be of minor importance. For every block the promille of the total number of recoveries in the group investigated was computed.

The material has been split up in several ways:

1) The total number of recoveries
2) Recoveries of birds found dead
3) Recoveries where the bird has been reported as breeding.

For each of these groups the geographical distribution in five 'seasons' of the year has been tabulated:

a) January to March (winter)

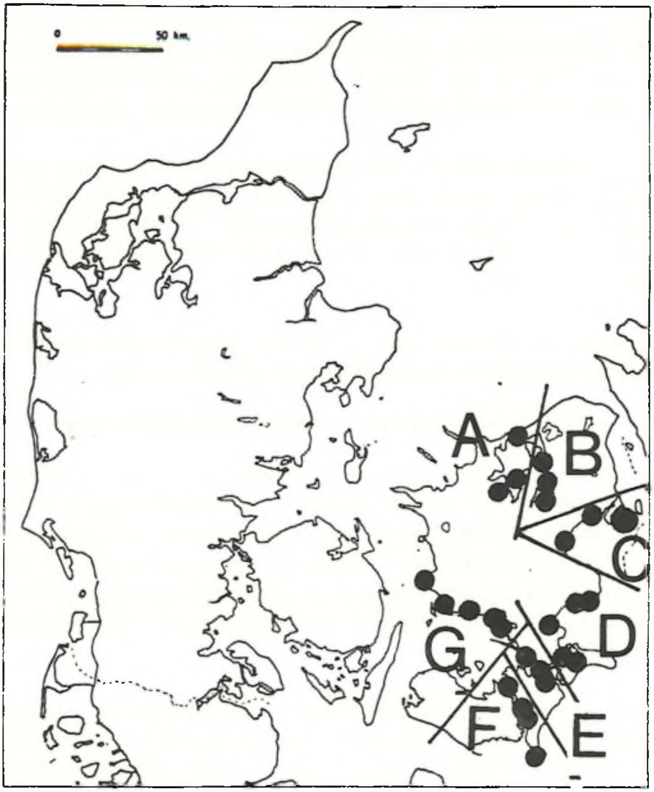


Fig 1. Main ringing localities in winter for *Cygnus olor*. The localities have been grouped as follows: A: Isefjord. B: Roskilde Fjord. C: Køge Bugt. D: Møn. E: Grønsund. F: Guldborgsund. G: Southwest Sjaelland.

b) April to May (spring dispersal of non-breeders)
c) June to August (moulting and breeding)
d) September to October (post-moulting)
e) November to December (autumn migration)

This will, of course, give a great number of distribution maps difficult to interpret. An easy and quick way of getting an impression of the distribution patterns is to have the ellipse of concentration plotted on the grid. The mathematical way of computing the ellipse of concentration is described in the appendix.

Bias in the materials

If distribution maps for birds recovered alive and birds recovered dead are compared, it is obvious that these two groups are not identically distributed. The resightings are concentrated at certain places in the southeastern part of Denmark, along the coast of the German Democratic Republic and the west coast of Sweden, depending on where enthusiastic amateur 'swan-ring-readers' are resident.

It is therefore concluded that the distribution of birds found dead will be the least biased. But when giving percentages, one must bear in mind that these reflect only the distribution of recoveries and not necessarily the distribution of the population. However, it is thought that differences between populations are reflected in the material.

Multiple resightings of the same bird, as is often possible when using neck-collars, are most valuable, but will not be specially treated in this paper.

Ice conditions and distribution of *C. olor* in the Baltic area

The breeding distribution of *C. olor* in the Baltic area appears to be determined mostly by the length of the ice-free period at the breeding places. This will allow the swans to breed as far north as 62°N in Sweden and along the coast of southeastern Norway and southwestern Finland. In Estonia, Latvia and Lithuania the population is increasing but an extension of the breeding range farther to the east and southeast will hardly be possible if the birds are still bound to use the Baltic Sea as a wintering area.

The distribution in winter is restricted mostly to areas around or west of the 0°C isotherm, which runs through Denmark. The birds gather in the shallow coastal waters in Denmark and along the German Baltic coast. Along the North Sea coast the swans find hardly any suitable feeding places. Along the Swedish and Polish Baltic coast the few shallow areas suitable to the swans are ice-covered for too long a period to allow the swans to survive under natural conditions. Swans wintering in this area normally benefit from the activity of man (harbours, sewage outlets, feeding, etc).

About every seven to nine years the winter climate in the Baltic Sea is much more severe than average. Cold winters occurred in 1962/63, 1969/70 and 1978/79. In these winters the shallow areas were frozen for about three months, and the swans suffered severe losses (Andersen-Harild 1981). In 'normal' winters the shallower parts of the western part of the Baltic Sea and the Danish waters freeze over only for a few weeks. Most of the birds are then able to feed at holes in the ice. Most ringing in winter has taken place in years with severe ice conditions. In such winters considerably higher numbers (70 000) of birds winter in Denmark than usual (40 000).

Results of ringing moulting swans

Large-scale ringing of moulting swans has taken place at Rødsand, Saltholm, Skalø,

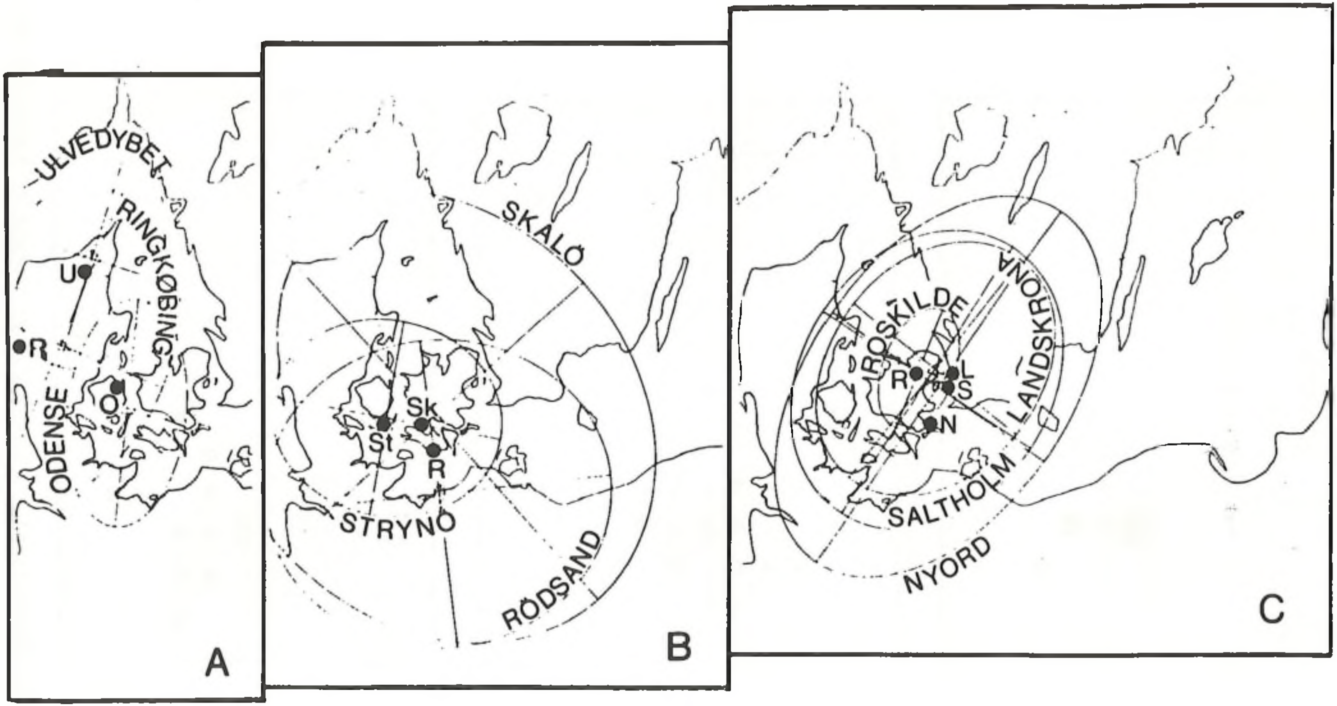


Fig 2. The ellipse of concentration for the recoveries of *Cygnus olor* ringed at various moulting places in Denmark.

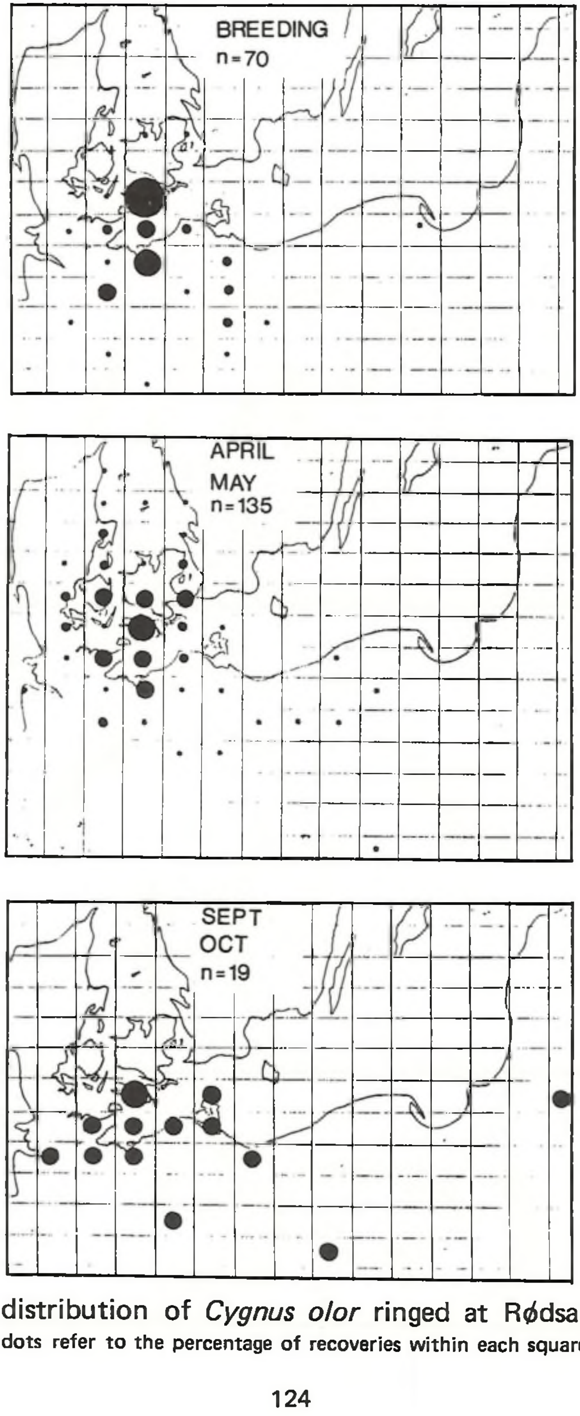
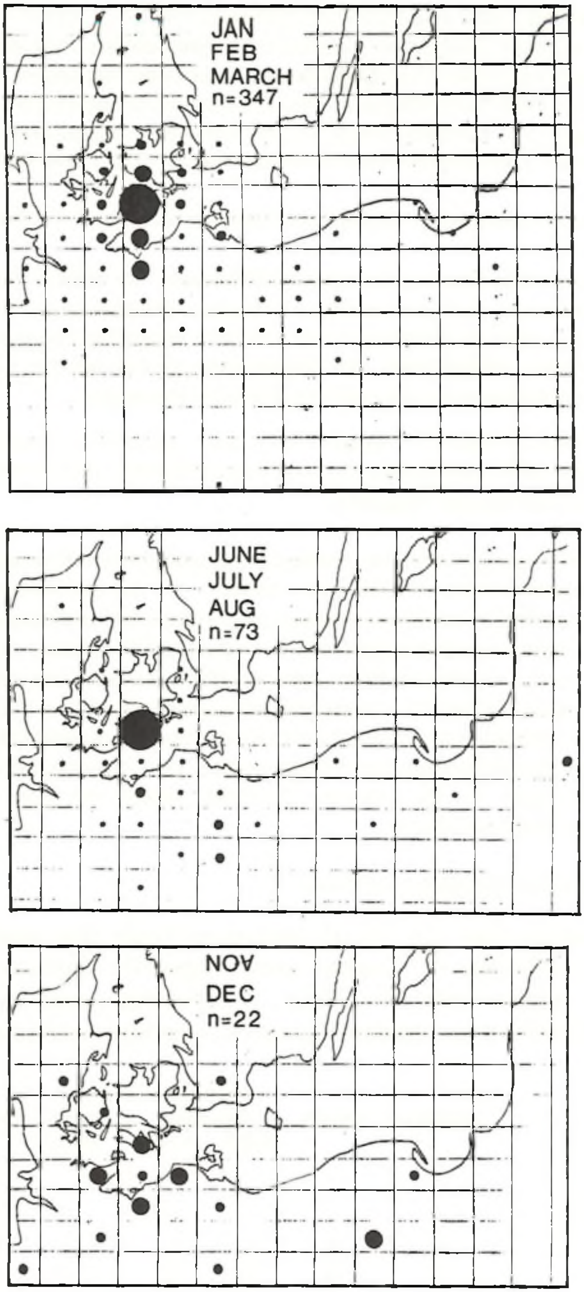


Fig 3. The distribution of *Cygnus olor* ringed at Rødsand and later
The size of the dots refer to the percentage of recoveries within each square. Smallest dot =



recovered dead.

less than 2%, then 2.0 to 4.9%, 5.0 to 14.9%, 15.0 to 24.9% and the biggest dot more than 25%.

Strynø, Ringkøbing Fjord and Roskilde Fjord. At Rødsand, Nyord and Ringkøbing Fjord a small number have been marked with neck-collars, but only in Roskilde Fjord has a majority (more than 50%) of the birds been marked in this way. A few birds (50 to 175) have been ringed at Ulvedybet and Odense Fjord – most of them with neck-collars. For further details on the moulting places and the number of *C. olor* moulting in Danish waters see Andersen-Harild (1971 and 1981).

Fig 2 shows the concentration ellipse for all recoveries from the moulting localities.

Fig 3 shows the results from birds ringed at Rødsand. The birds arrive at the moulting place in June and July and leave in August and September. Birds previously ringed and then caught at Rødsand show that this moulting place is used by birds hatched in an area ranging from the Netherlands in the west to Lithuania in the east and from Copenhagen in the north to Berlin in the south.

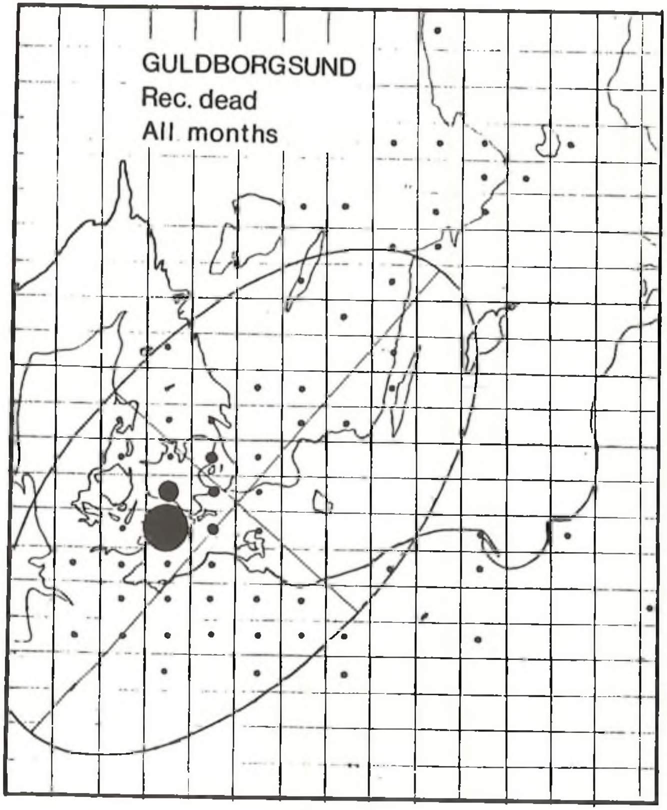
Recoveries of birds ringed at Rødsand and later reported as breeding birds show that most of the birds later breed around Lolland-Falster and in the northern part of the Germany Democratic Republic.

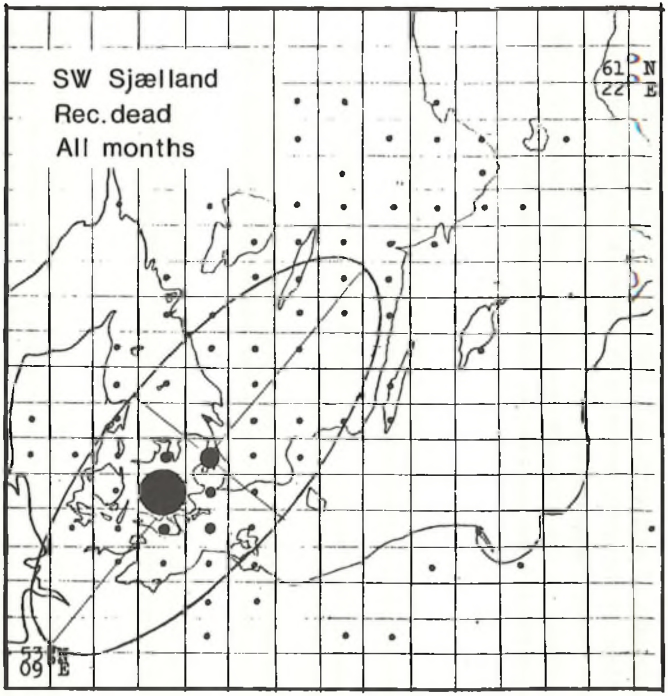
The main winter quarters for the Rødsand population is the western part of the Baltic Sea (Lolland-Falster and Rostock, Wismar). In the hard winter of 1978/79, recoveries showed that a small proportion of the birds left the normal winter range and spent the winter in northeastern Holland (outside the map). In April and May the birds are found in the southern part of Denmark and the northern part of Germany. At moulting time the recoveries are concentrated near Rødsand. Most of the birds still not breeding will return to the moulting-place used the previous year. Swans changing moulting-place are for the greater part young birds ringed in their second calendar year. In the autumn the birds spread out over the whole distribution area of the population.

Results from birds ringed in winter

Table 1. Distribution (in %) of recoveries from the months June to September (inclusive) of *Cygnus olor* ringed in eastern Denmark in winter. The letters refer to Fig 1. Resightings made by ringers and co-operators in the swan research project have been excluded.

Place of ringing		Country of recovery						
	Lithuania	Poland	Germany GDR	Germany FRG	Netherlands	Sweden	Denmark
A Isefjord	–	–	–	–	–	83	17
B Roskilde Fjord	–	–	3	–	–	53	43
C Køge Bugt	4	–	–	–	–	62	33
D Møn	3	5	13	–	–	52	27
E Grønsund	1	5	11	2	–	69	14
F Guldborgsund	–	4	49	3	1	32	11
G Southwest Sjaelland	1	–	2	–	–	65	32





It is obvious that the birds of map C belong to the same population. The small ellipse of concentration for Roskilde is due to a very high observation intensity for neck-collared swans in the area of ringing.

Fig 4. The recoveries and ellipses of concentration for *Cygnus olor* ringed in two areas in Denmark in winter.

The number of recoveries is: Odense 70, Ulvedybet 328, Ringkøbing 175, Skalø 189, Strynø 313, Rødsand 1716, Roskilde 3785, Landskrona 227, Saltholm 753, Nyord 406.

Fig 4 shows the distribution of recoveries of *C. olor* ringed at Guldborgsund and southwest Sjaelland. Most of the birds wintering in Denmark are of Danish and Swedish origin. Only in the southernmost part of Denmark do birds from Germany and Poland form a majority of the wintering population. Table 1 shows the percentage of birds found in the different countries in the breeding season.

Acknowledgements

I would like to thank all the persons who have helped in ringing operations and all those who have sent reports on ringed swans to the ringing centre in Copenhagen.

Large-scale ringing was initiated by P Tholstrup and A Schat-Kielberg. Later Peter Hermansen, Hans Lind and Leif Clausen have ringed thousands of swans.

The computer programmes were written by Erik Hansen and Preben Foldkaer, Risø National Laboratory. Jon Fjeldsa read the manuscript and suggested improvements. My sincere thanks are due to them all.

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Summary

Since 1963, 9000 moulting and 8000 wintering *Cygnus olor* have been ringed in Denmark, giving large numbers of recoveries. The plotting of an ellipse of concentration of recoveries to show recoveries is described and illustrated. Bias in recoveries is introduced by uneven observer effort and distribution of birds found dead shows least bias. Breeding distribution in the Baltic is determined by the length of ice-free period; wintering distribution is mostly around the $0^{o}C$ isotherm, but severe losses occur in severe winters which occur every seven to nine years.

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Appendix

The ellipse of concentration

A tool for mapping of geographical point distributions

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When the geographical distribution of a population is to be described, primary data often consist of a number of observations of individuals with corresponding co-ordinates. The most common method for displaying such data is the use of dot-maps (scatter-maps). However, such maps suffer from several inadequacies:

1) When many specimens are observed at the same co-ordinates or at co-ordinates close to each other, the maps become very confusing due to mingling of the dots.
2) When several populations are to be compared, the visual impressions of such maps are often very difficult to correlate, especially when the number of observations of the populations differ in magnitude and when this number is large.
3) For many purposes such a description is too detailed and thus confusing for the reader.

In an attempt to eliminate these problems we introduced the concept of the ellipse of concentration. The idea is to describe the distribution by the well-known geometrical concept of an ellipse. The ellipse is not influenced by the size of the population but immediately displays:

1) The centre of the population by the intersection of the axes.
2) The orientation of the population by the direction of the major axis.
3) The eccentricity of the population by the eccentricity of the ellipse.
4) The range of the population by the size of the ellipse.

By overlaying more ellipses of concentration with a geographical map, even small variations in the properties mentioned above are clearly displayed.

The mathematical tools for the calculation of the ellipse of concentration are taken from mechanical physics, where the ellipse of inertia is used to describe the behaviour of mass distribution in two dimensions.

The properties of the ellipse of concentration and their relation to the properties of the point distribution are most easily described in the system of co-ordinates formed by the major and minor axes of the ellipse. If we assign a weight equal to the number of specimens of the point to every point in the point distribution, and a uniform weight function to the ellipse so that the sum of the weights of the points is equal to the weight of the ellipse, the following relations define the ellipse:

1) The momentum of first order around the major and minor axes must be the same for the point distribution and the uniform distribution.
2) The momentum of second order around the major and minor axes must be the same for the point distribution and the uniform distribution.

Pragmatics:

ad 1) This relation simply states that the two distributions must have the same 'centre of gravity' which is the intersection of the axes. The momentum of first order is the weight multiplied by the distance from the axis.

ad 2) This statement 'defines' the size, eccentricity and orientation of the ellipse. The momentum of second order is the weight multiplied by the square of the distance from the axis; thus points far from the axis contribute more to the momentum of second order than points close to the axis.

The parameters of the ellipse of concentration are calculated by the following algorithm:

Let the points be given by their co-ordinates in a normal cartesian system of co-ordinates (west—east south—north).

$$x_i \text{ and } y_i \qquad i = 1, 2, 3, \ldots N$$

Let W denote the sum of the weights w_i, $\quad W = \sum_{i=1}^{N} w_i$

1) Calculate the centre of the concentration (x_c, y_c)

$$x_c = \frac{\sum_{i=1}^{N} x_i}{W} \qquad y_c = \frac{\sum_{i=1}^{N} y_i}{W}$$

2) Calculate the momenta of second order around axes through the centre of gravity and parallel to the original axes, and the hybrid momentum of second order around the same axes.

$$\mu_{20} = \frac{\sum_{i=1}^{N} (x_i - x_c)^2 \, w_i}{W} \qquad \mu_{02} = \frac{\sum_{i=1}^{N} (y_i - y_c)^2 \, w_i}{W}$$

$$\mu_{11} = \frac{\sum_{i=1}^{N} (x_i - x_c)\,(y_i - y_c)\,w_i}{w}$$

3) Calculate the correlation coefficient of the two-dimensional distribution (see Cramer p 277).

$$\varrho = \frac{\mu_{11}}{\sqrt{\mu_{20}\,\mu_{02}}}$$

4) Calculate the angle $\varnothing$ between the x-axis and the major axis.

$$\tan \varnothing \text{ major} = \frac{2\,\mu_{11}}{\mu_{20} - \mu_{02} + \sqrt{(\mu_{20} - \mu_{02})^2 + 4\,\mu_{11}^2}}$$

5) Calculate the length of the major and minor axis.

$$L = \frac{4\sqrt{1-\varrho^2}}{\sqrt{\dfrac{\cos^2\varnothing}{\mu_{20}} - \dfrac{2\mu_{11}\sin\varnothing\cos\varnothing}{\mu_{20}\,\mu_{02}} + \dfrac{\sin^2\varnothing}{\mu_{02}}}}$$

where $\varnothing = \varnothing$ major for major axis and
$\varnothing = \varnothing \text{ major} + \frac{\pi}{2}$ for minor axis.

I want to thank my colleague Peter Kirkegaard for his participation in evaluating the formulae.

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THE MOULTING GROUND'S RELATION TO BREEDING AND WINTERING AREAS AS REVEALED BY NECK-BANDED *CYGNUS OLOR*

S MATHIASSON

Introduction

There are three important biological and geographical elements in the annual life cycle of *Cygnus olor:* the reproduction and the breeding area; the moult and the moulting ground; and the winter quarters. They are connected by migration and resting grounds.

Before the 1930s *C. olor* was unknown as a breeding bird along the Swedish west coast. The swans had traditional haunts in eastern Sweden, where they have been known since the 17th century (Fig 1). These ancestral Swedish swans passed western Sweden on their migration to winter quarters along the coasts of southern Sweden and Denmark, as their descendants still do (Mathiasson 1973a). Gradually

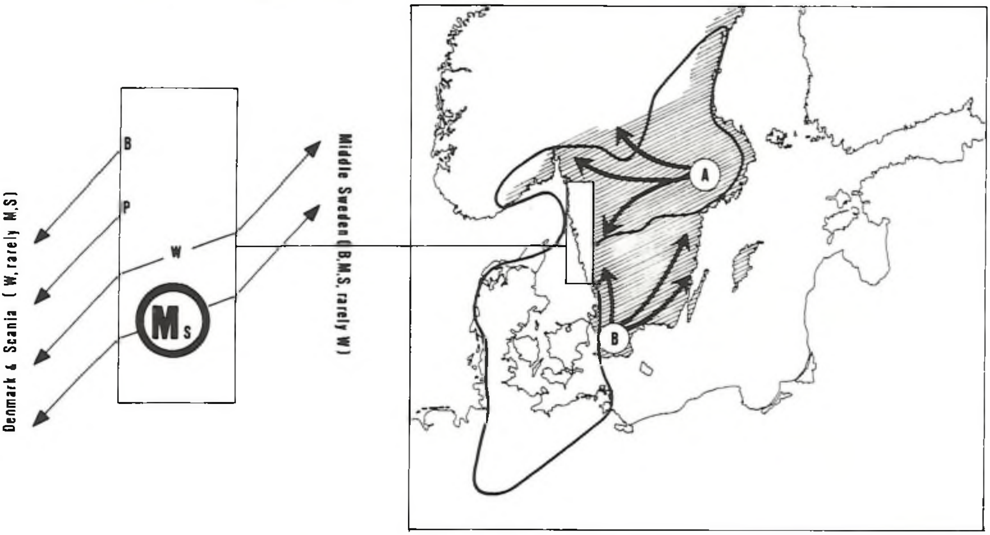

Fig 1. The present breeding distribution of *C. olor* in Sweden and Norway (hatched area), the preceding geographical extension of the former bicentric breeding populations (A and B) and the living space (all the year round) of swans occurring on the Swedish west coast (broad solid line).

The schematic illustration shows the migratory behaviour of different categories of west coast swans. Breeding birds (B) and their cygnets (P) occur only in the west coast area (rectangle) or migrate towards the southwest to winter. West coast winter swans (W) may use the whole living space, as do the moulting non-breeders of the summer (M_S).

they extended their breeding range to westernmost Sweden. The coast nowadays harbours no less than 83% of the population of about 300 pairs breeding in the Swedish west coast counties (total area 10 000 km^2). The coastal breeders have become more or less resident. The inland swans are still migratory and contribute non-breeders to the western Swedish moulting grounds and summer haunts.

More than 2500 moulting *C. olor* have been ringed in the 1960s and 1970s.

The moulting ground and the moulting flock

The moulting ground of Kungsbackafjorden (Mathiasson 1973a, 1973b) provides food and shelter. The total water area is about 53 km^2, of which 13 km^2 is of a depth less than 2 m. The vegetation of the latter area is accessible to the swans, in its deeper parts only during low water (Fig 1). It has been calculated that during their stay the moulting flock of about 1000 swans eat about 425 tonnes of seaweed, mainly *Zostera marina* but to a smaller extent also *Ulva lactuca.* This means that not more than 8% of the total production of *Z. marina* is consumed by that number of swans (Mathiasson 1973b and Borjesson 1974). The length of stay of the swans depends mainly on intrinsic factors connected with the moult. Fig 2 shows the regularity in annual fluctuation of numbers of swans at Kungsbackafjorden.

Counts throughout the year, biometrical data and movements of marked birds present general information on the migratory behaviour of *C. olor* in the Swedish west coast area as well as special information on the 'demographic' structure of the moulting flock and the behaviour of its members.

Fig 3 illustrates the structure of the moulting flock and the dynamic involved in the annual change of numbers. As can be seen from the graph to the left there has been a decline in the number of moulting swans during the decade of studies. The same graph shows the proportion of one-year old swans (hatched in the previous year). It is clear that the number of young produced in the preceding year (average 20%) strongly affects the total number of moulting swans present. There is also a clear decline of the proportion of one-year old birds, from 30% in 1972 to 6% in 1979. The very low figure of 1971 reflects lowered reproduction in 1970 due to the effect of the severe winter of 1969/70. The decreasing number of swans is also brought about by increased death rates (Fig 3: categories 6 and 4).

Shift of moulting ground has also had a strong influence. In the early 1960s up to 1800 moulting swans were present at Kungsbackafjorden and no other grounds were found along the Swedish west coast. Today there are six additional moulting grounds, established in the 1960s, which in 1978 held about 2500 moulting swans, compared with 625 at Kungsbackafjorden. Today such shifts seem to play a minor role. The numbers coming or going balance one another.

We find three clearly definable categories in the moulting flock. The 'floating'

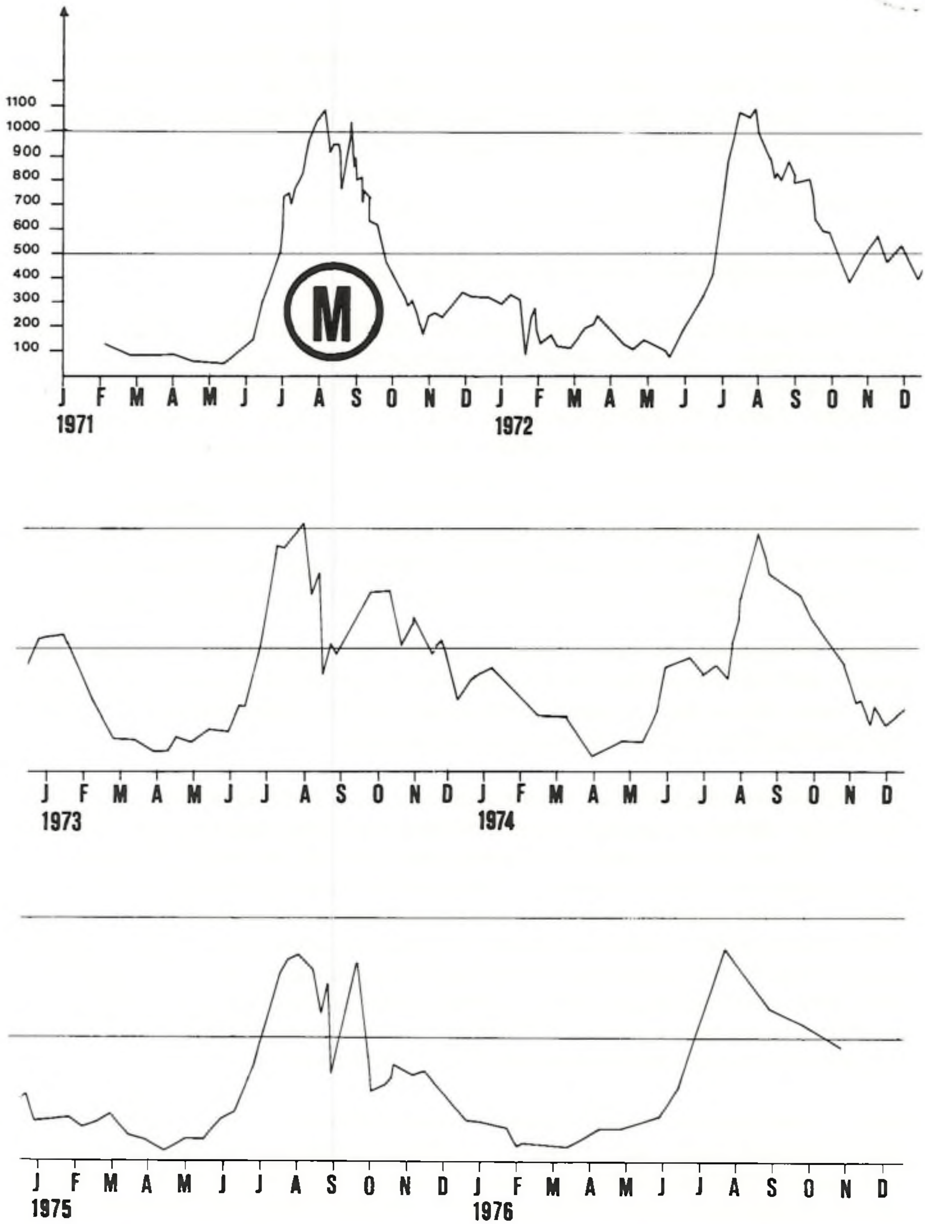

Fig 2. Annual fluctuations of *C. olor* at the Kungsbackafjorden moulting ground.

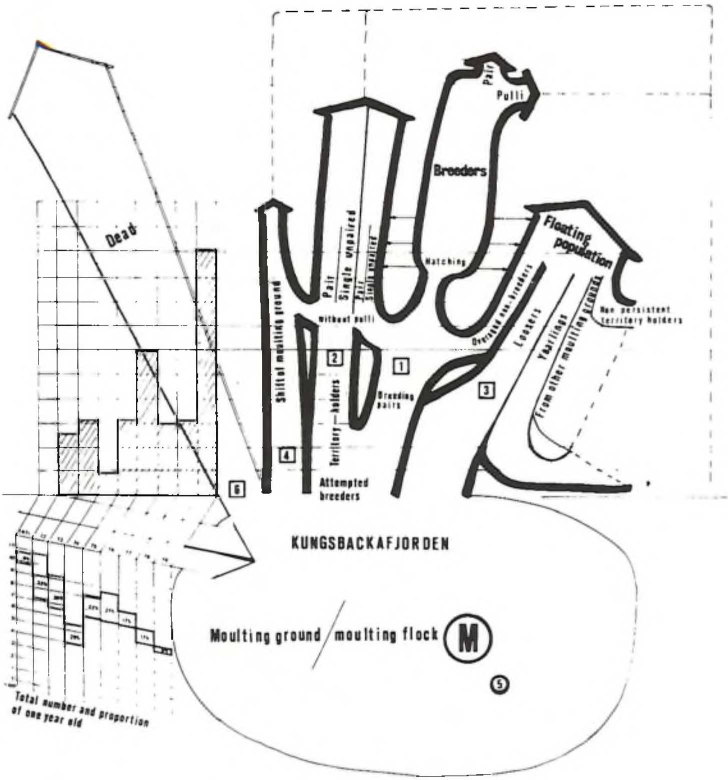

Fig 3. Illustration of the structure of the moulting flock at numerical peak (category 2) and the dynamic involved in the annual dispersal over the living space (category 1) and the rebuilding of the moulting flock.

The percentage of one-year-old swans in different years is presented to the left. The percentage of swans reported dead is also shown.

population which circulates between moulting ground, resting grounds and winter quarters (Fig 3: 3) and is built up mainly of yearlings, subadult non-breeders (but presumptive breeders), non-persistent territory-holders, over-aged breeders, swans which shift from other moulting grounds, and a large number of 'loosers', which never or very rarely attempt to breed, in spite of having reached the age of sexual maturity. The attempted breeders may take up a territory and stay there even during the moult and thus break the annual circulation characteristic of the first category (Fig 3: 2). The breeders, having reached sexual maturity, become successful territory-holders and stay at the breeding ground to moult (Fig 3:1). If the eggs are destroyed or the cygnets lost, they may, however, return for that particular season to their former moulting ground.

Migratory behaviour of individuals representing different categories of moulting swans

Mathiasson (1976) discussed the role of learned behaviour and tradition in the migratory habits of *C. olor.* Here are some examples of migratory behaviour connected to the function of the moulting flock model in Fig 3 and its relations to breeding grounds and place of birth, respectively, and winter quarters.

The way of the cygnet to its winter quarters, its future moulting ground and its subsequent breeding place (Fig 3: categories 1 and 2)

a) A pair of coastal breeders (female H4252, male H4154) of the Gothenburg archipelago produced four cygnets (001H—004H) in 1972 (Fig 4). The parents

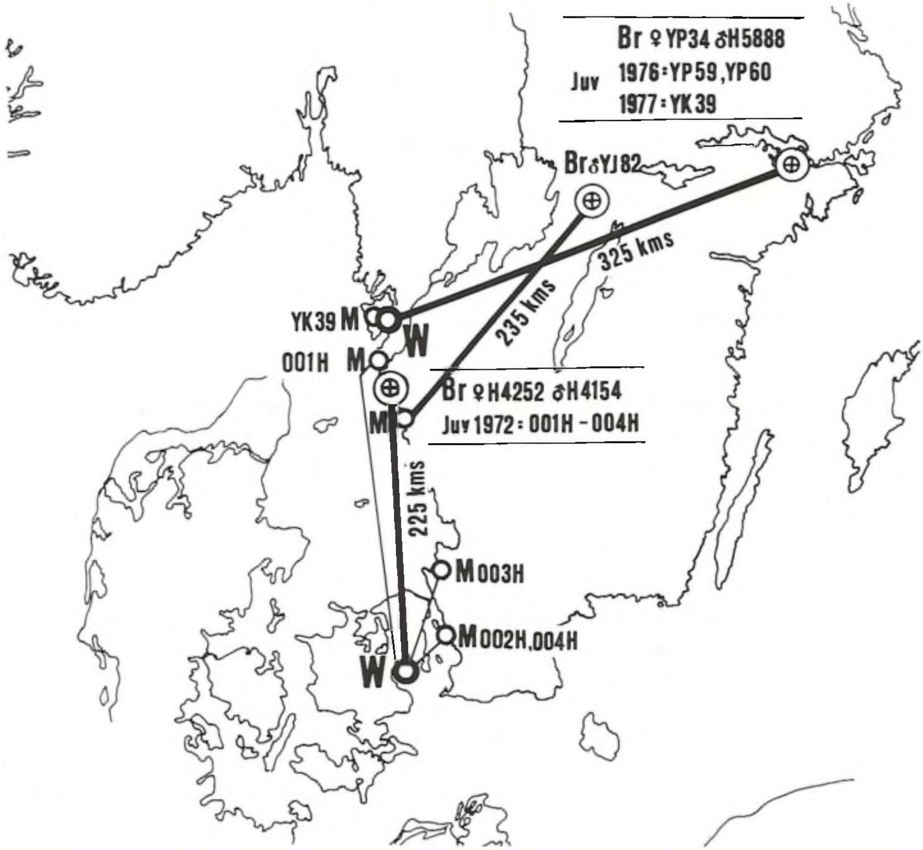

Fig 4. Three different migratory patterns between breeding places (birth places), winter quarters and moulting grounds.

reared their young and moulted as usual in the breeding ground. The cygnets wintered in Denmark, at Køge Bugt, southern Sjaelland. From there they dispersed the following spring. As yearlings, three of them were at different moulting grounds in Scania (southernmost Sweden) and Sjaelland (southern Denmark). From those moulting grounds they returned to their former and common winter quarters. They did so up to the age of 2 to 4 years. At that age they also returned for spring visits to the vicinity of their birth place but still recurred at their southern moulting grounds (about 225 km south). One female (004H) recurred during breeding time in 1976 with her mate at her birth place at the age of four. Being non-persistent territory-holders the pair disappeared. She was seen later on at her southern moulting ground (Landskrona, Scania), still later at her winter quarters. The following spring she returned to her place of birth and laid her first clutch of eggs but failed to incubate them. She returned to her winter quarters at the age of six (in 1979) and she succeeded in raising two cygnets in a nest 12 m from her own birth place. The pair that year moulted with their cygnets at the breeding place.

b) One pair of inland *C. olor* (female YP 34, male H5888) has its breeding place at Lake Hjalmaren, eastern central Sweden (Fig 4B). For five years they regularly changed between their breeding place at Lake Hjalmaren and their winter quarters 325 km away at Svanesund on the Swedish west coast. They arrive at their winter quarters in December and depart in late March or early April. In 1976 they brought two cygnets with them, in 1977 one (1976: YP 59, YP 60; 1977: YK 39). These cygnets stayed, as far as we know (records in summer), at west coast haunts when their parents left for their breeding ground in spring. The cygnets mingled with west coast non-breeders. One of them joined the moulting flock at Kalvofjorden. During subsequent winters the offspring rejoined their parents at Svanesund.

Shift of unsuccessful breeders between breeding ground and moulting ground (Fig 3: category 1)

A male (YJ 82/H4534) was ringed at Kungsbackafjorden moulting ground on 25 August 1973. Between 19 and 21 September 1974 it was caught when moulting there. On 23 November 1974 it was reported from Laxa, Narke, central Sweden, where it was courting one of two females (Fig 4C). They formed a pair and stayed for the winter. The following spring (1975) they bred and six cygnets were hatched but perished in June. On 17 June the parents were seen without cygnets at Laxa and in July they disappeared. On 20 August the pair was moulting at Kungsbackafjorden moulting ground, where they were still seen on 28 September. On 16 November they recurred at the breeding place at Laxa. Thus, when failing to breed, they left the breeding place for a flight of 235 km to the west coast moulting ground whence they returned, having completed the moult.

The examples given illustrate the traditional shifts between breeding place, moulting ground and winter quarters. The cygnets learn their way between birth place and their first winter quarters with their parents, because of family bonds.

Repelled by their parents in the winter quarters they join by chance flocks of older, more experienced swans from which they learn the way to their first moulting ground. Programmed in this way, they then continue their shifts year after year in the same manner. When reproductively mature, they reorientate themselves to their place of birth, where they settle to breed. Failing to breed, they go back to their programmed movements.

'Floating' population (Fig 3: category 3)

Obviously the moulting flock includes a number of less clearly definable groups. One such seems to be overaged non-breeders (eg former breeders). There also seems to be a fairly high number of swans never making any attempt to breed. We may name them 'loosers' as they seem to be of a low rank in both social and physical hierarchies. We have many records of neck-banded as well as tarsus-ringed swans of advanced age which have never bred. No less than 38% of the swans moulting at Kungsbackafjorden in 1979 (about 600) were considered to be at least six years old (a rough calculation based on capture/recapture). However, we need to be careful in judging whether a certain bird belongs to the 'loosers'. The start of breeding may take place very late in life. Continuous observations of single swans showing a permanent state of non-breeding are so far limited.

There are technical difficulties in permanent monitoring due to the long time span from the date of ringing (our oldest swan up to 1979 is 16 years old). Two examples of permanent non-breeders were:

- In July 1979 a healthy 9-year-old moulting female (3756) was controlled on Kungsbackafjorden, where she had been ringed as a moulting yearling in 1972. The shape of the cloaca showed that she had never laid eggs. As she was only tarsus-ringed, the records from the elapsed period were few. But she wintered at Hammer Bakke, Sjaelland, Denmark, prior to moving 200 km to the moulting ground;
- YA 94 (H4297), a female neck-banded as an adult (3 years old or more) in 1973 at the Lake Takern moulting ground. In 1974, 1975, 1976, 1977, 1978 and 1979 she was recorded in the moulting flock at Kungsbackafjorden. All the year round she was observed at the Swedish west coast and proved not to breed.

Shift of moulting ground (Fig 3: category 4)

Swans from the Kungsbackafjorden moulting ground have been found moulting not only at adjacent moulting grounds along the Swedish west coast, but also elsewhere within the living space of that population, as shown in Fig 1.

The rate of recurrence at a moulting ground of two-year old swans marked there as yearlings is between 55% and 70%. The recurrence in 1979 of swans marked as

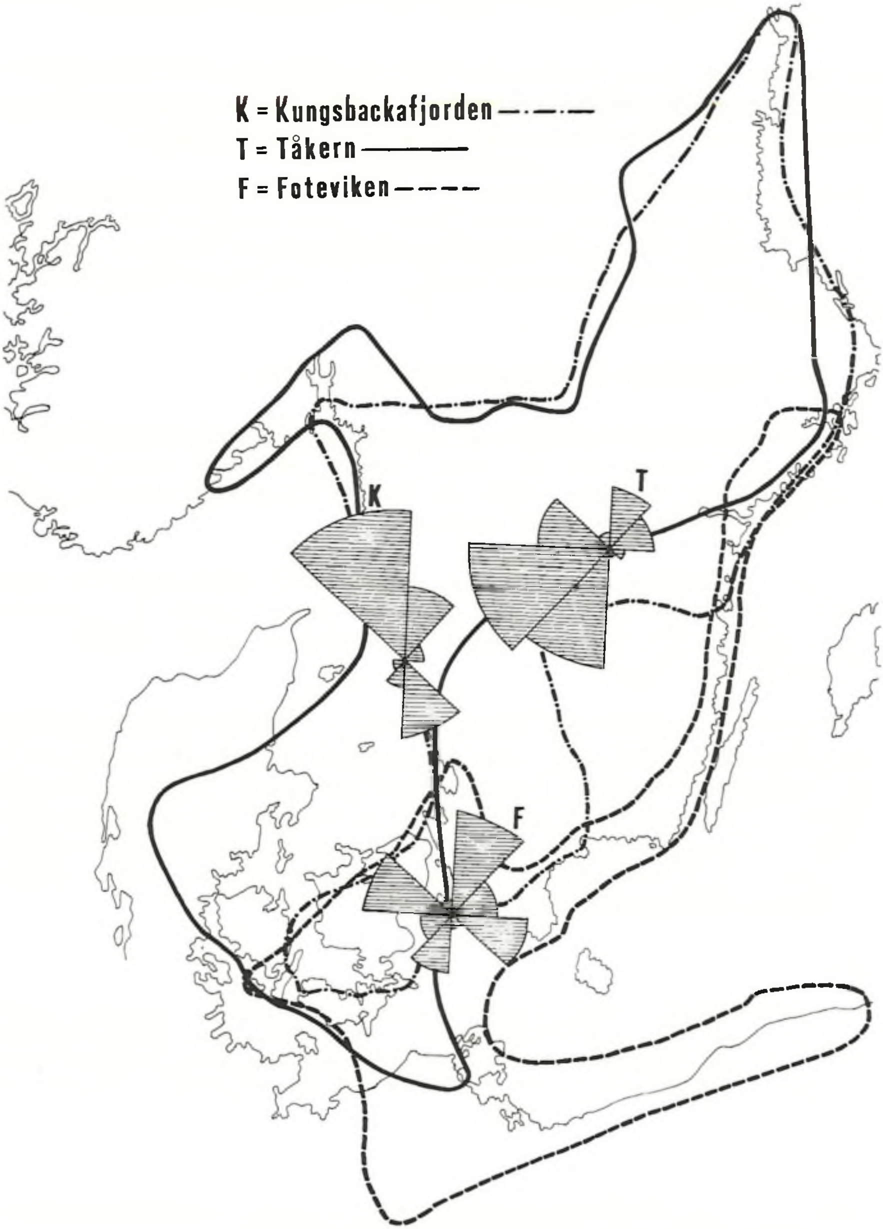

Fig 5. Geographical distribution during breeding season of *C. olor* ringed in preceding years at three important Swedish moulting grounds.

T = Lake Takern, K = Kungsbackafjorden, F = Foteviken-Hollviken. The circle diagrams show the proportional distribution in various directions from the moulting ground during breeding season.

two-year olds and older at Kungsbackafjorden moulting ground in 1978 was 37%, as compared to 65% for those marked as yearlings. Those figures are not compensated for mortality, so they should probably be at least 10% higher.

The lower recurrence rate of adult swans is connected with their incorporation into the breeding population and territory holders, which moult in their territories. There is, however, also a slight indication that adults shift more than yearlings; 15% of 85 swans shifted moulting ground in their second year of life, against an average of 20% yearlings.

The relations between different moulting grounds

The Swedish swans can be divided into two geographical populations. Their main living space is separate, but the winter quarters overlap to some extent (cf Mathiasson 1973a, Mathiasson 1976). The separate living spaces can be studied in relation to the main Swedish moulting grounds.

Numerical investigations show that the moulting swans of the different grounds have an identical time schedule in their in- and outflux, as well as synchronous numerical peaks. The different moulting flocks also seem to function as in Kungsbackafjorden (Fig 3).

Fig 5 shows the geographical affinities of the two moulting grounds of Kungsbackafjorden and Lake Takern, and the segregation between those two and the moulting ground of Foteviken, southern part of the Sound. The close connection between Kungsbackafjorden and Lake Takern is indicated by 22 swans alternating between the two grounds, but only 2 between Foteviken and Kungsbackafjorden and Takern. Fig 5 also indicates the clear connection between a certain breeding area (population) and special moulting grounds.

Summary

Cygnus olor has since the 1930s extended its breeding range to the west coast of Sweden. Kungsbackafjorden is the main moulting ground, and 2500 have been ringed since 1960. Marking with neck-collars allows different categories (floating population, attempted breeders and breeders) to be defined in the moulting flock and to illustrate subsequent movements and behaviour.

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PRELIMINARY RESULTS OF NECK-COLLARED *CYGNUS CYGNUS CYGNUS*

N O PREUSS

Introduction

During unusually cold weather, 129 *Cygnus cygnus cygnus* were ringed in Denmark during the first three months of 1979. Of these, 116 were additionally marked with a plastic neck-collar and a plastic tarsus-ring, both engraved with letters and ciphers. The neck-collar is 85 mm high with an inside diameter of 57 mm, the inscription is white on blue, 3 mm wide and 27 mm high. The tarsus-ring (94 mm high and 27 mm inside diameter), having the same inscription as the neck-collar, is engraved with 2 mm wide and 17 mm high ciphers and letters. With a telescope these neck-collars can be read from up to a distance of 500 m in good viewing conditions. This form of marking facilitates control in nature of live birds and does not depend entirely on recoveries of dead birds.

Up to 1 February 1980, we have received information concerning 40 such sight records from Denmark in the period up to April 1979, when the swans left for their breeding grounds. From Sweden we have sight records up to the end of April and from Finland from May. The autumn migration was demonstrated by records from south Finland and Sweden in October and November. From December and January 1980 we have received some records from the Danish winter-quarters.

Even at this early stage of the programme it is evident that the 116 neck-collared swans produced much more information that the 266 *C. c. cygnus* ringed without neck-collars in the period 1953 to 1978. Of the 116 neck-collared swans 26 (22.4%) were seen abroad (some individuals were recorded several times), compared with 24 (9.0%) recoveries of the 266 previous ringed.

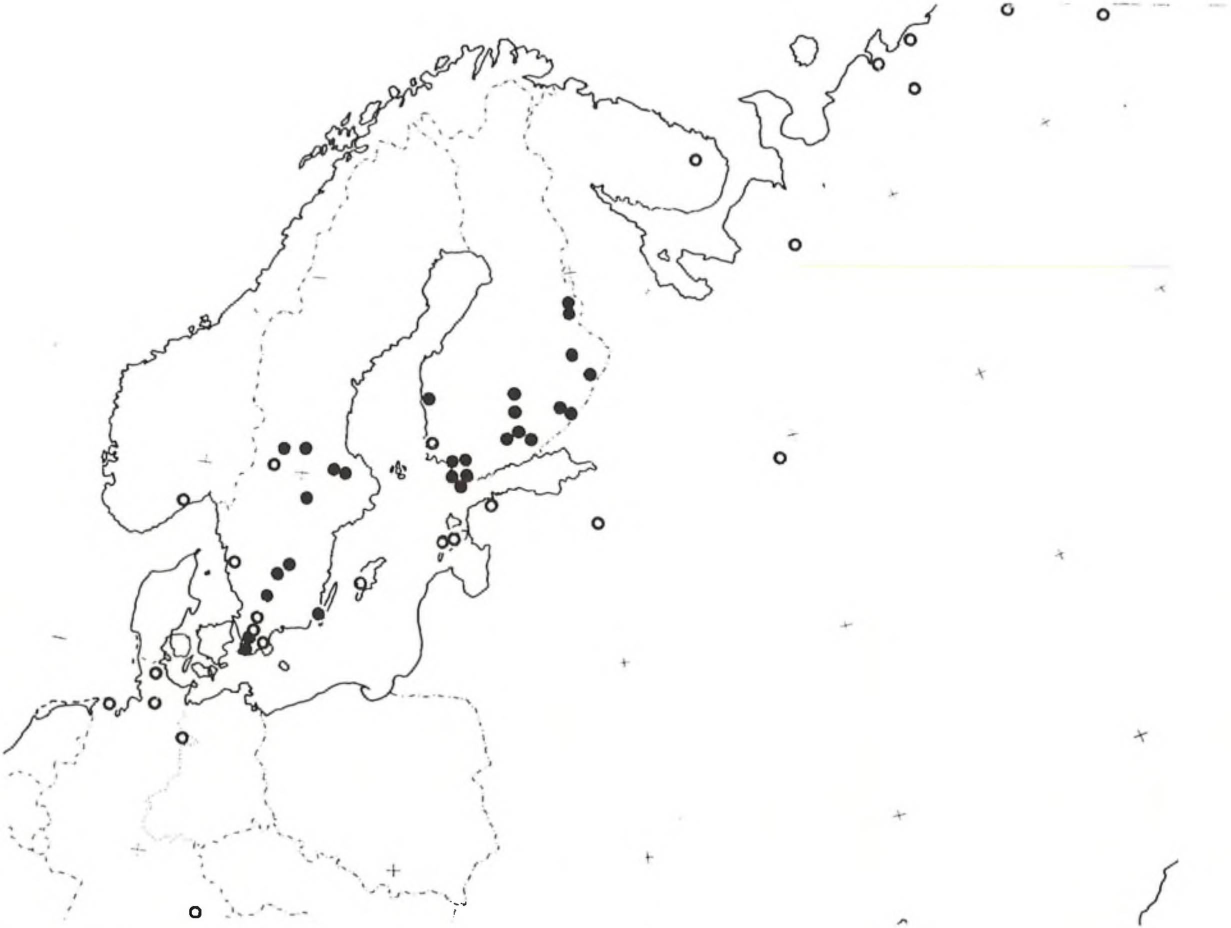

Fig 1. Sightings of neck-collared *Cygnus cygnus cygnus*.

On the map (Fig 1) sight records of neck-collared swans are indicated by a black dot and the previous recoveries by an open circle. Up to now no sight records have been received from the Soviet Union but we hope that we will get them from that area.

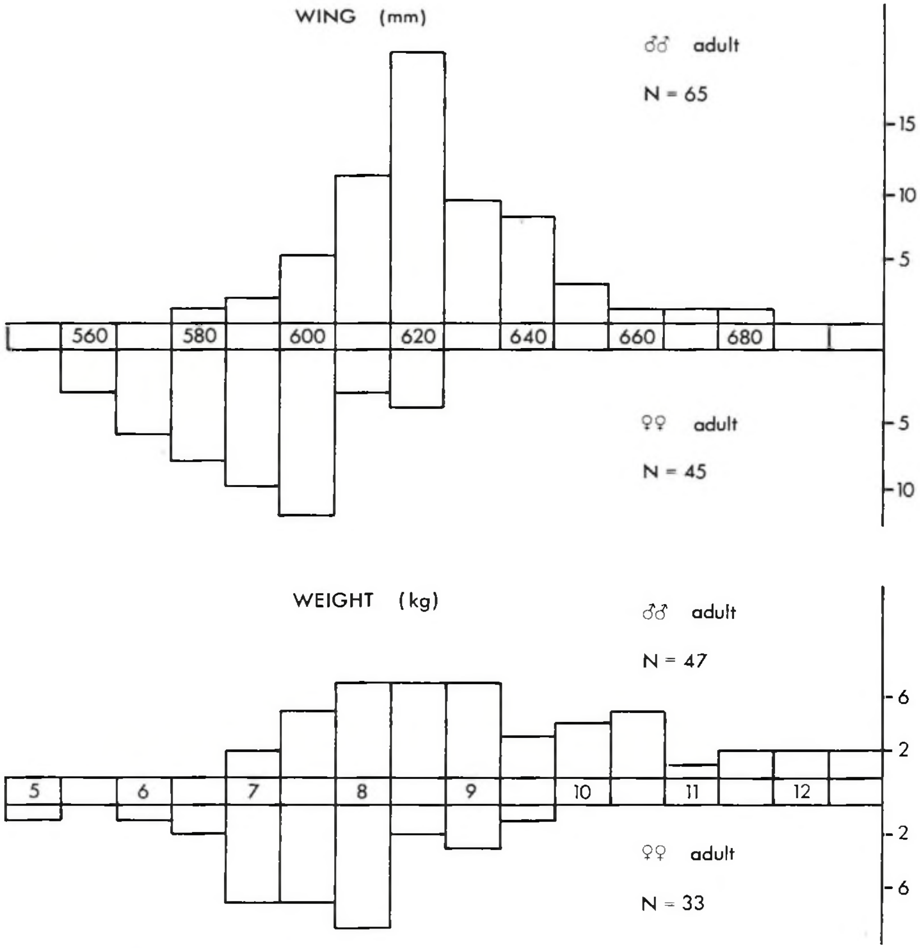

Fig 2. Weights and measurements of *Cygnus cygnus cygnus.*

C. c. cygnus parameters

In connection with the Danish *C. olor* ringing programme we have caught a small number of *C. c. cygnus.* In the severe winters of 1970 and 1979 a number were measured and weighed, the results being presented here as there is little information in the literature (Table 1).

Table 1. Weights and measurements of *C. c. cygnus* (in kg and mm)

	Males			Females		
	N	x ± sd	min–max	N	x ± sd	min–max
1st winter						
Wing	2		580–622	8	575 ± 24	541–605
Longest primary	2		317–325	7	304 ± 18	285–340
Foot span	2		160–179	8	166 ± 8	148–175
Weight	2		7.3–9.0	6	7.4 ± 1.2	5.9–9.3
2nd winter						
Wing	2		600–645	4	608 ± 26	575–635
Longest primary	2		320–347	3	312 ± 8	305–320
Foot span	2		165–169	4	181 ± 12	165–190
Weight	2		9.4–9.9	4	8.2 ± 1.1	6.9–9.6
Adults						
Wing	65	625 ± 18	580–686	46	593 ± 16	560–625
Longest primary	42	332 ± 13	305–360	33	319 ± 13	295–350
Foot span	44	181 ± 9	160–205	37	171 ± 9	155–186
Weight	55	9.2 ± 1.5	6.4–12.9	36	7.8 ± 0.9	5.2–9.8

In *C. olor* we know that the weight may decrease during long spells of low temperatures. It is our impression that *C. cygnus* stands low temperatures and strong wind much better than *C. olor.* Over icing, which is often seen in *C. olor* under cold and windy conditions, has never been noticed in *C. c. cygnus.*

Summary

116 *Cygnus cygnus cygnus* were marked with neck-collars in severe weather in unusually cold weather in early 1979. Resightings in the first year produced much more information (22.4%) than the 266 swans ringed without neck-collars in the previous 25 years (9.0%). Measurements and weights of trapped *C. c. cygnus* are also given.

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Breeding Biology
and
Population Dynamics

THE LIFE SPAN OF SWANS

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No difference has been discovered in the age of the adults of *Cygnus cygnus cygnus* and *Cygnus columbianus bewickii.* Their life spans can be estimated by matching recruitment to, and losses from, the population. In *C. c. bewickii* observed in the field, juveniles amount to between 25% and 43% (30.5% on average). Colour marking clearly shows that four juveniles (of 10 in two broods) survived till the migration season, ie the rate of elimination is 60%. Thus, in 43 swans, the number of adults will be 30 (69.9%) and that of juveniles 13 (30.2%) of all the swans in the first year. This result is roughly consistent with the average in the field.

Furthermore, we suppose that they come into breeding condition from the third year and that in this case the 13 juveniles are composed of two broods of five and a brood of three. On this assumption we add another, that the rate of elimination up to the second year is also 60%. Therefore, five juveniles survive as sub-adults.

If we compose an age pyramid style figure on the basis of these five sub-adults, we can get the result that in the second year the number of adults (including sub-adults) is 30, so the balance is kept. Therefore, in relation to the procreation coefficient of juveniles, if this cycle is maintained, the population of *C. c. bewickii* is kept constant.

In the 'Investigation Report on Hurt, Sick, and Dead Swans' (the Swan Society of Japan: 1977/78), the number of dead swans was 257. The dead adults and juveniles were in the ratio of 27 : 42 (= 39.4% : 60.6%).

While it is difficult to conclude that the actual condition of the whole population is directly reflected in this result, it may be helpful in examining the relation between breeding and selection.

Judging from these results, the average life span is ten years.

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THE DEMOGRAPHY OF NEW ZEALAND'S *CYGNUS ATRATUS* POPULATION

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Introduction

Cygnus atratus is a conspicuous inhabitant of the lakes, lagoons and estuaries of New Zealand. Native to Australia, it was first introduced to New Zealand in 1864 (Thompson 1922) but, coincidental with this, natural immigration seems also to have occurred (Kirk 1895). The species acclimatized very rapidly, exploiting a niche unoccupied since the extinction, several centuries previously, of the closely related *Cygnus sumnerensis,* and by 1900 breeding populations were established on all major freshwater lakes in both North and South Island (Thompson 1926) and on Chatham Island (Richards 1950).

Throughout almost all of its history in New Zealand, *C. atratus* has been exploited as a game-bird and its eggs have been collected. Because of its recreational value and because, in some areas, it is becoming an agricultural pest, current management practices include biannual monitoring of the national population by means of aerial surveys and the annual banding of about 4000 moulting adults and cygnets to determine dispersal, survival and levels of exploitation.

Population dispersion, size and structure

Within New Zealand, swans prefer the large permanent bodies of fresh water, avoiding small impoundments and flowing water. They are quick to exploit the food available in temporarily flooded swamplands and farmland, and they occur throughout the year on most coastal lagoons and large estuaries. All of the principal habitats are sampled during the biannual aerial surveys and estimates of the birds present are made. Surveys in November record the dispersion of the population at the height of the breeding season, while those made in January distinguish between cygnets and birds in adult plumage and so provide an estimate of that season's production.

The dispersion of the population in January 1979 is shown in Fig 1. The population on the New Zealand mainland at that time was estimated to be 60 000, of which approximately 5000 were fledged or near-fledged cygnets. Swans on Chatham Island, 800 km east of New Zealand, are not regularly surveyed. The most recent estimate is approximately 3000 birds (in 1978, E S Bucknell pers comm), although previous estimates there were as high as 10 000 (Lindsay *et al* 1959, Internal Affairs Dept files).

Estimates of the number of breeding pairs at most breeding areas have been made

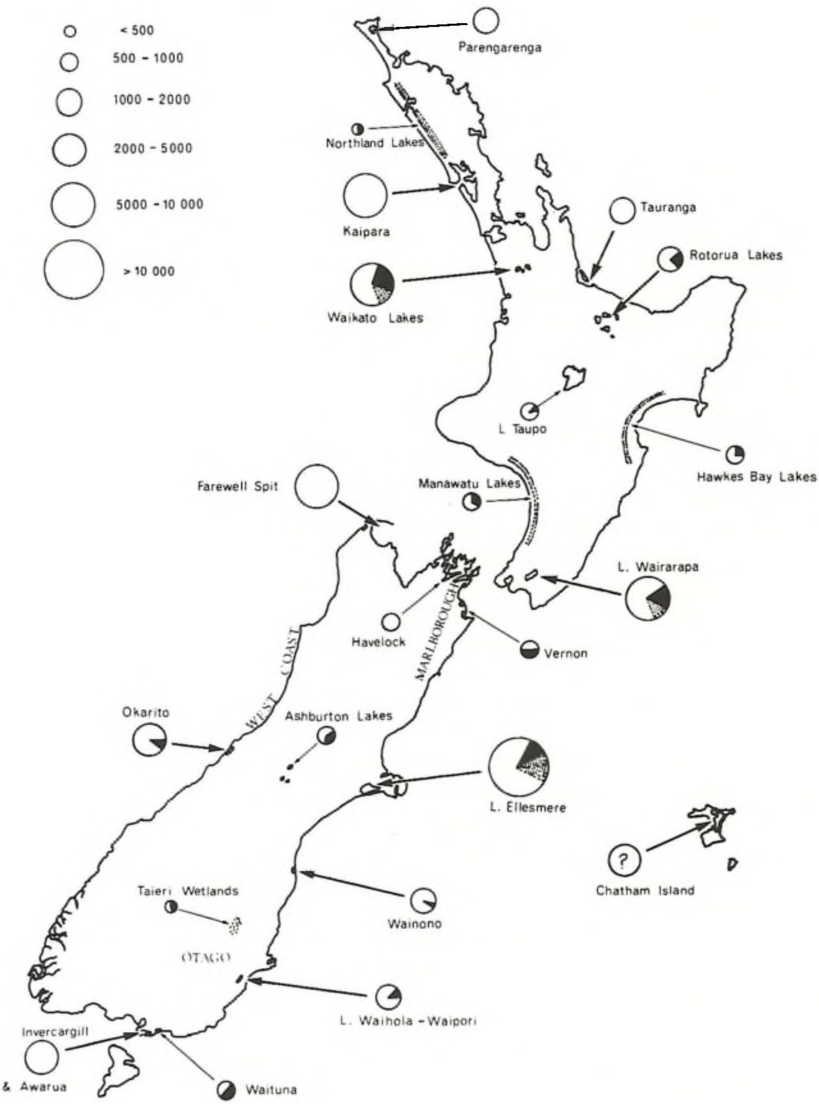

Fig 1. Principal concentrations of *Cygnus atratus* in New Zealand in January 1979, showing the proportion of the population at each locality which bred (black sector), an additional proportion which in the past three years has also bred (stippled sector) and the non-breeding fraction (open).

(Table 2) and the 1978/79 national breeding population was about 4600 pairs, approximately 17% of the national adult population. However, the number of pairs nesting annually varies and this is incorporated diagrammatically into Fig 1 and discussed further in the section on 'Population characteristics'.

Breeding does not occur on any of the marine habitats but swans are present there at all times of the year. This suggests that there may be two separate elements within the population which contribute to the distribution observed during each breeding season — adults which attempt breeding and non-breeders, the latter perhaps a combination of birds too young to breed plus adults of breeding age which make no nesting attempt. The ages of birds present at one marine habitat (Farewell Spit) towards the end of the breeding season have been investigated; during the period 1976 to 1980, 153 swans originally banded as cygnets were caught during their wing moult; 70 (46%) were one year old, 47 (30%) between one and three years of age (it is thought that most swans first commence breeding when four years old), 32 (21%) between four and eight years old and 4 (3%) older than eight years. Perhaps the marine and estuarine inhabitants are mainly pre-breeders.

Non-breeders seem also to comprise the major proportion of the swans present on the principal breeding areas. At all nesting localities where the numbers of nests in colonies were counted (Table 1), a maximum of one-third of the swans present

Table 1. The number of nests counted and the number of swans present in breeding areas

Breeding area and date		Number of nests	Number of swans present	% total swans breeding
Lake Ellesmere	1974	900	13 000	16
Lake Ellesmere	1977	1 600	9 300	34
Lake Emma	1973	71	454	31
Lake Heron	1973	23	164	28
Okarito Lagoon	1973	70	1 500	9
Vernon Lagoon	1974	101	574	35
Lake Waihola	1971	23	246	19

seem to have participated in nesting. Censuses of broods at three areas (Lake Emma 1973, Lake Waihola 1971 and Lake Whangape 1975) recorded that 15% to 27% of the swans present were attending broods. The ages of swans present at these principal breeding sites during a breeding season have been estimated only for Lake Ellesmere. There, at the end of 1977, 70% of the 9300 adults present were estimated to be older than four years (Williams 1979). Are the birds present at these principal breeding areas mostly the older birds? If so, why do so few attempt to breed?

Population dispersal

Should New Zealand's population of *C. atratus* be managed on a national basis or is there evidence that the population is sub-divided regionally? Attempts to answer this question have initially involved determining the limits of dispersal of swans reared at major breeding localities and examining the extent to which these areas of dispersal overlap.

Information about movements of swans from Lake Ellesmere and Waikato lakes has been derived from the analysis of bands returned by hunters (Williams 1977). Most swans banded as cygnets on Lake Ellesmere (Fig 1) were recovered either at the lake itself or from coastal wetlands to the south. Although some birds were shot in North Island there was no evidence of major movements in that direction. Hunting ceased in South Island in 1974 but aerial surveys confirm that movement between Lake Ellesmere and all points south to Invercargill Estuary continues. Waikato swans (Fig 1) were also recovered in a clearly defined region. Almost 90% of the band recoveries were made within 80 km radius of the banding site and most of the more distant recoveries were from Northland. Aerial surveys confirm very large movements of swans from the Waikato lakes to the enclosed harbours in Northland.

These findings tell as much about the dispersion of hunters as about that of swans, but to the wildlife manager this is extremely useful. However, hunting of swans is no longer permitted widely throughout the country. To describe more completely the dispersion of swans both during the hunting season and at other times of the year, banding and collaring programmes commenced in 1974 at four localities. The results of these studies (Williams in prep) may be briefly summarized:

Lake Wairarapa: 500 cygnets banded and collared annually for five years.

(i) Collar sightings: approximately 1200. Those reported away from the lake were mainly at Farewell Spit, in Marlborough or on lakes in Manawatu. Small numbers were regularly seen at Lake Ellesmere but sightings elsewhere were rare.

(ii) Band returns: almost 90% of 355 were made at Lake Wairarapa, the remainder in Marlborough and Hawkes Bay (an area where few collar sightings were made).

Thus, Lake Wairarapa swans remain mostly in the area of Farewell Spit, Marlborough and the lake itself with some birds regularly reaching Hawkes Bay and Manawatu.

Hawkes Bay: 100 to 150 cygnets banded and collared annually for five years.

(i) Collar sightings: 120, 50% within the Hawkes Bay district and a further 20% at Lake Wairarapa. Other sightings were scattered throughout Manawatu, Marlborough and at Farewell Spit. No sightings were made in the northern half of North Island and only four south of the Marlborough district.

(ii) Band returns: 56, 15 of which come from beyond Hawkes Bay. Two swans were shot at Rotorua where no collared birds have been reported, and 10 from Lake Wairarapa and Marlborough.

This small population shows only limited dispersal beyond its natal area, most of this south of Lake Wairarapa.

Rotorua lakes: 686 cygnets banded and collared over four years.

(i) Collar sightings: 300, 70% of which were in the immediate area of the Rotorua lakes and Lake Taupo. Most other sightings were from the Waikato area but Rotorua swans have been seen in Manawatu, at Farewell Spit, on Lake Wairarapa and Lake Ellesmere and in Otago.

(ii) Band returns: 48, 10 of which came from areas other than the Rotorua lakes and Lake Taupo. Four birds were shot on the Waikato lakes, three in the Hawkes Bay district and three on coastal lagoons of the Bay of Plenty. No banded birds have been shot on Tauranga Harbour.

Dispersal characteristics of this population are not yet clear. Considerable movement to the Waikato wetlands seems to occur, especially in winter when water levels in the Rotorua lakes are high. However, numerous swans, sometimes in excess of 1500, are present throughout most of the year on nearby Tauranga Harbour. Their origin is unknown but it is assumed that they may comprise birds from both the Waikato and Rotorua populations.

Farewell Spit: This area, a designated wetland of international importance, is the major moulting site for swans in New Zealand and, at the peak of the moult, approximately 15% of New Zealand's *C. atratus* are present. Almost 4500 moulting swans have been banded and collared over five years.

(i) Collar sightings: almost 1200, scattered from Northland to Otago. Most sightings have been from Marlborough, Manawatu and Lake Wairarapa. Collared swans have been observed breeding in these localities and also in Hawkes Bay, Rotorua and at Lake Ellesmere.

(ii) Band returns: 204, the majority from Lake Wairarapa and Marlborough but also from Hawkes Bay and Waikato.

(iii) Recapture of banded birds: 153 swans, banded as cygnets at various localities, have been recaptured at Farewell Spit, 90 (59%) from Lake Wairarapa, 28 (18%) from Okarito Lagoon, 14 (9%) from Waikato lakes, 10 (7%) from Lake Ellesmere

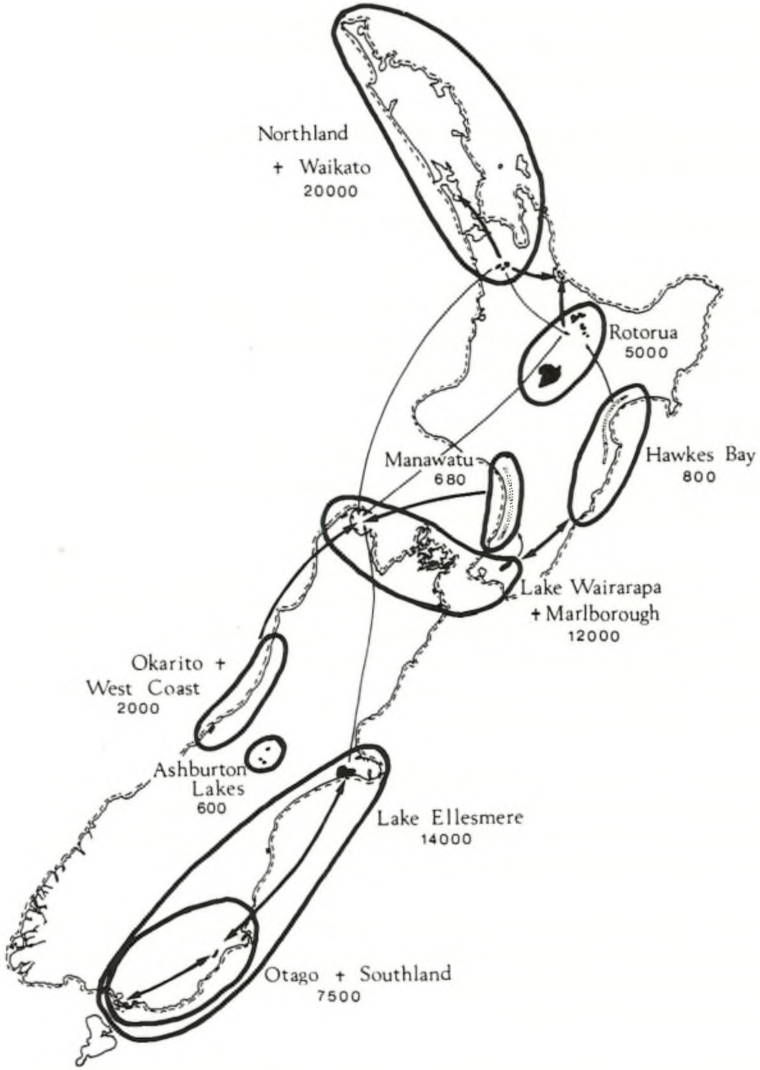

Fig 2. The geographic sub-division and size of New Zealand's mainland *Cygnus atratus* population and the pattern of major (thick arrow) and minor (thin arrow) movements between sub-populations.

and 11 (7%) from Hawkes Bay. No birds banded on the Rotorua lakes (the only other banding site) have been caught although sightings of Rotorua collared swans have been made.

Thus, swans present at Farewell Spit during the peak of moulting are drawn from a wide area but predominantly from nearby breeding areas in Marlborough and Lake Wairarapa, from Okarito Lagoon and probably Manawatu.

Okarito Lagoon: Approximately 100 cygnets have been banded annually since 1973 but not marked with collars. All but four of 51 band returns have come from the West Coast area and, apart from the presence of birds moulting at Farewell Spit, it seems the Okarito population is a sedentary one.

These data on movements and the changes in numbers and distribution revealed during the twice-yearly aerial surveys indicate that there are several discrete or partially discrete populations of *C. atratus* in New Zealand, as illustrated in Fig 2. Without doubt, some of these populations overlap, sharing a common winter feeding area (eg Ellesmere and Otago/Southland, Waikato and Rotorua) but there is no evidence of widespread intermingling throughout the year nor of interbreeding consistent with the hypothesis of a mobile national population.

Population characteristics

In Table 2 principal characteristics of the various regional swan populations are summarized.

Nesting method

C. atratus is popularly considered to be a colonial nesting species (Kear 1972). However, in many situations in New Zealand it is classically territorial, each breeding pair defending several hectares of open water (to which they confine all of their feeding activities) and swamp edge (where the nest is constructed). This territory may be established several months prior to laying, is usually vigorously maintained throughout the full period of the cygnets' development, and is vacated only briefly during the period of the wing moult. Solitary nesting and the establishment of a territory occurs on:

(a) small water bodies (5 to 20 ha);

(b) large water bodies ($>$ 20 ha) where non-breeding birds do not permanently reside throughout the breeding season;

(c) large water bodies where aquatic macrophytes are distributed in a thin band around the margins and not distributed throughout;

(d) areas where the water level is constant or almost so throughout the winter and spring period.

By contrast, colonial nesting, characterized by some nests being spaced a mere pecking distance apart and defence being restricted to the immediate area of the nest, is usually the nesting method adopted at:

(a) large water areas;

(b) areas where large numbers of non-breeders are present throughout the breeding season;

(c) areas where water levels fluctuate throughout the winter and spring period and experience considerable summer drawdown;

(d) areas where food is patchily distributed or is distributed all over the wetland — in both circumstances being extremely abundant;

(e) estuarine areas.

Colonial nesting appears to be, as Kear (1972) has suggested, an adaptation which allows abundant food in areas of unstable water levels to be exploited.

Timing and length of breeding season

On those wetlands with stable winter and spring water levels, where most solitary nesting occurs, the timing of nesting is regular, commencing in July and extended to early October. The timing of breeding of colonial nesters is irregular and is determined by water levels. Colonial nesting occurs as levels decline from the winter peak and seldom commences before September. However, high water levels during spring may delay any nesting attempt until November and, in some cases, into the new year. Once commenced, however, nesting in colonies is highly synchronous and more than three weeks seldom elapse between the first and last egg in a colony.

There are numerous examples of fluctuating water levels inhibiting breeding. At Lake Whangape in 1978 water levels gradually declined from the winter peak in July and early nesting commenced in late September as traditional nesting areas became exposed. However, in late October levels increased again and remained high throughout November. Most of the adult male swans sampled in October, November and December of this year showed testicular regression and when water levels declined throughout December and January to expose the usual colonial nesting sites, few pairs were able to respond and nest. At Waituna Lagoon in 1973, the outlet to the sea became blocked in September and high water levels remained throughout the summer. In February 1974, however, the blockage was breached and, once the water level declined, nesting commenced, approximately five months later than usual.

These two examples indicate that in New Zealand *C. atratus* is a strictly seasonal breeder but is able to delay the onset of nesting until water levels allow access to suitable nesting sites and food becomes readily available. Variations in water levels during the breeding season can stop all nesting activity and prevent further breeding attempts that season.

Clutch size

An extensive study at Lake Ellesmere almost 20 years ago (Miers and Williams 1969) recorded the mean clutch as 5.4, the most common clutch being 5 eggs. The clutch sizes at Ellesmere have been recorded every year since 1975, each year's sample comprising at least 500 nests. There has been a progressive decline, the mean clutch being 5.0, 4.9, 4.0, 4.3, 4.0 in 1975 to 1979 respectively, reflecting the deteriorating state of Lake Ellesmere as swan habitat (Williams 1979).

Clutch size data are available from four other areas, all colonial nesting situations: the mean sizes of clutches were 4.9 at Okarito Lagoon (23 nests in 1973), 5.2 at Lake Wairarapa (70 nests in 1979), 5.1 at Lake Whangape (538 nests in 1974) and 5.7 at Vernon Lagoon (225 nests in 1975). In all cases, the most common clutch was of five eggs.

There are too few data to determine what differences may occur (a) between nesting areas, (b) at the same nesting area between years and (c) between solitary and colonial nesters.

Brood rearing

Cygnets are reared either in family broods, guarded and attended by their parents, or they may be reared in creches which appear to be attended by only one pair of adults. Family broods occur in all situations where pairs nest solitarily, and, where colonial nesting occurs, at least some of the broods are raised by their parents. Work at Lake Ellesmere in 1976 which involved tagging entire broods of cygnets at hatching showed that 32% of the cygnets were reared in family units; the remainder were distributed in creches of various sizes. One extreme example was a creche of 40 which contained 19 tagged cygnets, derived from 15 different broods. If the untagged cygnets were similarly derived, this creche may have contained cygnets from up to 30 different broods. However, approximately 70% of the creches handled contained cygnets derived from two, three or four broods (Williams unpubl data).

At Lake Ellesmere, broods reared as family units were mostly those hatched early and taken by their parents to the more remote parts of the lake. Creching occurred when large numbers of broods attempted to feed simultaneously in the same confined area. The patchy distribution of food there forced broods into close contact and the apparent lack of aggression between guardian adults allowed frequent interchange of cygnets between broods.

Table 2. The demographic characteristics of the various sub-populations of *C. atratus* on the North and South Islands of New Zealand. Little is known of the Chatham Island population. It numbers 3000 swans and is believed not to move beyond the Chatham group of islands.

	NORTHLAND/ WAIKATO	ROTORUA	HAWKES BAY	MANAWATU	WAIRARAPA/ MARLBOROUGH
Principal breeding area	Lake Whangape, Wahi and other scattered lakes in Waikato basin — all freshwater. Few on Northland fresh-water wetlands.	Widely scattered on all lakes but mainly Lakes Rotorua and Rotoehu — all freshwater	Small numbers on all freshwater wetlands	Small numbers on all freshwater wetlands	Lake Wairarapa (freshwater) Vernon Lagoon (freshwater)
Main location of non-breeders in breeding season	Lake Whangape (freshwater), Kaipara and Parengarenga Harbours (estuarine/marine)	Tauranga Harbour (marine), Lake Taupo (freshwater)	Small numbers widely scattered. All fresh-water. Possibly some movement south to Lake Wairarapa	Widely scattered on all freshwater wet-lands. Concentrations on Lakes Horowhenua and Papaitonga to-ward end of season	At main breeding areas plus marine areas at Havelock and Farewell Spit
Breeding season	Variable on Lake Whangape but seems to have two peaks, one in August/September following initial water level decline from winter peak and another in November to January following further dec-line which exposes islands in lake. Else-where regular September to November	August to October — regular	August to October — regular	July to October — regular	Lake Wairarapa — onset is irregular but mostly August to October. Vernon Lagoon — irregular, mainly July to September
Nesting method	Early nesting at Lake Whangape and else-where solitary. Late nesting at Lake Whangape is colonial	Solitary	Solitary	Solitary	Lake Wairarapa — both solitary and colonial. Vernon Lagoon — colonial
Clutch sizes	Lake Whangape 1974, 5.1 in 538 colonial nests. No records for solitary nesters	No records	No records	No records	Lake Wairarapa 1979, 5.2 in 70 colonial nests. Vernon Lagoon 1975, 5.7 in 225 colonial nests
Brood rearing	Family broods. No observations of creches	Family broods	Family broods	Family broods	Lake Wairarapa — broods reared on main water bodies remain in families. Those reared in pasture or on ephe-meral waters creche. Vernon Lagoon — both family broods and creches
Cygnet production	1978: 500—800. 1200—2600 range in past five years	1978: 280. 180—320 range in past four years	1978: 220. Recent counts all about 200	1978: 200. Annual increase of 20—30 over past three years	Lake Wairarapa 1978: approximately 2400 but ex-tended breeding made estimate very difficult. Average annual production probably within range 1500—2500. Vernon Lagoon 1978: 120. Highly variable nil—800 in past five years

Estimated breeding pairs	No satisfactory estimate. Guesses range 600–2000	150–250	80–100	70–100	Lake Wairarapa: no satisfactory estimate. Guesses range 600–1000. Vernon Lagoon: highly variable, 250 in 1979
Total population January 1979	20 000	5000	800	680	12 000

	OKARITO/ WEST COAST	LAKE ELLESMERE	OTAGO/ SOUTHLAND	ASHBURTON LAKES
Principal breeding area	Okarito Lagoon (estuarine)	Lake Ellesmere – fresh/brackish	Waituna Lagoon (estuarine); Lake Waihola/Waipori (freshwater); Taieri River wetland (freshwater)	Lake Emma; Lake Heron; both freshwater
Main location of non-breeders in breeding season	Okarito Lagoon but straying to Farewell Spit near end of season	Lake Ellesmere; Lake Wainono (estuarine); Washdyke Lagoon (estuarine)	Awarua Bay (marine); Invercargill Estuary and Otago Heads (marine). Scattered over various freshwater lakes in Otago	Lake Emma; Lake Heron
Breeding season	Starting date variable and season prolonged due to flooding and frequent closing of lagoon from sea July to February	September to November. Onset closely follows water level decline from winter peak. This is artificially controlled	Waituna: highly variable due to frequent blocking of lagoon outlet to sea. September to March. Elsewhere regularly September to November	September to November regular
Nesting method	Colonial	Colonial	Solitary but sometimes colonial at Waituna	Solitary and colonial
Clutch sizes	4.9 in 23 colonial nests in 1973	1975: 5.0, 1034 nests 1976: 4.9, 1400 nests 1977: 4.0, 1229 nests 1978: 4.3, 586 nests 1979: 4.0, 500 nests	No records but average size of 42 newly-hatched broods in 1971 was 4.3	No records
Brood rearing	Family broods but creches reported	32% cygnets reared in family broods, rest in creches at Lake Ellesmere 1976	Family broods but creches occasionally reported at Waituna	Family broods
Cygnet production	1978: 180. 50–350 range over past five years	1978: 450–600. 200–1500 range over past six years	1978: 260–300. Waituna variable, 50–350 over past five years. Taieri wetlands variable 100–350. Otago lakes constant 100–120	1978:50. 90–250 over past five years
Estimated breeding pairs	50–100	Variable but apparently declining. 1977: 1600 1978: 700–800 1979: 600–700	Waituna: variable, 50–100. Otago lakes: 100. Taieri wetlands: 100 and increasing	80–100
Total population January 1979	2000	14 000	7500	600

Creching has been reported or observed at Lake Wairarapa, Vernon Lagoon and Okarito, all areas where nesting occurs in colonies and where food is patchily distributed. At Lake Whangape, food is available all over the lake and the progeny of colonial nesting there are all apparently reared in family broods.

Creching, like the colonial nesting habit, appears to be an adaptation to ensure the exploitation of abundant but patchily distributed food in areas of unstable water levels.

Cygnet production

At Lake Ellesmere in 1976, 65% of the cygnets which remained in family broods fledged and, overall, 52.2% of the nesting colony survived to independence. At Okarito Lagoon in 1975, 42% of the cygnets hatched were still alive when half-grown. At Lake Wairarapa in 1971, the average size of broods when cygnets were almost fledged was 71% of that recorded when cygnets were newly hatched and at Lake Whangape in 1974, 72% — but these are over-estimates of survival because they exclude the possibility that some broods may have become extinct. These data are all from areas where colonial nesting occurs. At Pukepuke Lagoon in the Manawatu district, 29 broods reared by solitary nesting swans over the years 1974 to 1978 have been followed. All cygnets hatched were reared to fledging in 20 of these broods and, overall, 87.5% of the cygnets fledged (T A Caithness pers comm).

Aerial counts of cygnets on all major breeding areas are made annually to provide an 'order of magnitude' of cygnet production. These counts are made in January when most cygnets have fledged. Estimates of annual productions are listed in Table 2; in 1978, the national production was approximately 5000, almost half of which was raised at Lake Wairarapa, and represents a production slightly in excess of one cygnet per breeding pair.

Estimates of survival

Survival rates have been calculated only for the Lake Ellesmere and Lake Whangape populations (Williams 1973, 1979 and unpubl). At Lake Ellesmere over the period 1956 to 1974, the average annual survival of adults (five to ten year olds) was approximately 84%; for swans in their first two years of life 67%; and, during years two to four, 78%. Bands have been returned from birds exceeding 20 years of age. Data from Lake Whangape contrast with those above. No recovery of a swan older than nine years has been made since banding commenced there in 1962. Survival during the first year was approximately 30%, with an average of 40% over years two to five.

These data are derived from the banding of cygnets and have been analysed by the method of Seber (1971). However, assumptions implicit in the Seber model cannot be satisfied by the data and the observed band recoveries depart significantly from model predictions. Recently derived life-table methodology (Brownie *et al* 1978) allows many of the problems associated with exploited species (eg annual variation in band reporting) to be overcome but it demands that data derived from the banding of cygnets be analysed in association with similar data obtained from the banding of adults. All but one of the swan banding programmes in New Zealand have concentrated on cygnets.

Although the above estimates of survival must be treated with suspicion, it is clear that real differences in survival exist between the Lake Ellesmere and Lake Whangape populations and perhaps it is not an unreasonable working hypothesis that survival rates differ considerably between the various regional populations.

Some questions

Knowledge of the biology of *C. atratus* in New Zealand has many fundamental gaps. The distribution, movements and abundance of the species throughout the country is now adequately understood but breeding biology is very poorly known. The age of first breeding has not yet been established in the field and until this is done we cannot correctly interpret the composition of the large non-breeding population. That only about 20% breed in any year implies either that the onset of breeding is long delayed (yet in Australia some males have been sexually active in their second and third years – Braithwaite and Frith 1969) or that not all mature adults breed every year, or both. There is also the possibility that the age of sexual maturity varies between populations.

At some breeding areas, eg Lake Ellesmere, there are large annual variations in the number of nests constructed (900, 1300, 2200, 1600, 750, 600 in 1974 to 1979 inclusive) yet at other areas, eg Okarito Lagoon, the numbers of nests located have varied by less than 15% over the past four years. What are the factors which determine whether a pair will attempt breeding? There are almost no data on clutch sizes and whether they vary between years and nesting areas and if so, why?

There are intriguing behavioural questions raised by a species which shows two distinct types of social structure on nesting grounds. Why do some pairs nest solitarily and what is missing from the behavioural repertoire of birds nesting in colonies? Can individuals adopt either nesting method at will or, once they first attempt nesting, are they restricted throughout their life to that particular breeding strategy?

C. atratus has a long history of exploitation as a game-bird in New Zealand. Despite this, the dynamics of the hunting populations have never been satisfactorily studied – indeed, there has been no long-term population study of *C. atratus* at all – and there is a strong need for a better understanding of the ways by which hunting affects the age structure, breeding output and survival of swans.

Extensive wetland drainage and modification is taking place. The levels of many lakes are being lowered or controlled and the ephemeral wetlands typically associated with lakes and rivers have almost all disappeared. The effect of these changes on a species more dependent on the wetland than most of New Zealand's waterfowl is poorly understood because basic information on such topics as habitat, food, nesting and cygnet-rearing requirements is lacking. The recent decline of the Lake Ellesmere population (Williams 1979) and the increased trophic state of some Waikato and other lakes suggest that these topics need attention just as urgently as the dynamics of *C. atratus* populations.

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Summary

New Zealand's 60 000 *Cygnus atratus* inhabit the large lowland lakes, coastal lagoons, estuaries and some marine areas of both North and South Island and Chatham Island. Swans present at marine areas, where no breeding occurs, are mostly pre-breeders; 76% at Farewell Spit were three years old or less. Of those swans present at the principal freshwater nesting areas during the breeding season, less than one-third has been recorded nesting. However, until the age of first breeding is established it is not possible to determine whether some swans of breeding age fail to nest each year.

Studies of dispersal using collar resightings and band recoveries suggest that swans in New Zealand may be divided into a series of regional populations between which only limited intermingling occurs and, as yet, no recorded interbreeding. The timing and method of nesting (solitary or colonial) and length of breeding season vary between these populations, depending mainly on water level stability, and the methods of brood rearing are dependent on the distribution and abundance of food in the lakes. Breeding rate and adult survival probably differ considerably between populations although substantive data are lacking at present.

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POPULATION STRUCTURE AND PRODUCTIVITY OF *CYGNUS COLUMBIANUS COLUMBIANUS* ON THE YUKON DELTA, ALASKA

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Introduction

The broad, flat delta between the Yukon and Kuskokwim Rivers covers an area of approximately 67 340 km^2 in southwestern Alaska. Here *Cygnus columbianus columbianus* is an abundant nesting species occurring in higher densities than elsewhere in its breeding range (King 1973). The swans nest throughout the Yukon-Kuskokwim Delta, which extends approximately 376 km north to south at the coast and 320 km east to west. The mid-portion of the delta lies at about 61°30'N.

Variations in population characteristics, have been demonstrated by standardized survey methods, exploratory searches and on-site nesting studies along the coastal fringe (King 1973; Clarence Rhode National Wildlife Range unpubl data). These evaluations have shown that areas within 32 km of the coastline usually support the greatest nesting densities.

Lensink (1973) analysed the population structure and productivity of *C. c. columbianus* on the delta between 1963 and 1971. Since 1971 several studies have expanded knowledge of nesting waterfowl on the Yukon-Kuskokwim Delta (Boise 1977; Dau 1974; Dau and Mickelson 1979; Eisenhauer and Kirkpatrick 1977; Eisenhauer 1977; Mickelson 1975; Scott 1977). These and continuing field investigations performed by the refuge staff have provided data expanding knowledge of the nesting biology of *C. c. columbianus* in selected habitats along the coastal fringe (Clarence Rhode National Wildlife Range unpubl data).

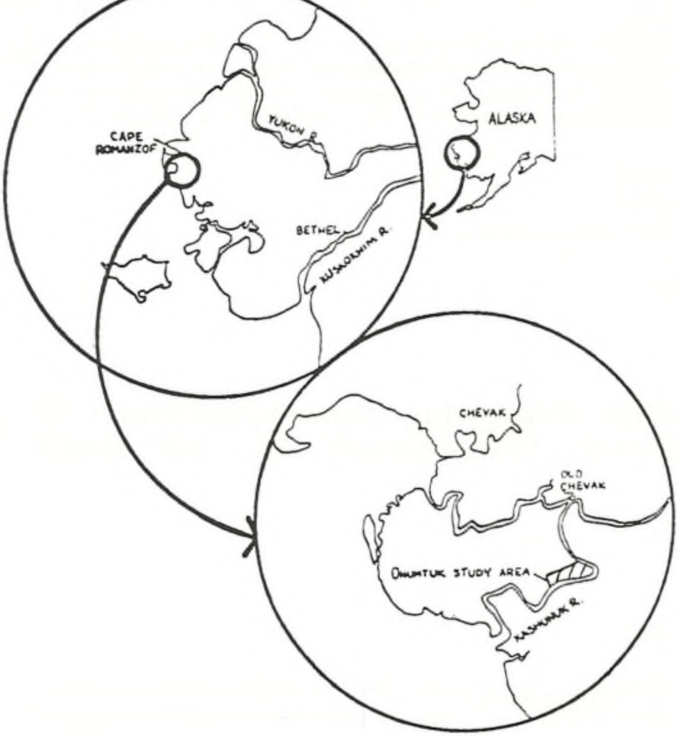

Fig 1. Location of the Onumtuk study area on the Yukon-Kuskokwim Delta, Alaska.

The present paper is an up-date of data on population structure and productivity for 1972 to 1979. An evaluation is provided of the phenology of weather patterns during the spring/early summer period and the resulting effects on the nesting distribution, densities and production of swans on the 10.4 km^2 Onumtuk study area situated 11.2 km from the Bering Sea coast (Fig 1).

Results

Distribution and productivity

The Onumtuk study area is dominated by low, wet sedge/grass meadow with numerous small, irregularly shaped ponds, typical of this habitat type within the coastal fringe of the delta. In some climatically early years *C. c. columbianus* nests in such areas in densities averaging over 0.4 nests per km^2. Areas of upland, ericaceous tundra interspersed with areas of wet meadow along the coastal fringe seem to be preferred areas for nesting and may support densities up to 1.5 nests per km^2, probably averaging nearly 0.8 nests per km^2.

Lensink stated that most *C. c. columbianus* arrive on the Yukon-Kuskokwim Delta by mid-May. On the Onumtuk study area it is one of the first species to arrive. First arrivals and peak influxes seem to relate to fluctuations in the timing of the snow-melt period and the subsequent availability of nest sites (Table 1). The years of 1974, 1978 and 1979 were climatically early and the first arrival and peak influxes of swans were also advanced. In the late years of 1972 and 1977 the timing of spring migration and ice break-up were delayed.

Table 1. Phenology of habitat availability and *Cygnus columbianus columbianus* nesting on the coastal fringe of the Yukon Delta.

A = April, M = May, Jn = June

Year		Snow cover 100% meadow	Snow cover 10% meadow	Nest sites available meadow	First arrival	Peak arrival	Onset laying (n)
1972		10M	28M	6Jn	8M	–	–
1973		16M	23M	29M	6M	13M	1Jn (1)
1974		26A	4M	12M	26A	2M	–
1975		–	–	–	2M	–	15M– 1Jn (8)
1976		16M	23M	24M	2M	9M	28M (1)
1977		19M	1Jn	3Jn	7M	11M	24M (1)
1978		2M	13M	14M	24A	30A	14–17M (2)
1979	pre	28A	10M	11M	28A	2M	13–21M (8)
Av		10M	17M	23M	1M	3M	24M

Weather conditions from late March to mid-May dictate to a large extent the timing and duration of the snow-melt and runoff period in May. This affects the nesting distribution of swans in areas dominated by wet meadow. Dau and Mickelson (1979) have described some relationships of spring weather to the nesting of *Branta canadensis minima* on the Onumtuk study area. Weather data presented by Searby *et al* (1977), shown in Fig 2, closely approximate to that recorded on the Onumtuk study area. Cloud conditions in late March are not as extensive, falling in the 50% cloud cover bracket (Searby *et al* 1977). Comparative figures for early versus late years on the Onumtuk study area suggest that temperatures and cloud cover in April and May are the primary factors determining the phenology of the season (Table 2).

Climatically late years prevent swans from nesting in some wet meadow areas and hence have an obvious effect on nesting distribution and potentially overall nesting density. Productivity may also be affected if predation rates differ among habitat types.

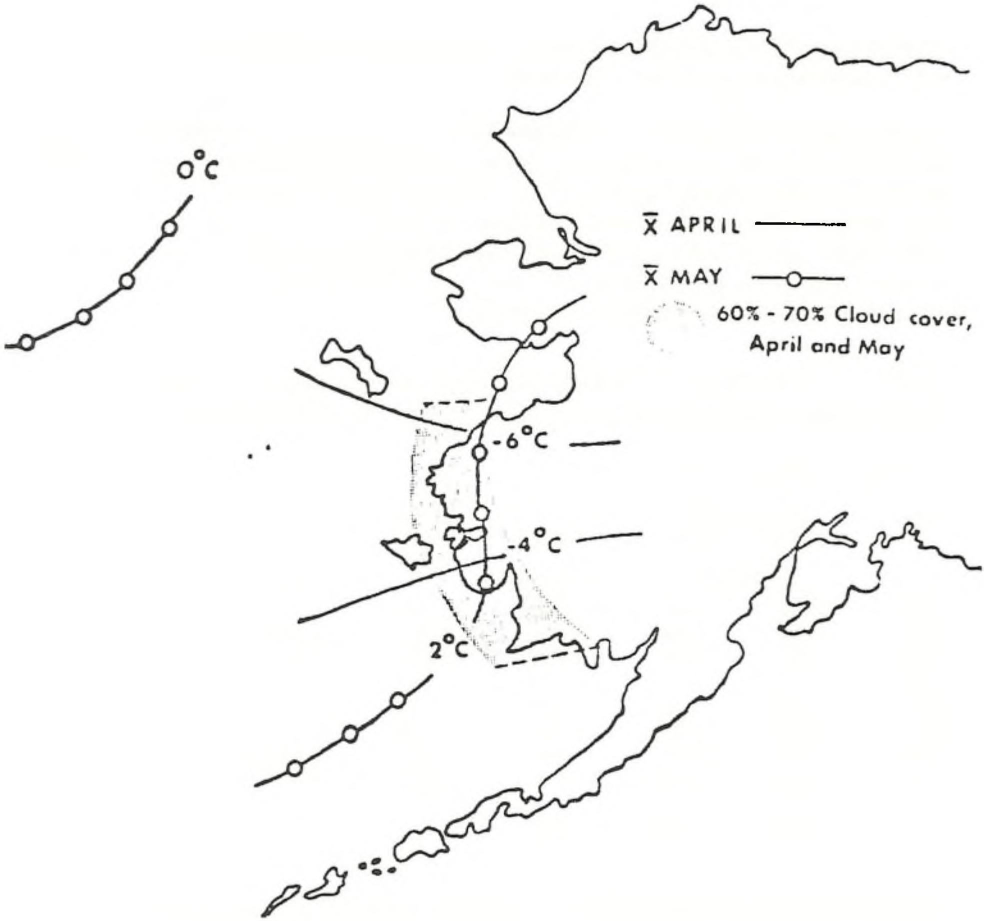

Fig 2. Average air temperatures and percent cloud cover for April and May on the Yukon-Kuskokwim Delta, Alaska (after Searby *et al* 1977).

Table 2. Comparative climatological data for a late year (1977) and early year (1978) recorded at Cape Romanzof and average percent cloud cover for the Onumtuk Study Area

Year	Month	Temperatures (°C) Av min	Av max	Average	Precipitation No. days ≥2.5mm	Total (in mm)	Av % cloud cover
1977	April	−13.3	−6.9	−10.0	4	33.8	—
	May	− 3.3	+0.9	− 1.3	4	22.1	77
1978	April	− 4.6	−0.1	− 2.4	4	32.3	—
	May	+ 0.8	+6.4	+ 3.6	3	29.2	62

Analysis of aerial survey data over two coastal transects dominated by wet, sedge/grass meadows and two other transects over mixed upland/wet meadow habitat for two climatically late years versus three climatically early years showed two-fold increases in nests observed in early years for both strata (Table 3; Fig 3). Observations of pairs, singles or flocks for these years did not show an obvious response in habitat selection in relation to spring climate.

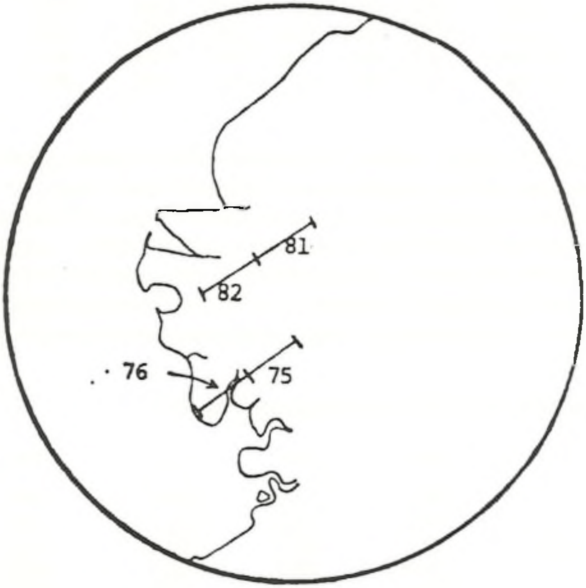

Fig 3. Four 25 km spring aerial transects utilized to assess response of *Cygnus columbianus columbianus* to climatically late versus early years (segments 76 and 82 predominately wet sedge-grass meadow; segments 75 and 81 mixed upland-wet meadow).

Table 3. Analysis of swan numbers on two coastal transects during climatically late versus early years

	Late years [1]				Early years [2]			
Transect	82	81	76	75	82	81	76	75
No. nests	1	0	2	5	4	3	5	12
No. single birds	5	7	13	9	22	12	16	23
No. pairs	6	5	27	5	8	3	11	21
Est. total pairs [3]	9.5	8.5	33.5	9.5	19.0	9.0	19.0	32.5
Birds in flocks	0	0	386	25	10	0	307	23

1) 1972 and 1977. 2) 1974, 1978 and 1979. 3) Pairs plus half the number of singles.

Table 4. Comparison of climatic factors and productivity

Year	Ice breakup		Mean temp (°C Bethel)				Av	Pairs with	Survival	
	Bethel	Chevak	April	May	June	July	Clutch	broods (%)	Sept.	Winter
1972	24 May	6 Jun	–9.8	2.9	9.2	14.3	3.50	21.9	91.1	60.6
1973	13 May	1 Jun	–3.8	4.3	9.9	11.8	4.18	34.2	75.6	62.2
1974	5 May	18 May	–1.8	7.4	10.8	12.6	4.33	46.7	68.6	53.4
1975	17 May	8 Jun	–6.4	4.3	9.7	13.6	3.38	25.2	87.9	73.1
1976	19 May	10 Jun	–8.3	3.1	9.7	12.7	5.00	13.8	66.0	52.2
1977	22 May	6 Jun	–10.1	1.9	11.4	13.4	4.50	12.6	62.2	52.9
1978	11 May	17 May	–0.9	6.6	7.3	12.2	5.20	35.1	51.7	43.5
1979	27 Apr	14 May	–0.3	6.8	8.8	12.0	4.60	48.9	60.7	–

The comparison of climatic factors and productivity of swans presented in Table 4 shows that decreases in the proportion of successful pairs occur in late years. This relationship is further exemplified in a temporal analysis of the proportion of pairs with nests or broods (Table 5). These data provide further support of the supposition by Lensink that there is a stabilization of the number of pairs with nests or broods from June to August. Variables such as human disturbance and predation have adverse effects on the survival of eggs and young but to an unknown degree.

Table 5. Percent of pairs with nest or brood

Year	May	June	July	Aug	Sept	Oct
1972	–	26.4	18.9	20.9	35.7	–
1973	–	27.6	40.8	32.8	29.2	–
1974	34.8	43.1	54.0	50.0	50.3	–
1975	–	30.0	38.3	45.5	45.5	(74.4)
1976	–	50.7	27.5	43.5	(43.5)	70.6
1977	–	20.7	38.0	45.7	(31.9)	(70.0)
1978	(40.9)	38.9	36.5	12.5	40.2	–
1979	39.6	64.4	34.4	(48.5)	52.3	(30.8)

Samples less than 100 pairs bracketed.

Lensink suggests that swan pairs with young remain near their nesting site until fledging. This seems to be the case in upland or mixed upland/wet meadow locations and is supported by the observations of Scott (1977) who maintained surveillance of several pairs and their young. However, pairs nesting in open meadow situations can move considerable distances with broods to large lake networks in meadows or, more preferably, in mixed upland/wet meadow situations.

Table 6 depicts survival throughout the brood rearing period, fall migration and into the winter. Lensink showed that most losses occur within the month after the hatch, with relatively constant rates of survival persisting throughout the remainder of the summer. This pattern is reinforced by the present analysis, as is his supposition that losses throughout the brood rearing period appear independent of the

Table 6. Survival of cygnets as indicated by changes in size of broods expressed as percentage of the average clutch size for year

	Clutches		Percent survival/average brood size					
Year	No.	Average	June	July	Aug	Sept	Oct	Winter
1972	14	3.50	(102.0)/3.57	88.3 /3.09	92.2 /3.25	91.1 /3.19	–/–	60.0/2.4
1973	22	4.18	(79.7)/3.33	(80.9)/3.38	(74.7)/3.12	75.6 /3.16	(60.3)/2.52	62.2/2.6
1974	21	4.33	100.9 /4.37	78.5 /3.40	74.8 /3.24	(68.6)/2.97	–/–	53.4/2.3
1975	8	3.38	(59.2)/2.00	(92.3)/3.12	(87.9)/2.97	(87.9)/2.97	(97.0)/3.28	73.1/2.4
1976	1	5.00	–/–	(70.0)/3.50	(60.0)/3.00	(66.0)/3.30	(63.4)/3.17	52.2/2.6
1977	2	4.50	(88.9)/4.00	67.3 /3.03	79.6 /3.58	(62.2)/2.80	74.4 /3.35	52.9/2.5
1978	13	5.20	(67.3)/3.50	65.0 /3.38	(54.0)/2.81	(51.7)/2.69	–/–	43.5/2.4
1979	12	4.60	–/–	(60.9)/2.80	(48.9)/2.25	60.7 /2.97	81.5 /3.75	–/–

Samples of less than 50 broods are bracketed; samples with more than 200 observations in California and Utah during December or January are summarized in various reports by J J Lynch or J Voelzer.

original clutch or brood size. Attrition of young swans during fall migration from 1963 to 1979 ranged from 8.3% to 31.1% (16.9% average) reductions in brood size from September/October to December.

Lensink suggests that determining the proportion of single and paired swans in May, June and September is hampered by the non-random distribution of flocks of non-breeders. This problem exists to a variable extent throughout the summer and increasingly so in mid- to late August (Table 7). Losses of nests or young may induce failed breeders to join existing flocks of non-breeders.

Table 7. Percent of adult or subadult swans identified as singles or pairs

Year	May	June	July	Aug	Sept	Oct
1972	–	62.1	65.2	83.1	16.8**	–
1973	–	43.2	55.6	(62.9)	(49.8)	–
1974	37.7	51.8*	43.0	35.0*	(17.6)	–
1975	–	(80.0)	60.1	(66.2)	(80.1)	44.3
1976	–	12.5	46.7	(79.2)	10.9	(15.9)
1977	–	12.0	52.4	(77.2)	(34.5)	4.4*
1978	(86.3)	(95.1)	(83.3)	(71.6)	(24.0)	–
1979	66.3	35.7	(72.1)	14.0*	12.1**	(50.9)

Samples of less than 1000 swans are bracketed; * samples larger than 2000; ** samples larger than 3000.

Conclusions

Timing of snow-melt and runoff in spring determines the utilization of low, wet meadow areas in the coastal fringe of the Yukon-Kuskokwim Delta by swans.

Climatic conditions, primarily temperature and cloud cover, dictate the phenology of spring break-up and, as was pointed out by Lensink, these factors can affect productivity via clutch size. Nesting distribution and density is also affected by snow-melt patterns, especially in late years. The relationship between spring climate and length of the nesting season on productivity of *C. c. columbianus* at other coastal locations in Alaska was presented by Lensink and recent data do not suggest a different appraisal (J G King pers comm).

There is no obvious relationship between timing of nesting and clutch size versus family group size and percentage of young in the winter population (Norman 1977, 1978; Voelzer and Wade 1979). This suggests that variability in the annual winter estimates of productivity probably reflects differential mortality during migration or on the winter grounds.

Summary

Observations on the population dynamics of the Yukon-Kuskokwim Delta *Cygnus columbianus*

columbianus population were reported for the nine-year period 1963 to 1971 (Lensink 1973). The present paper presents continuing data on this population for the eight-year period 1972 to 1979.

The high visibility of this species has permitted the collection of data relating to population status by aerial survey techniques. Clutch and brood sizes as well as flock size and composition are collected in this manner and relate productivity to the phenology of the spring snow-melt. Data relating to spring climate were collected on study areas within 30 km of the Bering Sea coast where nesting densities are approximately 0.4 nests per km^2.

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BREEDING ECOLOGY OF *CYGNUS CYGNUS BUCCINATOR* IN WYOMING

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Cygnus cygnus buccinator breeding in the mountain lake habitat of northwestern Wyoming was studied during the 1977, 1978 and 1979 nesting seasons. From 72 nesting attempts the swans hatched 1.8 and fledged 0.47 cygnets per active nest. Clutch size at 55 nests averaged 4.05. Hatching rate of eggs (n = 270) was 48.5%; nesting success was 71% in 1977, 41% in 1978 and 71% in 1979. Flooding of nests was the major cause of egg loss and nest failure.

Swans that laid above-average clutches incubated with higher constancy, longer sessions, shorter recesses and fewer recesses per day than swans with below-average clutches. Cygnets from large clutches suffered significantly lower mortality than those from clutches of four eggs or fewer.

Pre-fledging cygnet mortality totalled 75% of the surviving cygnets; 23% were conspicuously retarded in growth. Moribund cygnets showed extreme weakness, emaciation, deformities and leech parasitism.

Stability of the *C. c. buccinator* population in Idaho-Montana-Wyoming depends upon cygnet production at Red Rock Lakes National Wildlife Refuge. Cygnet production in off-refuge habitats is inadequate to maintain the current number of off-refuge breeding pairs. Without expansion or qualitative improvement of winter food resources, population growth is unlikely.

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BREEDING OF *CYGNUS CYGNUS CYGNUS* IN A COASTAL AREA OF NORTHERN NORWAY

S MYRBERGET

Introduction

Round about 1950, *Cygnus c. cygnus* bred only in small numbers in Norway and was restricted to the northernmost county, Finnmark. About 1960, a few breeding pairs were recorded on certain coastal islands in the county of Troms, and during the 1970s swans were found breeding in increasing numbers in many coastal areas north of the Arctic Circle to about 70°N in the counties of Nordland and Troms (eg Fjeldsa 1972). In Finnmark, however, the present development of the breeding population is uncertain (NOU 1978).

Study area

The area is situated at 69°30'N in the county of Troms. Senja is Norway's second largest island (1590 km^2) with mountains reaching heights of 1000 m. The island is located within the submaritime zone of forests dominated by *Betula pubescens.* The outer parts of the island are much steeper than the inner districts, where there are large bogs with floating wetland systems and also some *Pinus silvestris* forests.

Material

The study is based mainly on contact with local inhabitats who have submitted written accounts of breeding in different water systems. Most of the data come from Hans Kristian Eriksen, Stonglandseidet, but data were also furnished by Hakon Elveland, Hallvard Hanssen, Hans Helge Jørgensen, Alida Nylund, Sverre Nylund, Olav Olsen Jr and Ørjan Olsvik. In addition, the author has visited most of the lakes in question.

Results

Breeding population

The known breeding localities between 1960 and 1978 are shown on the map (Fig 1). The swans have bred in nine wetland systems, in some cases using a number of lakes within the same system (Table 1).

In area 1, the swans were first found breeding in the central lake (1b) of three small lakes between 1960 and 1962 (Myrberget 1962, 1963). Between 1963 and 1965 the pair used the lower lake (1a). From 1966 to 1969 the pair used lakes 1a or 1b, but since 1970 they have used lake 1a every year except 1971. In the 1970s, breed-

Fig 1. Map of Senja with numbered breeding areas.

ing in lake 1a has been encouraged by artificially building up the small nesting islet so that it becomes free of snow early in the spring. In 1965, another pair laid three eggs in the upper lake (1c), but this pair was apparently driven away by the first pair before incubation, and three fresh eggs were found in June. The distance between lakes 1a and 1c is 1.5 km. In 1971, the thaw came very late. The swans from area 1 then moved to a small holm in the sea just outside the river mouth, where the first egg was laid on 14 May.

In area 2, swans have been observed every year since 1960. The first nest was found in 1967. In area 3, nesting also started about 1967. Nesting then occurred every year until 1971 and also most years in the 1970s (Table 1).

In 1970 three breeding pairs were known on Senja, the minimum figures for the breeding population in subsequent years being three, three, four, five, three, five, six and seven.

The northeastern part of Senja comprises areas 3, 4, 5 and 6. It was believed locally that pair 3 moved to area 4 in 1972, but this is not substantiated by the development of the population. It is possible that pairs 4, 5 and 6 are the same swans. An

Table 1. Review of the swan breeding localities on Senja from 1960 to 1978.

Area number refers to the map (Fig 1).

Area number	Size in km	m above sea level	Distance from sea in km	Breeding years 1970–1978
1a	0.9 x 0.5	14	1	1970, 1972–78*
1b	0.5 x 0.5	15	2	(Last in 1969)
1c	0.5 x 0.1	20	3	(Unsuccessful 1965)
2	0.6 x 0.3	60	1	1970–78
3	0.5 x 0.2	52	0.5	1970–71, 1973–74, 1976–78
4	1.5 x 0.5	88	1.5	1972, 1974–78
5	(6 x 1)	25	2	1973
6	1.8 x 0.6	18	1	1974, 1976
7	2.0 x 1.5	19	4	1977–78
8	0.1 x 0.2	10	2.5	1977–78
9	0.5 x 0.5	305	8.5	Unsuccessful 1978

* In 1971 on a small holm in the sea close by.

adult pair, probably from area 3, was killed when it collided with a power line in early July 1976. Collectively, these four areas have been inhabited by at least three pairs of swans in the later 1970s.

In area 9, breeding attempts were recorded only in 1978. Pairs 1, 2, 7 and 8 are definitely separate pairs. Thus it is estimated that, round about 1978, the total breeding swan population was seven or eight pairs.

Breeding habitats

As shown in Table 1, most lakes are rather small, 0.5 to 2 km long and 0.5 to 1 km wide. Only one locality, area 5, is markedly larger.

All successful breeding attempts occurred below 100 m above sea level. Most localities lay 1 to 2 km from the nearest sea. (In one case a small islet in the sea was used for the nest).

The vegetation is fairly rich in most breeding localities. Common species in most lakes are *Equisetum fluviatile, Menyantes trifoliata* and *Carex spp* such as *C. vesicaria. Equisetum* seems to be an important food plant for the swans in the middle of the summer.

The closest distance between successful breeding pairs was 3 km.

Reproduction

Most of the eggs were laid in the latter half of May. The number of eggs in 12 clutches varied between three and six, the average being 4.8 (Table 2).

Table 2. Clutch and brood size distribution.

In calculating the mean, zero is excluded.

	0	1	2	3	4	5	6	Sample size	Mean
Number of eggs	–	–	–	1	4	4	3	12	4.8
Young in early July	3	1	3	6	7	7	–	27	3.7
Young Aug/Sept	6	6	9	12	6	1	–	40	2.6

It was never shown that a nest was predated, even if predators such as *Aquila chrysaetos* and red fox *Vulpes vulpes* obviously showed interest in the incubating swans. In 1961 a nest in area 1b was probably destroyed due to human disturbance during egg-laying (Myrberget 1962). In the late spring 1971, the nest in area 2 was flooded in early July. We have occasionally found unfertilized eggs or dead newly-hatched young in the nests but, in general, hatching losses seem to be low.

Brood size was, on average, 3.7 in July and 2.6 in August/September (Table 2). In three of 37 hatched broods, all young disappeared soon after hatching.

In three cases the brood contained one young which was unable to fly and was left by the parents. In one case it is possible that the parents returned for the young. In both of the other cases the young died shortly after the parents had departed. One of these chicks was dissected, but there appeared to be nothing wrong with the anatomy of the wing (Eriksen 1971 and pers comm).

In 1977 and 1978 the nest in area 8 was on a very small lake in bog land. The parents soon took the young to a nearby and obviously more favourable lake but in both cases only one young survived. In 1979 the pair nested in a small lake in the immediate vicinity and bred three young.

In the period 1970 to 1978, there were at least 38 breeding attempts within the area. It is probable that 35 pairs hatched young and 32 pairs raised about 80 fledging young. Reproduction was particularly poor in 1971 and 1975. In 1971, with a late thaw, three pairs produced two fledgelings. In 1975 three pairs produced one cygnet, the number of hatched young that survived the first days determining the net production. In these two years, production was also poor for terrestrial birds such as *Lagopus lagopus* (Myrberget 1978) and 1975 was poor also for *Larus spp* (Myrberget *et al* 1976). Unfavourable weather was probably the main reason for bad production in both years. In 1975 the main proximate cause may have been a poor production of insects, which are the main food for the young during the first days (Blomgren 1974; Haapanen *et al* 1977).

The families usually leave the breeding lakes during the period 20 September to 10 October, but have been known to remain until 20 October.

Discussion

The increase in the Senja population of *C. cygnus* during the last 20 years may continue, since there are other potential breeding areas on the island. The reasons for the increase must be the same as those which have led to the general increase in Fennoscandinavian swan populations in the period (Fjeldsa 1972, Haapanen *et al* 1973) and will not be discussed here. Some of the swans on Senja are very tame, just like those in many other newly inhabited Nordic areas.

The net reproduction rate, 2.6 cygnets per successful pair, is approximately the same as that found in other northern areas in Fennoscandia (Fjeldsa 1972; Blomgren 1974; Haapanen *et al* 1977) but less than in the eutrophic lakes in southern Sweden (Elmelid *et al* 1977).

Summary

On Senja island (1590 km^2, 69^{o}30'N) the breeding population of *Cygnus c. cygnus* increased from one pair in 1960 to seven to eight pairs in 1978. Of 38 recorded breeding attempts in 1970 to 1978, 35 hatched young and 32 produced about 80 fledging cygnets. Two bad production years coincided with bad production in other birds.

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POPULATION DYNAMICS OF *CYGNUS OLOR* IN DENMARK

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Introduction

The Zoological Museum started swan investigations in 1966 on a breeding population of solitary *Cygnus olor* pairs nesting in Copenhagen and North Sjaelland. Since 1971 they have been enlarged bv investigations on colonially breeding swans in Roskilde Fjord, a brackish water area 30 km west of Copenhagen.

In addition, about 17 000 swans were ringed in winter and during moult in summer. All data concerning ringed swans are transferred to Electronic Data Processing (EDP), but computer processing has not yet started. It has therefore been possible to make only a few preliminary calculations.

Climatic conditions

The data on which the main part of this paper is based can be divided into two parts: 1964 to 1969 and 1971 to 1978. The first period was quite normal as far as the severity of the winters is concerned, whereas there has been a series of very mild winters in the 1970s. In 1963, 1970 and 1979 the winters were very severe. This must be kept in mind as the mortality, shown below, is especially high during the winter months.

Production of young

Solitary breeding swans: As there is little variation from year to year in the onset of the breeding, 1 October has been taken as the time for fledging, even though poorly developed young actually fledge later.

In the period from 1966 to 1975 the number of young in North Sjaelland varied between 1.9 and 3.8 per pair, with 2.6 as the average. A breeding pair is one which built a nest and laid at least one egg.

Colonially breeding swans: Colonially breeding swans in Roskilde Fjord generally had a lower production than solitary swans. By the end of September (1971 to 1979) it varied between 0.6 and 1.5 young per pair, average 0.9. The production is very low even in areas in Guldborgsund (Clausen and Lind *in litt* and the author's own observations) and Ringkøbing Fjord (Eskildsen 1979), and it is possible that the numbers on more exposed areas are lower still. It has been possible to find only a few broods from the big colony of about 100 pairs at Ragø north of Lolland (Preuss pers comm).

In North Sjaelland the proportion of solitary pairs which do not start the breeding cycle at all varies. Normally it lies between 10% and 20%, but after the very severe winter in 1970, 42% of all surviving potential breeders did not nest. The total production of young in North Sjaelland appears to have varied from about 75 to 200. The lowest number was produced in 1970 but those birds which actually bred had the highest average brood size ever found. A part of the colonially breeding swans also did not start to breed.

Age at first breeding

Estimates made in 1975 on data from cygnets ringed from 1967 to 1969 show that the average age of first breeding for females was 4.7 years (n = 24), and for males 5.0 years (n = 19). However, it was clear that some birds from the years in question had not yet bred, so that the values most probably should be higher. Less than 10% of the birds in their fourth calendar year breed, and swans breeding in their third calendar year have not been found in Denmark at all. Indeed, we have the impression that a few birds never join the breeding population, even at the age of more than ten years.

Below we have used five years as the mean age of the first breeding.

These figures refer to solitary swans in North Sjaelland. Corresponding values for colonially breeding birds are not yet known but may be still higher.

Mortality before fledging

Calculation of mortality up to 1 October is based on direct observation.

The average number of eggs per breeding pair in North Sjaelland is 5.6. For colonially breeding swans the corresponding value is 5.2. As the figures for fledged young are 2.6 and 0.9 respectively, the loss is 54% for solitary breeding and 83% for colonially breeding swans. Solitary breeding swans lose young especially during their first month of life. Colonially breeding swans also lose many young during the first month, but in addition 40% to 50% of the eggs are lost, so that the number of young hatched in colonies is about 2.6 per pair, equal to what is left with a solitary pair four months later.

There is more disturbance in colonies, where nests are situated close together. There is much walking about during the egg-laying period, and the consequent conflicts among the pairs result in many eggs being broken. The higher the density of nests, the more eggs will be lost.

The mortality among young is higher among colonially breeding than in solitary breeding swans because the former are in more open and wind-exposed areas. The young weigh less in years with much wind and the average brood size is also lower in such years, which means that the mortality of young during the first four months is higher (Andersen-Harild 1981a).

Mortality after fledging

Material: The material can be subdivided as follows:

- Recoveries of *C. olor* ringed in Denmark and Sweden before 1957.
- Mortality calculations based on recoveries of birds ringed in the ice-winter 1962/63.
- Mortality calculations based on breeding birds in North Sjaelland in the period 1963 to 1974.
- Mortality calculations based on swans ringed as young at breeding places in North Sjaelland from 1961 to 1974.
- Estimate of the mortality among birds ringed as moulting non-breeding birds in 1970 and 1971.
- Estimate of the mortality of birds ringed as young in Roskilde Fjord and Guldborgsund 1972 to 1977.

Sources of error: This heterogeneous material contains a number of specific sources of error. Among the more general sources of error are loss of rings and differential chances of recovery of birds according to geographical area or age. Baltic swans stay in shallow areas near coasts until they start to breed, when the majority migrate to lakes and peatbogs. We do not know whether there is any difference in chances of recovery in these two habitats. Dead swans are so big that they take a long time to disappear on land, and they drift around on the surface before sinking. Thus the chances of recovery are high and it is assumed that all age groups have the same recovery chance.

Possible differences in recovery prospects between geographical areas are assumed to be without consequence as the population remains throughout the year in rather densely populated areas where ringing is well known and where there is good communication between ringing centres.

Loss of rings may therefore be the most serious source of error. The Zoological Museum in Copenhagen has used four different ring types for swans (see Table 1).

The highest loss occurs when rings of type 3 (with no clip) are used. In investigations in North Sjaelland and Copenhagen, swans were ringed with an aluminium ring of type 3 on one leg and an individually coded plastic ring on the other. It soon became obvious that there was extensive loss of the aluminium rings, estimated at 7% to 8% per annum, which is of almost the same order as the annual mortality (Andersen-Harild 1971). The loss of rings does not appear to be connected with wear or correlated with how long the ring has been on the swan. In several cases the ring, although correctly applied, was lost a few months after it

Table 1. Ring types used by the Zoological Museum in Copenhagen for ringing of swans.

No.	Material	Inner diameter (in mm)	Thickness (in mm)	Closing method	In use
1	Aluminium	32	1.5	Clip	1954–61
2	Aluminium	28	1.0	Clip	1962–68 (70)
3	Aluminium	20 x 30	1.0	No clip; butted	1964–66
4	Aluminium	28	1.5	Clip	1968–

had been put on. The data originating from this type of ring are without value and are not included in the mortality calculations.

As far as the other ring types are concerned, the loss (according to calculations on birds with coloured plastic rings) is much lower. The loss of type 2 and 4 is less than 0.5% annually and, therefore, we do not consider it necessary to correct calculations. The cause of loss is not quite clear but it seems that rings with clips can be so distorted by a blow that another blow can open them completely.

Wear of rings: As far as ring type 1 is concerned, the wear is rather limited, even after ten years. In addition, some of the rings were applied above the heel joint, which further reduced wear.

Ring type 2 wears much more quickly and some were nearly worn down after five years. In most cases the wear was not so extensive as to cause loss of the ring but in some the address was difficult or impossible to read. In many cases worn rings were replaced by new ones. In this way ring type 4 replaced more than half of the older ring types on swans which were still alive in the winter of 1969/70. Wear of rings does not seem to have had essential influence on the recovery frequency.

Mortality during the first winter (1 October to 31 May)

Solitary breeding swans: In the Copenhagen area the swans are ringed with an aluminium ring and mostly with additional colour rings. Since 1971, a 40 mm wide plastic ring with a number consisting of three cyphers was used. It can be read from a distance of up to 100 m. During the preceding years about half of the birds were ringed with an individual combination of colour rings. As the birds are rather tame and congregate in spring, it has been possible to check a rather large portion of them in the study area.

It is difficult to calculate the mortality during the first winter of cygnets of solitary breeding swans. The birds leave the breeding places during the first autumn or winter and most of them leave the study area during their first flight-feather moult. Thereafter they usually spend some years away from the study area but return for shorter or longer periods in spring until they settle down as breeding birds.

As only rather few young were ringed (usually 100 to 175 annually) recoveries of dead birds are insufficient for mortality estimates. It is possible only to calculate a 'disappearance percentage' based on birds which have not been recorded after 31 May in their second calendar year. However, a bird may be found dead and reported to the ringing centre, it may be observed in the study area or it may be controlled alive on a winter feeding place or on a moulting place. Some of the birds surviving the first winter are never recorded, so the disappearance percentage is a maximum figure. This will apply to birds which die after the first winter and before their potential return to the breeding area up to five years later. However, since the mortality in this period is very low (see page 170) the margin of error will, at most, be 10% to 12%.

Table 2 shows the 'disappearance percentage' for 1967 to 1974 (1970 being excluded). The latter was the year after the severe ice-winter, and only a few birds produced young for ringing. The Table shows 56% as the mean, which, as mentioned above, should be reduced to about 45%. The highest losses occurred in 1969 when the young had to face the severe ice-winter. Some 10% to 30% of the cygnets fledged in the study area spent the winter there and, being fed by man, were subject to less starvation than cygnets which emigrated. On the other hand, they were more endangered by collisions with wires. A disappearance percentage of 74% in the study area was thus relatively low and probably 90% of the young died in Denmark during this very severe winter.

Table 2. The percentage of young in solitary breeding swans in North Sjaelland and Copenhagen which have not been observed later than 31 May in their second calendar year.

Year of ringing	'Disappearance percentage'
1967	63
1968	50
1969	74
1971	58
1972	45
1973	48
1974	54
Average	56

Colonially bred swans: Mortality during the first winter of colonially bred swans can be followed better as they have been marked with neck-collars and 'mortality' is close to the true die-off (Table 3).

Table 3. Mortality during the first winter (1 October to 31 May) of cygnets of colonially breeding swans from eastern Denmark.

Year of ringing	Mortality percentage	
	Roskilde Fjord	Guldborgsund
1972	24	
1973	54	6
1974	21	
1975	13	75
1976	71	95
1977	78	81
Average	44	(64)

Mortality in this group varies much more than in those from solitary breeders because of the greater variation in weight from year to year (Andersen-Harild 1981). The mild winters in the 1970s resulted in a very good survival rate, certainly higher than in the 1960s.

Proportion of second calendar year birds in the moulting places

The proportion of second calendar year birds present on the moulting places is highly variable and was lowest in 1970 after the severe ice-winter (Fig 1).

The moulting flocks in Roskilde Fjord consist mainly of local swans (Andersen-Harild 1981b) and the proportion of young birds closely reflects the mortality data of cygnets fledged in this area (Table 3).

Swans from Sjaelland and southern Sweden moult at Saltholm and the proportion of second calendar year *C. olor* recorded accords well with that in midwinter in southern Sweden (Nilsson 1979). Nilsson did not find any correlation between the winter temperatures and the percentage of young (ie second calendar year birds) the following winter, indicating that breeding success in *C. olor* does not depend on weather conditions in the previous winter.

The percentage of second calendar year birds moulting does, however, correlate with the temperature and ice conditions in the preceding winter, but it must be remembered that the age composition of the total population varies from year to year. Therefore differences in the second year percentage do not reflect only differences in production and/or mortality.

The moulting swans at Rødsand come mainly from the German Democratic Republic and the conditions influencing this population differ from those affecting birds moulting at Saltholm.

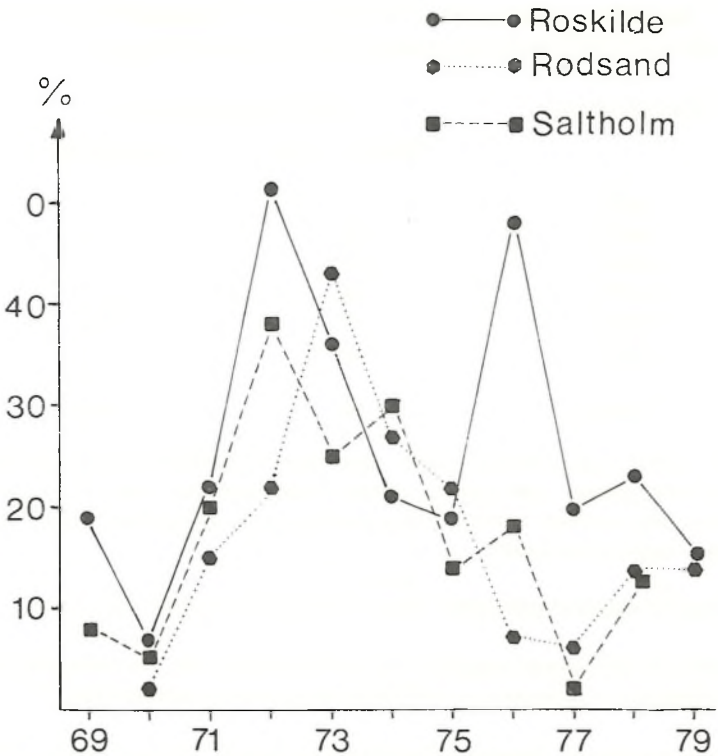

Fig 1. Variation in the percentage of second calendar year birds at three moulting places, 1969 to 1979.

Mortality of older swans

Here different material has been used:

1) *Birds ringed before 1957:* All recoveries are of birds ringed in winter in North Sjaelland (1953, 1954, 1956) or of birds ringed on the Swedish coast of Øresund (1941, 1947). All birds reported dead before 1 January 1977 are included. Table 4 shows the age of the birds when recovered. The average annual mortality is calculated using the formulae in Lack (1951) and Haldane (1955): $m = N/\sum xd_x$, where N represents the total number of recoveries, x the age group and d_x the total number of recoveries in a given age group. This gives m = 36/271 = 0.133. The uncertainty $\delta = m\sqrt{(\frac{1-m}{N})}$ is 0.021. Thus the annual mortality will be 13.3% ± 2.1%. This calculation is based on the assumption that the original ringed population is extinct. We can still expect one or two recoveries of birds ringed between 1954 and 1956, so the mortality rate will decrease to below 13%.

Table 4. Number of recoveries of swans found dead in different age groups.

The age groups follow the calendar year. Recoveries in the same calendar year as ringing have been omitted.

Age group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
No. recovered	5	2	3	2	3	3	3	2	1	3	0	2	1	2	0	1	1	1	0	1

2) *Birds ringed in winter 1962/63:* The winter of 1962/63 was more severe and longer than usual. *C. olor* gathered in big flocks in places where currents maintained open water, and in many there was extensive artificial feeding activity. Some 1800 *C. olor* were ringed, most of them in the beginning of March 1963. It can be assumed that about 1500 of these survived the winter. The number reported dead up to 31 December 1976 is shown in Table 5.

Table 5. Recoveries of *Cygnus olor* ringed in winter quarters in east Denmark during the ice-winter of 1962/63.

The recovery year runs from 1 June to 31 May.

Year of recovery	Number of recoveries Actual	Number of recoveries Calculated (assuming constant mortality)	Mortality (%) calculated (assuming constant reporting rate)
1963/64	22	33	8
1964/65	34	29	15
1965/66	26	25	13
1966/67	14	22	8
1967/68	18	19	12
1968/69	23	17	17
1969/70	81	15	70
1970/71	7	13	7
1971/72	10	11	11
1972/73	10	10	13
1973/74	6	9	9
1974/75	4	7	7
1975/76	10	6	20

Calculations of the annual mortality based on these recoveries require that the frequency of reporting is constant during the whole period and that mortality does not fluctuate too much. The formula of Haldane (1955) can be used but if the recoveries involve only birds ringed in a single year it is easier to use a regression

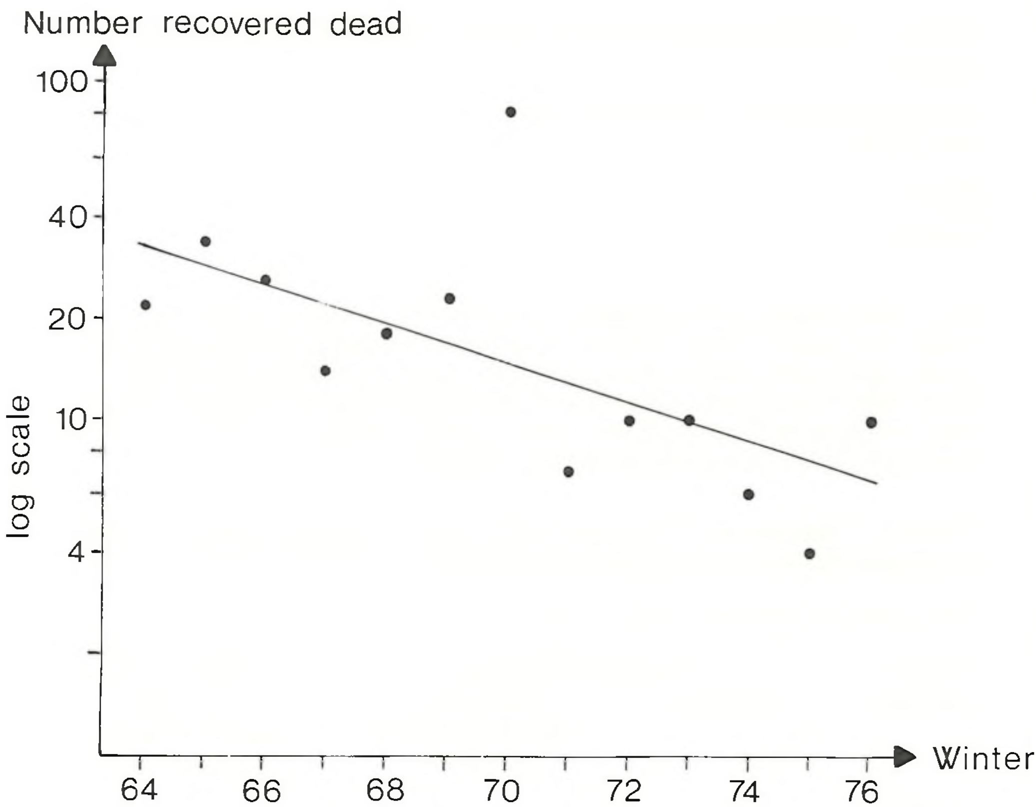

Fig 2. Number of recoveries of birds ringed in winter 1962/63 as a function of time.

The line is the regression line, the decline of which shows the average mortality.

analysis. Fig 2 shows the number of recoveries in relation to time, the line being the regression line. The regression coefficient shows the mortality, which is 12.8%.

We can calculate how many recoveries we should have received. If the result of the calculation differs from the number actually received, this can mean that the mortality has not been constant and/or that the reporting rate varies.

If it is assumed that the reporting rate is constant, the difference between expected and actual numbers of recoveries must be due to differences in mortality. The actual mortality can be found by multiplying the average mortality by a factor ^{y} actual/^{y} calculated. This has been done in Table 5.

The calculated mortality has been compared with the severity of the winter (Fig 3). This clearly indicates that those winters with the highest mortality have been the

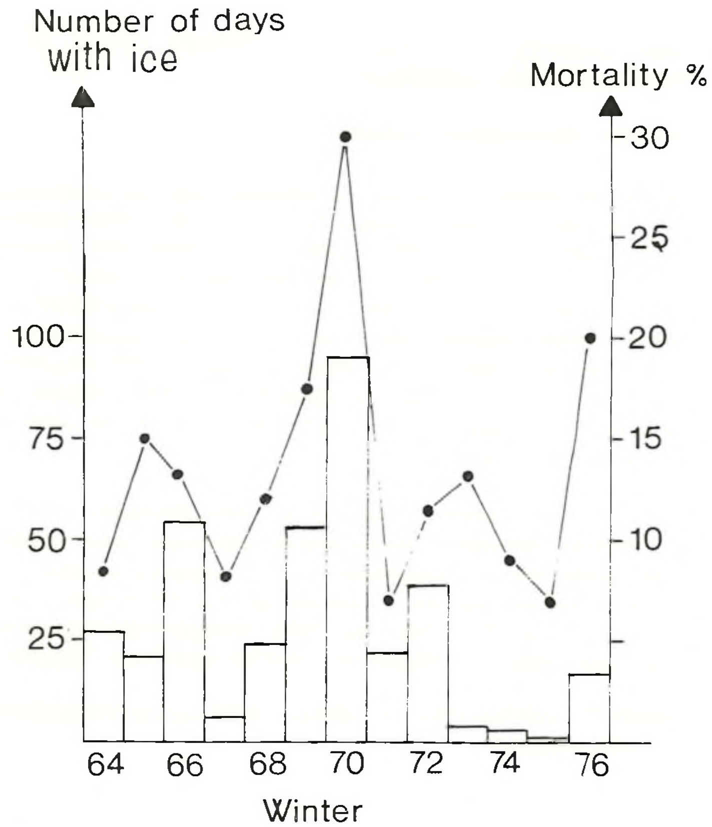

Fig 3. The calculated mortality (curve) during the winters 1963/64 to 1975/76 for *Cygnus olor* ringed in the ice-winter of 1962/63, in relation to the number of days with ice in the inner Danish waters (columns).

most severe (1968/69 and 1969/70) and mortality has been lowest in especially mild winters (1966/67, 1970/71 and 1973/74). There are indeed annual fluctuations in mortality.

On the other hand, the prospects for reporting in severe winters must be higher than normal because the birds gather in large numbers at a few localities visited by many people. The calculated mortality of 70% in 1969/70 is too high. Counts of the swan population in northern Europe (especially Denmark) suggested a much smaller reduction. Calculations of other parts of the population suggest 30% to 35% as more reasonable. Mathiasson (1974) has shown in Sweden that only 61% of the rings from dead swans were reported to the ringing centre, but the proportion would be higher in 1969/70 because of the intensive ringing activities which resulted in many additional ringed swans being collected directly and through contacts with local people at feeding places.

Mortality of birds ringed during moult

Since 1970 many birds have been ringed at moulting places, mainly younger ones (up to four to five years old) which have not yet bred and a few failed breeders. Only after severe winters did the latter increase. This means that there will be a higher proportion of potential breeders among those caught in the summer of 1970 than among those caught in 1971. In both years there would be relatively few birds in their second and third calendar year (Fig 1), these age groups having suffered severe losses during winter 1969/70. The breeding success in 1970 was very low, so that only a few young joined the moulting population in 1971. Thus the two years chosen are untypical but calculations for later years have not yet been made. It will always be hard to find a 'normal' year.

It is difficult to adjust the recovery material from moulting swans to formulae for calculation of mortality. We need to know what proportion of dead ringed swans is reported to the ringing centre. Even though we still receive recoveries for the 1963 group, the number is now so low that we can estimate the final recovery proportion with confidence as around 20%. Thus only 20% of dead birds are reported, and the mortality for birds ringed in 1970 and 1971 can be calculated (Table 6).

Table 6. Mortality calculations of swans ringed as non-breeders during moult in July and August.

The recovery year runs from 1 June to 31 May.

Year of recovery	Number recovered dead	Estimated total number of deaths	Number alive in the beginning of the period	Mortality (%)
a) Birds ringed in 1970:				
1970/71	11	55	931	6
1971/72	15	75	876	9
1972/73	23	115	801	14
1973/74	20	100	686	15
1974/75	15	75	586	13
1975/76	23	115	511	23
b) Birds ringed in 1971:				
1971/72	15	75	948	8
1972/73	17	85	873	10
1973/74	10	50	788	6
1974/75	17	85	738	12
1975/76	20	100	653	15

Mortality is somewhat lower during the first year than during later years because moulting birds stay in a marine environment during the first three to four years of their lives. A large part of Danish swans die by collision with wires when flying to potential breeding places and this hazard is lower for non-breeding swans.

Mortality in the birds' second winter

Mortality seems to be considerably reduced in the second winter. This is shown by ringing of moulting birds in 1970 and 1971. Of swans ringed in their second calendar year, 1.7% were recovered during the year after ringing, compared with 1.6% of those older swans. The 1970/71 winter was mild but the 1971/72 winter normal (Fig 3).

Mortality of breeding birds

In North Sjaelland most of the breeding birds were ringed with an aluminium ring and additional colour rings which enabled individual recognition at some distance. The mortality may be calculated from the number of ringed birds that disappears between two breeding seasons (Table 7). Usually *C. olor* is faithful to the breeding territory and even when partners are changed a new territory is rarely established more than a few kilometres away. Only a small part of those swans which disappear are reported to the ringing centre as dead. In the severe winter of 1969/70, when there was an exceptional opportunity to control birds on the wintering places, only one of those which had disappeared from a breeding site was seen alive and this bird actually returned to breed one year later.

Table 7. Mortality in solitary breeding swans in North Sjaelland.

Breeding seasons	Number alive in the preceding breeding season	Number disappeared before the next breeding season	Mortality (%)
1963/64	7	1	(14)
1964/65	20	2	(10)
1965/66	27	5	19
1966/67	70	8	11
1967/68	100	21	21
1968/69	90	22	24
1969/70	104	37	36
1970/71	49	6	12
1971/72	90	9	10
1972/73	120	20	17

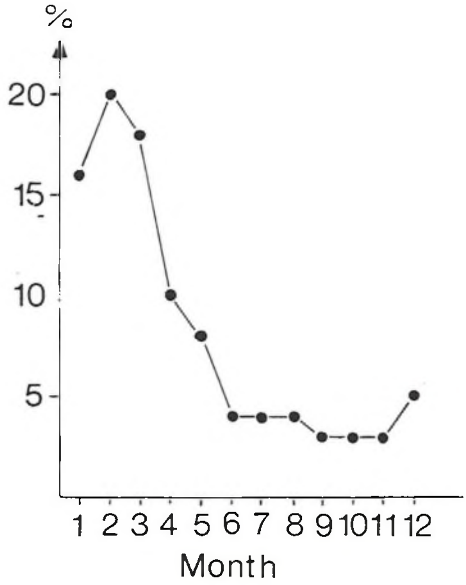

Fig 4. Distribution by month of ringed swans found dead.

The mortality rate in colonially breeding swans seems to be similar to that of solitary breeding ones.

Causes of death during the year

By far the majority of swans ringed in Denmark die in the winter. Fig 4 shows the distribution by month of all swans recovered as dead. About 54% are recovered from January to March. In severe winters thousands of swans die, usually from starvation.

Oil pollution is a special problem in the early spring (Fig 5) and occurs at the same time as oil catastrophes for diving ducks. Most oil pollution occurs in the Kattegat area where swans are sparse (Joensen 1972 and 1977). Extensive oil pollution in southern Danish waters might have very serious consequences for the population, even though *C. olor* seems to have a better chance of surviving oiling than other waterfowl.

Of recoveries received with an indication of the cause of death, 14% died from oil pollution and 36% by collision with overhead wires. However, many reports give no cause of death, many being from winter and probably involving starvation. Collisions with wires occur mostly in spring, when the birds fly to the breeding places, and in autumn, when they leave them again.

It has to be added that even though swans are totally protected in Denmark some illegal shooting takes place. X-ray investigations of dead birds have shown that about one-fifth had pellets in their tissues.

In later years several cases of lead poisoning caused by ingestion of spent lead pellets have been observed in areas where there are shooting-ranges orientated towards shallow coastal waters. Up to 150 to 200 dead swans were found in such areas (Clausen and Wolstrup 1979). The usual concentration of lead pellets in shallow areas in West Jutland is so high that death by lead poisoning seems to be fairly common (Petersen and Meltofte 1979).

Balance in the population

It is difficult to make calculations on the balance of the populations because of the variation in winter mortality and in age composition. In order to maintain the population level, production of about 1.5 young per pair is necessary, but calculations show that enough young from solitary breeding swans survive to give an annual population increase of about 15%. Contrary to this, the population of colonially breeding birds should decline.

The increase in colonially breeding swans would seem to be due to immigration of surplus young from the solitary breeding population. In North Sjaelland we have controlled about 15 swans breeding in colonies which had been hatched in lakes. Young hatched in colonies have never been found breeding as solitary pairs.

Variations in the age of first breeding do not change the calculations much and cold winters seem to occur at such long intervals that their overall effect must be comparatively small.

Even though the Danish swan population has increased considerably, the breeding population rising from 750 pairs in 1954 to 2800 in 1966 (Block 1971), mortality of swans after their second calendar year does not seem to have changed since 1950.

On the other hand, a change in mortality during the first four months of life could be documented. In 1954, when no colonially breeding swans existed, 3.1 fledged young were produced per pair (Paludan and Fog 1956). In 1966 Bloch (1971) gives an average in July of 3.5 young per pair in freshwater lakes and 1.9 for colonially breeding birds. The present material shows 2.6 young per pair for solitary breeding and 0.9 for colonially breeding swans in the period 1966 to 1975. This means that the change to colonially breeding has caused an increase in mortality of young. It is more difficult to ascertain whether mortality in young of solitary pairs has increased, but it seems likely that the spread to less appropriate lakes, caused by the increase in the population, has also resulted in a higher cygnet mortality rate in this group.

We cannot say for certain whether mortality during the first winter has also increased. Still, it has to be pointed out that the utilization of marginal habitats during the last 20 years has resulted in lower weights of young, probably causing increased winter mortality.

More detailed analysis of the relation of weight, sex, age and habitat on mortality are desirable.

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Summary

The paper presents preliminary data on studies carried out since 1966 on a solitary breeding population and since 1971 on a colonially breeding population of *Cygnus olor* in Denmark. Production of young was higher in solitary than colonial nesters and after severe winters many potential breeders did not nest. In solitary breeders, five was the mean age of first breeding. Mortality before fledging is higher in colonial breeders because of disturbance in the colonies, but mortality in young of solitary breeders is also high because of exposure to wind. Mortality during the first winter is calculated for solitary breeders by the 'disappearance percentage', normally 45%, but 90% in severe winters; in colonial breeders mortality in the first winter varies considerably from year to year because of variations in weight. Mortality in older birds averages under 13%, but there are considerable annual fluctuations, linked with the severity of the winter. Mortality of swans ringed during moult is difficult to calculate but is lower in the first year. Most swans die in winter, usually in severe winters from starvation; 14% of recoveries received come from oil pollution and 36% from collision with overhead wires. The population of solitary breeders shows a small increase, which compensates for a decrease in colonies. The change to colonial breeding apparently leads to increased mortality in young swans.

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AN ISOLATED POPULATION OF *CYGNUS OLOR* IN SCOTLAND

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Introduction

This paper presents a preliminary report on certain aspects of a study of *Cygnus olor,* begun in 1978, in the Outer Hebrides, Scotland. The main objective of the research project is to understand the processes underlying the regulation of numbers in a natural wild population.

Jenkins *et al* (1976) suggested that the numbers of adult *C. olor* were fairly constant between seasons, that an August peak might be due to a temporary immigration to the islands of 200 birds to moult, and that the constancy both of numbers of breeding pairs (around 86) and of adult non-breeders between seasons was due to regulation of numbers through social behaviour in relation to food supply. The population, unlike others studied in Britain recently, appeared to be stable, not declining in numbers, despite a low breeding output each year. Furthermore, being in a relatively isolated area, there was the possibility of being able to gather very complete data on population processes and their controls. Another important aspect is that although the population is an introduced one, dating back no further than the latter half of the 19th century (Harvie-Brown and Buckley 1888), it has never existed in close proximity to man as have populations studied elsewhere in Britain. It is essentially therefore a natural population, relying little on man's activities for its survival.

Study area

The Outer Hebrides are a group of islands, approximately 210 km in length, situated in the North Atlantic, some 50 km west of the Scottish mainland (Fig 1). Resident *C. olor* does not occur on the islands north of the Sound of Harris, nor south of Barra, and the study area is restricted to the island group of Uist and Benbecula. The nearest other breeding populations (Sharrock 1976) occur on the Isle of Tiree (80 km southsoutheast) and on the mainland around Loch Ewe (100 km eastnortheast).

The islands are composed almost entirely of Lewisian gneiss, overlain by peat deposits. Barra and South Uist are partially mountainous but the rest of the area is predominantly low-lying, with acid peat moorland and hundreds of lochs which vary greatly in size. Along the western seaboard, however, wind action has deposited a layer of calcareous marine shell-sand, which overlies the gneiss forming a narrow fertile coastal plain known as 'machair' (Ritchie 1976, 1979) (Fig 2).

The machair is used for cereal cultivation, while the less fertile 'blackland' area, lying between the machair and the peat moorland, is used for cattle and sheep grazing and the growing of potatoes and hay (Caird 1979). Little fertilizer is used, though shell-sand is occasionally spread on the blackland areas to improve grass production. There are no large urban concentrations or sewage outfalls and the *C. olor* population, unlike many others in Britain, lives with minimal assistance or interference from man's activities in an environment comparatively little altered by modern development.

Three categories of freshwater lochs can be identified on the Uist, on the basis of their water chemistry and vegetation (Waterston and Lyster 1979). The vast majority can be classed as oligotrophic, acidic peat lochs, very low in terms of biological productivity. These moorland lochs have pH values generally well below 7, and both conductivity and alkalinity are also very low, the latter below 10 mg/l $CaCO_3$ (Waterston *et al* 1979). The vegetation is characterized by an open *Littorella-Lobelia* association (Spence 1964) and is generally sparse, except in sheltered areas of silt where larger swards of *Myriophyllum alterniflorum, Isoetes lacustris* and *Potamogeton natans* may occur.

The machair lochs are quite different, being shallow areas of water, wholly or partially lying on shell-sand, and with high pH and alkalinity values. Alkalinity in these eutrophic lochs is generally greater than 25 mg/l $CaCO_3$ and may be as high as 100 mg/l or above, with pH values always greater than 7. The vegetation, especially in sheltered areas, may be extremely luxuriant, with the *Chara aspera-Potamogeton filiformis* association (Spence 1964) dominant. *Potamogeton gramineus* and *P. perfoliatus* may also occur in dense stands, with *Hippuris vulgaris* and *Myriophyllum spicatum* in nutrient-rich areas.

Lying between these two extremes are the lochs of the blackland area, which can be classed as mesotrophic. These lochs occupy an intermediate position, both geographically and in terms of productivity, between the acidic peat lochs and calcareous machair lochs (Spence *et al* 1979), and their conductivity, alkalinity and pH values reflect this. The *Chara aspera-Potamogeton filiformis* association is missing, but extensive beds of *Potamogeton perfoliatus, P. natans* and *P. gramineus* may occur.

A fourth category of loch can be identified on the Uists, as there are certain areas of shallow brackish water which are also regularly used by swans. Lochs in this category include both those under regular tidal influence and those which only occasionally receive a direct intrusion of sea water at extremely high tides. PH, conductivity and alkalinity vary considerably, but are generally much higher than found in the mesotrophic freshwater lochs. In sheltered and shallow silty locations dense stands of *Ruppia spiralis, R. maritima* and *Zostera marina* occur, with *P. pectinatus* and other euryhaline species distributed according to salinity tolerance and exposure.

Development of methods and techniques

Population censuses

Previous censuses (Jenkins *et al* 1976) have involved counting swans only on lochs accessible from the roads, concentrating on the machair and certain saline lochs, and were carried out within a two to three day period at the beginning of each month. The present study, however, has involved a series of complete surveys of the islands, though less often, visiting all lochs, except some of the remote oligotrophic ones, either by car or on foot. Such is the nature and extent of the study area, however, that it proved impossible, in the absence of aerial censuses, to check all water bodies on the island in less than ten days and frequently bad weather extended this time.

Accuracy of this counting method has been checked in a number of ways to ensure birds were not missed or counted twice. Financial and logistical constraints precluded the use of complete aerial censuses, but whenever possible ground counts were checked using aerial photography and the remote and inaccessible areas rapidly censused from the air as well. Such flights were used in particular to census

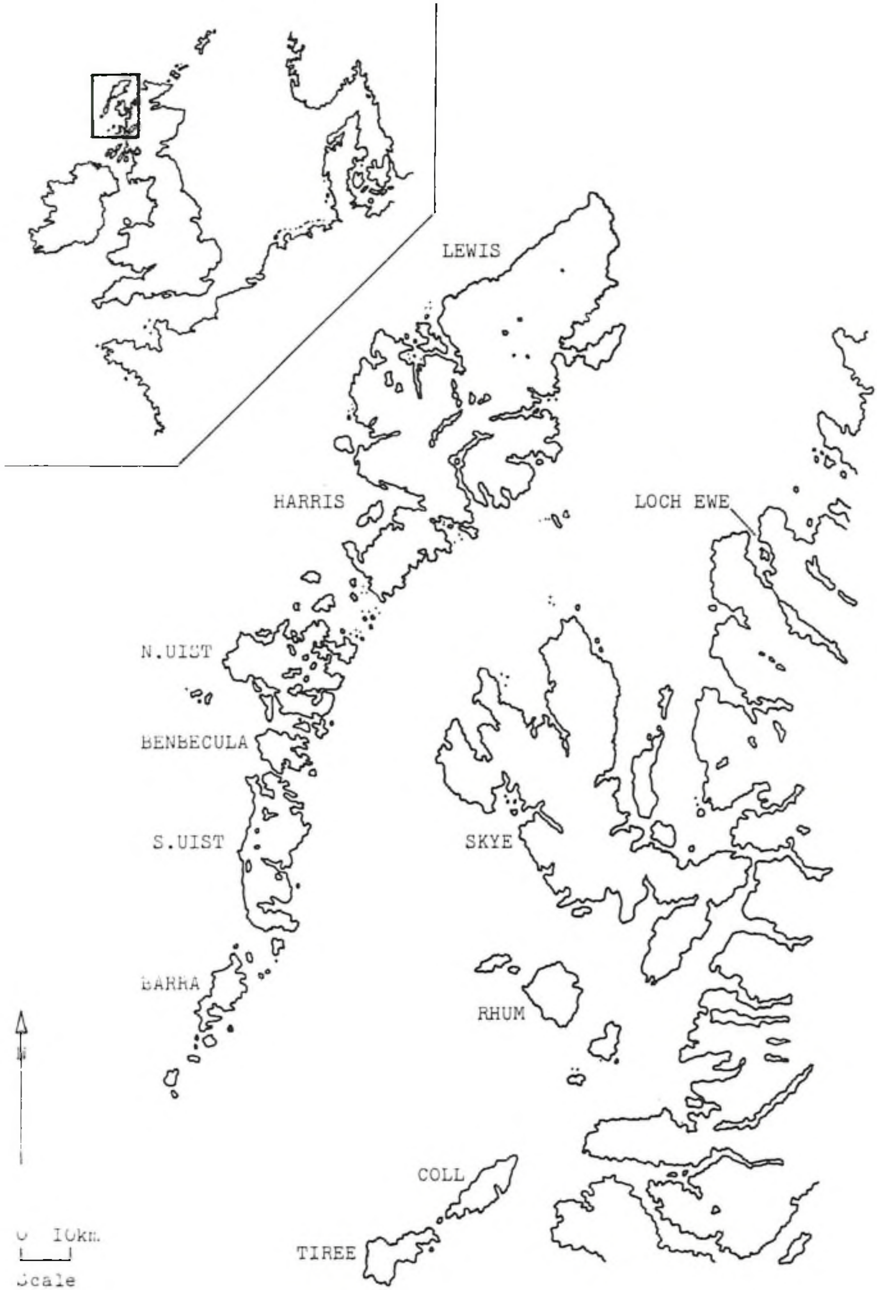

Fig 1. The Outer Hebrides.

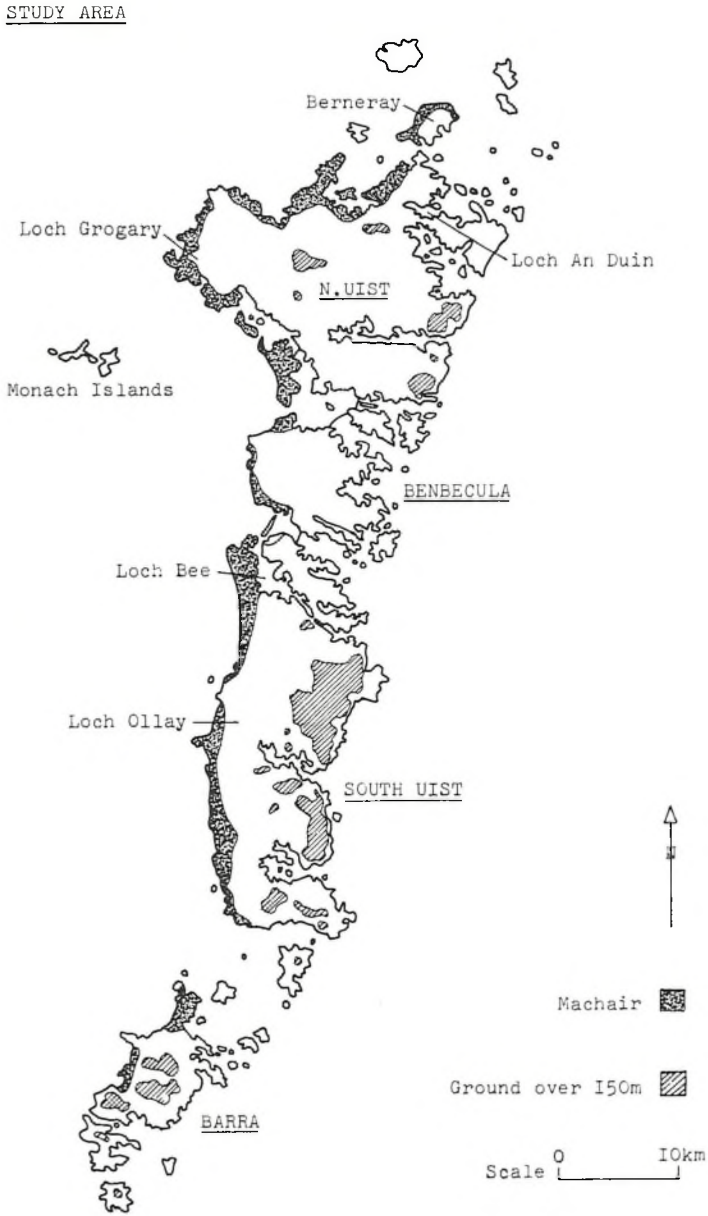

Fig 2. The study area within the Outer Hebrides.

the main non-breeding flocks on Loch Bee (South Uist) and Loch an Duin (North Uist) and to compare the numbers counted with figures obtained from ground counts (Table 1). Possible misidentification of *Cygnus cygnus cygnus* was a problem in the aerial counts.

Table 1. Comparison of aerial and ground censuses.

Number of adult swans counted in two flocks.

	Ground census	Aerial census	Dates
Loch Bee	224	248	15/13 December 1978
Loch Bee	204	211	14/16 February 1979
Loch an Duin	91	93	19/16 February 1979
Loch an Duin	90	85	19/13 March 1980

The counting method was also checked against another ground census technique by comparing the results of the usual autumn and winter censuses in 1979 with the results obtained by ten teams of observers covering the whole study area on one day (Table 2). A number of birds, mainly cygnets, were certainly missed by the teams of counters on 18 November, and some confusion with *C. c. cygnus* was also possible. Despite very bad weather conditions on 18 November, though, the numbers recorded by the two methods are remarkably close.

Table 2. Comparison of ground census techniques

13–26 September 1979	754 adults	179 cygnets	– autumn census
18 November 1979	743	112	– ten teams of observers
30 November–11 December 1979	738	152	– winter census

Where possible, the identity of all marked birds was recorded. The repeat sighting of a marked bird in the same census occurred so rarely that counting the same individuals twice in different locations is not considered to have affected the accuracy of the census technique. The possibility that certain birds were missed at each census remains. However, aerial surveys did not locate swans in areas where they were not expected, and the general consistency between the total numbers recorded in sequential censuses, rather than large random fluctuations, does not suggest this to be the case either.

Catching and marking

It has not been possible to catch breeding swans at the nest site, as the Hebridean birds, unlike most others in Britain, are extremely wary and do not stay to defend their nest, swimming away quickly when approached. Instead, adult birds have been captured during the moult period in July/August, when they are flightless, and cygnets caught in early October just prior to fledging. The autumn catching effort has been primarily directed at non-breeders and failed breeders gathered in moulting flocks, though a certain number of successful breeding adults, which moulted on territory, have also been caught. During 1978, 283 cygnets and 91 cygnets were ringed, with a further 47 adults and 130 cygnets in 1979.

Birds in the moulting flocks were caught by using teams of people on the bank, in canoes and in inflatable dinghies to herd the swans into temporary pens erected at the water's edge. This technique works best on small or confined water bodies and was only partially successful on the main loch used by moulting swans, Loch Bee, as it is so large. Cygnets were caught from a small inflatable dinghy fitted with an outboard engine, the catcher standing in the bows with a swan-hook while his assistant manoeuvred the boat.

All birds handled were weighed, aged, sexed and ringed, in addition to having measurements made of wing-, skull- and tarsus-length. Traditional plastic colour leg-rings were considered to be of little use as a marking technique, as they could not be identified at the distances to which the wary Hebridean swans could be approached. Instead, 330 adults and 162 cygnets have been marked with specially made and engraved plastic neck-collars, a technique not in use elsewhere in Britain, though widely used in America and some other countries.

The neck-collars were made at Aberdeen University, having been tested initially on tame birds kept at the Zoology Department's field station. In specification they follow broadly the outlines set in the IWRB Swan Research Group's Technical Note No 5 (Sept 1972). The collars are made of triple laminate 1.5 mm thick yellow 'Darvic' and weigh c 34 gm each (0.3% of the body weight of an adult *C. olor)*. They are 8 cm high x 23 cm in length, with the ends overlapped to give an internal diameter of 6 cm and the overlap glued using the plastic manufacturer's recommended PVC solvent cement. A three-digit combination of two letters and one number is engraved in black three times vertically around the collar, the individual digits being 23 mm high. Under favourable conditions they can be read at distances up to 600 m.

Results

Total population

The number of *C. olor* recorded in the study area for the two years 1978 to 1980 is shown in Table 3. Until December most young birds remained with their parents and so cygnets could be easily censused. Soon afterwards, however, they left their natal territories and dispersed widely, eventually joining the non-breeding flocks.

Table 3. Total population counts.

	1978 Full-grown	Cygnets	1979 Full-grown	Cygnets
April	892		838	
May	943		770	
June	948	+267		
July			753	+216
August	889	+218		(+194)
September			754	+179
October		(+182)		(+174)
November				(+158)
December	845	+156	738	+152
	1979		1980	
January				
February	820			
March			820	

During this period they gradually lost their brown juvenile colouring, so they were not separated from adults from January onwards.

The total population of full-grown swans in the Uists peaked at 948 in June 1978 and fell to 838 in April 1979 following severe winter mortality. The actual total fell from 1001 swans (of all ages) in December 1978 to 820 in February 1979. The total then stabilized at around 750 birds for the rest of the year, rising again to 820 by March 1980 with the inclusion of young birds in the total once more.

Immatures and non-territorial adults were found in two main flocks. That on the complex of saline lochs centred on Loch an Duin and Loch an Strumore (North Uist) regularly held over 100 birds, except during the winter 1978/79, when all but a small part of the loch was frozen (Fig 3). In addition mid Loch Ollay (South Uist) regularly held high numbers during the moult period, including many birds that had come from the non-breeding flock on Loch Bee, although birds also remained to moult on Loch Bee itself. Other moulting flocks occurred on Loch Grogary (North Uist) with a maximum of 43 birds in July 1978, and Loch Bhruist on the Island of Berneray, maximum 47 birds in August 1978. At other times of the year, like Loch Ollay, these two lochs had few, if any, swans.

Both Loch Bee and Loch an Duin are brackish water lochs and this is reflected by the fact that at all times of the year the majority of swans were found on lochs which have a saline influence (Table 4). Eutrophic machair lochs were important during winter, though numbers did not vary greatly, whereas mesotrophic lochs were important only during late summer. Oligotrophic lochs, despite their great

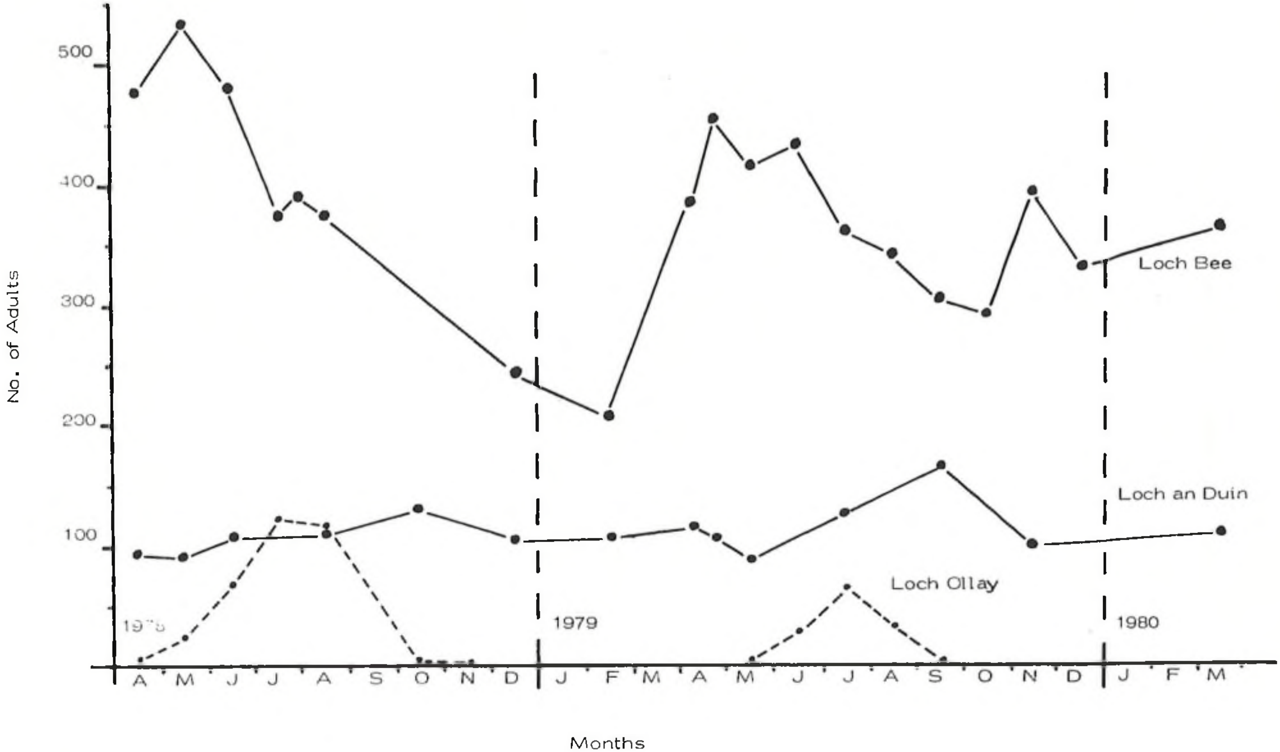

Fig 3. Numbers of adult *Cygnus olor* on three selected lochs.

Table 4. Dispersion of full-grown *Cygnus olor* in relation to loch type (as % of total population).

Date		Brackish	Eutrophic	Mesotrophic	Oligotrophic	Total numbers
April	1978	78.7	10.5	9.6	1.1	892
May	1978	76.6	9.8	12.9	0.7	943
June	1978	71.4	12.8	15.0	0.6	948
August	1978	62.5	15.5	22.0	–	889
December	1978	76.2	15.4	8.4	–	845
February	1979	75.7	18.1	6.0	0.2	820
April	1979	80.8	9.9	8.0	1.3	838
May	1979	79.6	11.1	8.1	1.2	770
July	1979	74.4	9.2	15.9	0.5	753
September	1979	76.7	13.1	9.8	0.4	754
December	1979	80.7	16.1	3.2	–	738

abundance, were hardly utilized at all.

Breeding population

A complete survey of the study area was undertaken from the air and from the ground during April and May each year to locate territorial pairs of swans. Not all pairs nested each year, about 12% apparently failing to build a nest and lay eggs, though it is possible that nests which were destroyed or deserted early in the season might have been missed. Wherever possible, clutch size, hatching and fledging success were also recorded and details are given in Table 5.

Table 5. Breeding of *Cygnus olor* in the Uists.

Number of territorial pairs	% of total population	Number of nesting pairs	% of total population	Clutch size	% nests hatching	% nests fledging	Young fledged per nesting pair
1978: 163	35%	143	31%	6.17 (n = 52)	56%	34%	1.22
1979: 116	27%	102	24%	5.66 (n = 68)	65%	49%	1.74

The density of breeding pairs is extremely high, with 1 nesting pair/5.4 km^2 in 1978 (1 territorial pair/4.7 km^2). The actual density of pairs on North Uist, Benbecula and South Uist alone, excluding offshore islands, is 1 nesting pair/4.7 km^2, nearly twice as dense as the highest density recorded in any area in Britain during the 1955 *C. olor* census (Campbell 1960) and four times as great as the density recorded in the Midlands during the 1960s (Minton 1968). These figures are even more impressive when one considers that several parts of the study area are mountainous and the majority of the low-lying ground is acid peat moorland. Breeding pairs were not colonial, though in 1978 four pairs attempted to nest on two islands in a small eutrophic loch of only 6 ha, and in both years the minimum distance recorded between any two nests was only 30 m.

The number of breeding birds as a percentage of the total population, however, is low compared with figures from other studies in Britain. Returns from the 1955 census (Rawcliffe 1958; Campbell 1960) give an estimate of 3500 to 4000 breeding pairs in Britain with another 11 000 non-breeders, indicating that about 40% of the total were nesting pairs, compared with only 24% to 31% in this study. Minton (1968) in a more detailed study in the Midlands reported that nesting pairs made up 39% of the population in 1966. At the same time the percentage of territorial pairs was 57% (Minton 1971).

Data from the two years of the present study show differences in almost every aspect of breeding biology examined and it is therefore very difficult to comment. Breeding success, however, was very much better in the second year, when, despite a 29% drop in the number of nesting pairs and a drop in clutch size, hatching and fledging success improved and the total number of cygnets alive at the end of each year was similar (156 vs 152). The mean number of young fledged per nesting pair, even in the better year, is still very low in comparison with other studies in Britain, eg 2.0 per breeding pair, Perrins and Reynolds (1967), Minton (1968); 2.3, Eltringham (1966); 2.4, Cramp (1957); 2.9, Reynolds (1965).

However, comparison of the breeding success of pairs nesting on different types of loch showed that there were marked differences in the production of young (Table 6).

Table 6. Breeding success in relation to loch type (1979 data only)

	Eutrophic (Machair)	Mesotrophic	Brackish	Totals
Number of pairs	20	10	68	(98)
Clutch size	*6.31 (n = 16)	*4.75 (n = 8)	5.49 (n = 43)	5.66
% nesting pairs that hatch at least 1 cygnet	90%	70%	56%	65%
% nesting pairs that fledge at least 1 cygnet	*80%	50%	*41%	49%
Number of cygnets fledged per nesting pair	3.00	1.40	1.44	1.74
Mean weight of cygnets at fledging (October)	8.00 kg 11 broods 40 cygnets	6.3 kg 5 broods 12 cygnets	8.1 kg 21 broods 71 cygnets	

* Significant at P = 0.05.

In both years birds nesting on the eutrophic machair lochs did considerably better than those using other habitats. Differences in clutch size between eutrophic and mesotrophic nests were statistically significant in both years. In 1979 there was also a statistical difference between the percentage of nesting pairs that fledged at least one cygnet on eutrophic and brackish water lochs. Differences in clutch size may possibly be related to weight and condition of the female in early spring, whereas differences in fledging success could be due to laying date, egg quality, feeding conditions for cygnets or parental care.

The majority of nests sites were on islands (75% in 1978, 81% in 1979) with inaccessible sites in reedbeds accounting for a further 6% each year. The remaining sites were along the edges of lochs, many on promontories and all close to the water. Had human interference been an important cause of clutch losses, as reported elsewhere (Minton 1968), one might expect hatching success to be lowest in these easily accessible nests. In fact, there was no statistical difference between hatching success at the three different nest sites in either year (Table 7).

Table 7. Hatching success in relation to nest site location (1978 data only).

	Nest site			
	Islands	Reedbeds	Bankside	Total examined
Number of nests	104	9	26	139
% nests hatching at least 1 cygnet	55%	78%	54%	56%

Movements and mortality

A total of only eight birds out of 551 ringed on the Uists during 1978 and 1979 has been reported from areas outside the study area. Seven of the eight were identified by their collar codes and are of known age. The collar of the eighth, a bird reported on the Isle of Tiree in April 1980, was not read.

All seven identified birds were immatures, having left the study area in their second calendar year. One bird hatched in 1979 had moved only 15 km north on to South Harris in January 1980; three cygnets hatched in 1979 moved as a group 85 km northnortheast on to Lewis during April 1980; two birds, both in their second winter, were recovered dead on Tiree (80 km southsoutheast), one each in the winters of 1978 and 1979; the longest movement involved a bird hatched on South Uist in 1978, which was reported on the Scottish mainland, 190 km southsoutheast, on the Mull of Kintyre in July 1979. It remained there until at least November 1979 and then in April 1980 it was reported near Port Stewart, County Derry, in Northern Ireland (a further 110 km southsouthwest and 225 km south from its ringing site), the first record of any *C. olor* moving from Britain to Ireland.

Table 8. Recovery distances of swans found dead within the study area.

	Distance moved from ringing site (km)						Mean distance
	0–1	2–5	6–10	11–20	21–50	50	
Cygnets (n = 30)	15	8	2	3	2	0	4.7 km
Adults (n = 43)	7	20	6	8	2	0	6.7 km (♂6.5, ♀7.1)

The recovery distances for swans found dead within the study area are shown in Table 8. 'Cygnets' are birds recovered within one year of fledging, while adults refer to all full-grown birds (minimum age two years) caught in moult flocks during 1978. This latter class includes a number of failed breeders which moult in the flocks, as well as non-breeding swans. Four adults ringed as breeding birds on territories have also been recovered. All were reported during winter icing of their territorial waters and had hit electricity cables nearby (mean distance of movement 2.5 km).

The pattern of recoveries follows closely those observed by Ogilvie (1967) and Minton (1971), with very few movements over 50 km, though to a certain extent the shape and size of the study area precludes much longer movements. No adult birds have been reported outside the study area at all, the only movements over 50 km involving six birds all in their second year, the age at which *C. olor* is most prone to wandering (Minton 1971). Collared swans are conspicuous and it is unlikely that many are leaving the islands undetected, as most of their likely destinations (Tiree, Rhum, Skye, Harris and Lewis) are being regularly checked.

Sightings of collared birds within the study area have shown that internal movements can be accounted for by the dispersal of juvenile birds from their natal territories to join the non-breeding flocks, by the movement of adults to and from the flocks, especially during the moulting period and in severe winter weather, and by the short term movements of paired birds prospecting for territories. Such movements are similar to those observed in the Midlands (Minton 1971) and the population therefore appears to be essentially a closed one, though a certain amount of emigration of immature birds may occur. Because of their size and conspicuousness, dead swans are easily discovered and a large number, including many collared ones, have been reported dead. The monthly distribution of deaths (Fig 4) shows a heavy concentration during winter 1978/79, with most birds having died between late December and April, similar to that reported by Ogilvie (1967). There is no indication of any tendency for more deaths to have occurred in spring and autumn than in summer and mid-winter, as suggested by Perrins and Reynolds (1967), although the number of deaths in summer is very low. However, the winter of 1978/79 was severe, even in the usually relatively mild maritime climate of the Outer Hebrides, with much icing of lochs, and the mortality pattern may be rather different from more normal years (Boyd and Ogilvie 1964).

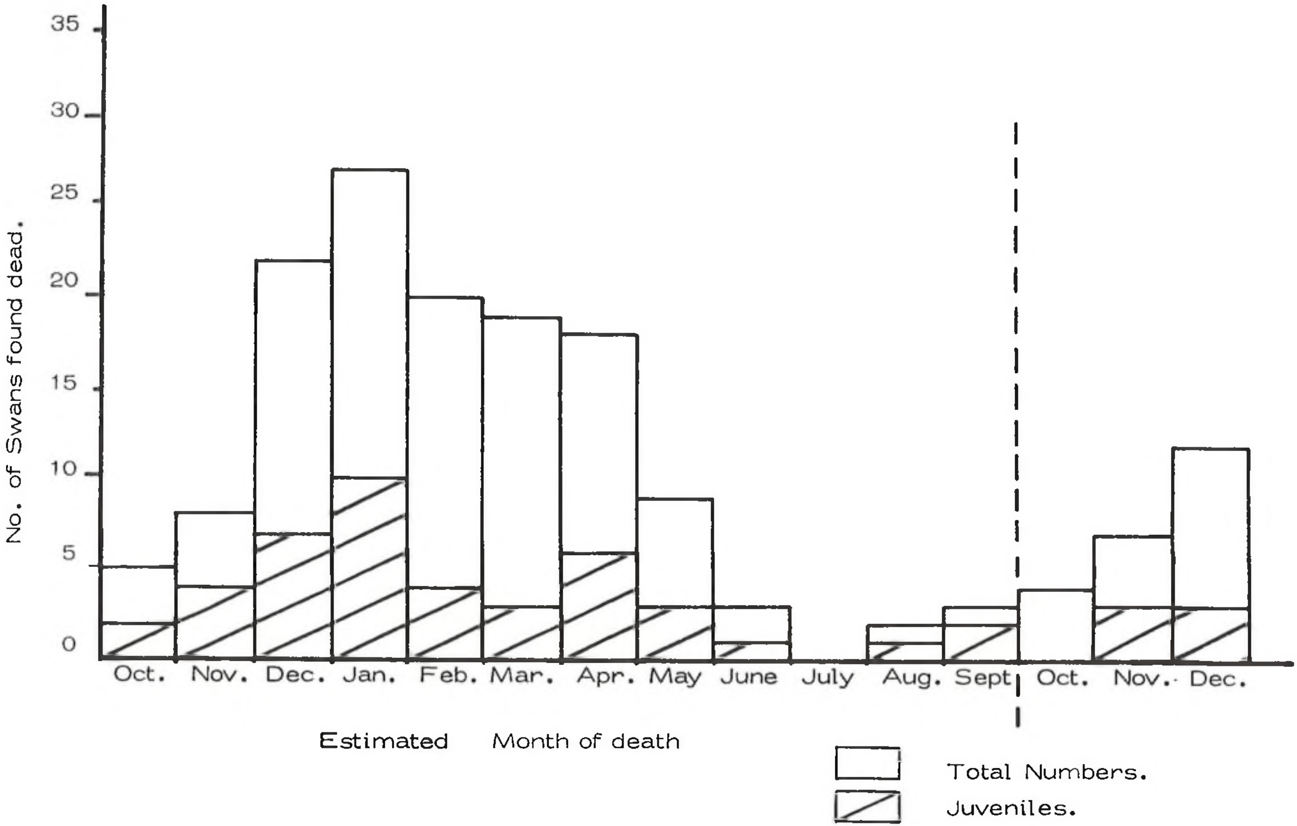

Fig 4. Mortality of *Cygnus olor* in Uists 1978 and 1979.

Table 9. Cause of death of *Cygnus olor* in the Uists 1978/79.

Cause of death	Numbers	%	% known causes
Unknown	76 (61)	52 (53)	
Powerline collisions	60 (44)	41 (38)	86 (81)
Shot	4 (4)	3 (3)	8 (7)
Fighting	3 (3)	2 (3)	4 (6)
Disease/starvation	3 (3)	2 (3)	4 (6)
TOTALS	146 (115)	100%	100%

(Figures given in brackets are those found by the author).

The causes of death are given in Table 9, though, as post-mortem examinations were not possible in most cases, the reported causes are probably biassed towards those that produced obvious characteristics of death. Linesmen working for the Hydro Electric Board were one obvious source of bias, as they were especially on the look-out for swans. However, even if birds found only by the author are included, the figures remain much the same, and it is apparent that death due to collision with electricity cables is the major cause of mortality in the Uists.

It should be noted that, although collision with overhead wires was indeed the commonest ultimate cause of death, the extremely cold weather may have caused birds to move off their usual haunts to find feeding grounds elsewhere, increasing the risk of collisions, and indeed several of the corpses were very low in weight. However, the percentage of deaths due to collision with wires (86%) is still nearly twice as high on the Uists as recorded for the whole of Britain, 44.1% (Ogilvie 1967) of the swans for which cause of death was specified, though very locally higher mortality rates may occur for a short time (Harrison 1963).

Discussion and conclusions

Data collected in the first two years of this present study differ markedly in several important aspects from those collected in the earlier study of this population between 1971 and 1974 (Jenkins *et al* 1976). In particular the present data show none of the regular large-scale seasonal fluctuations in the total numbers, while the number of breeding pairs observed is much higher than they reported. These differences could be due to the different census techniques being used, rather than to a real change in the numbers and pattern of movement of swans in the study area in the intervening years.

The two census methods were therefore compared directly, a simultaneous survey being carried out in June 1978, with Colin Brown (who did the actual counting in the censuses of 1971 to 1974) using the original method, while the author used the current technique. The results showed a disparity of 253 birds, with 695 adults counted by the former method and 948 by the present method, a 36% difference. This difference was due both to inadequate counting of several complex lochs which held large numbers of birds and to the fact that 54 lochs on which swans were seen in 1978 were not included in the former censuses.

A further suggestion that the previous census technique was not covering all birds came from the results of a Royal Society for the Protection of Birds (RSPB) group expedition which did an ornithological survey of the Uists in February 1975. The recorded a total of 1350 *C. olor,* in what they described as an unusually good year (Hammond 1975). This figure is over twice the number recorded during February in the years 1971 to 1974 (mean 526 swans) and compares with just 461 and 386 recorded in November and December 1974 only a few weeks before. It is also higher than any count in 1978 and 1979 but the present technique is considered to be accurate, whereas there are no checks on the accuracy of the RSPB count, done by people who had little previous knowledge of the study area or of censusing swans.

Had there been a moult migration to and from the study area, as was hypothesized, by Jenkins *et al,* it would surely have shown up with the ringing and collar-marking of so many birds during 1978. The wide discrepancy in the number of breeding pairs is also considered due to the counting techniques; indeed, the 54 lochs missed in the June 1978 census held 32 nesting pairs that year. It is possible, therefore, that the apparent stability in the number of territorial pairs reported in the study area in the years 1971 to 1974 was also just a product of the census method used.

It is difficult to draw any firm conclusions when the two breeding seasons of the present study were so very different. A number of points, though, do seem to have emerged that are worth very briefly speculating upon. The number of nesting pairs in the study area has not remained constant, showing a 29% drop between years as well as decreasing from 31% to 24% of the total population, despite the presence of a large number of non-breeding birds in the population. This differs from the situation reported by Minton (1971) in the Midlands where the number of breeding pairs remained relatively stable, with the non-breeding flock, which fluctuated more widely, acting as a reservoir of potential territorial pairs.

It is difficult at present in the Uist study area to distinguish between two possible reasons for this lack of stability in the number of breeding pairs: poor body condition of potential breeding adults or the physical state of the breeding territories. Following the severe winter of 1978/79 either or both of these factors may influence the number of breeding territories utilized.

The overall breeding success of the Uist population is very low (even in the better of the two years) when compared with figures from other population studies, and reworking the data on breeding success from Jenkins *et al* (1976) still gives a mean of only 1.36 cygnets fledged/nesting pair for the earlier years 1971 to 1974. If, however, breeding success is examined in relation to loch type, it is apparent that birds on the eutrophic machair lochs are the most successful. A small sub-section of the breeding population may thus be responsible for a disproportionately large percentage of the total breeding output each year.

Although colonial nesting is not found in the Uists, the density of breeding swans is far higher than recorded anywhere else in Britain. At the same time, though, breeding swans account for a lower percentage of the total population, suggesting that in the Uists some factor, such as a limited number of breeding sites, may be setting an upper limit to the number of breeding pairs, whereas availability of suitable habitat for non-breeding birds has not so far limited their build-up in numbers.

These observations, taken together with the conclusions from ringing results and movements, suggest that the population structure of such an isolated and closed community of *C. olor* may well differ from those studied elsewhere in Britain, which are in effect just small parts of a continuous population.

Acknowledgements

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Summary

A study of the population of *Cygnus olor* in the Outer Hebrides, which, though originally introduced, is now isolated and essentially natural, may allow understanding of the processes regulating numbers. Data collected in this study differ markedly from those in an earlier study, perhaps because of differing methods. The present study shows no large-scale seasonal fluctuations in numbers and many more breeding pairs, and the earlier hypothesis of an influx of moulting birds therefore seems unjustified.

The number of breeding pairs has not — unlike conditions elsewhere in Britain — remained

constant. Overall breeding success is comparatively low and pairs breeding on eutrophic lakes produce a disproportionately large percentage of the total output. Density of breeding swans is higher than elsewhere in Britain. The population structure of the island community clearly differs from that in the main British population.

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Behaviour

HIERARCHY IN THE FAMILY GROUP AND SOCIAL BEHAVIOUR IN WINTERING *CYGNUS CYGNUS CYGNUS*

R KAKIZAWA

Introduction

I have been studying the social behaviour in *Cygnus cygnus cygnus* since the winter of 1974/75.

The study area is Lake Hyoko in Niigata Prefecture in the central part of Honshu Island on the coast of the Sea of Japan. Hyoko, a well-known wintering ground for many waterfowl species, is a small lake covering about 9 ha. Every year several hundred swans, along with numerous ducks, winter here. They are fed three times daily, enabling researchers to study these birds at close range.

Methods

I used the method described by Scott (1966), identifying individual swans by the difference in black and yellow patterns on the beaks. Behaviour was recorded every two minutes by continually observing family groups (adult pairs, or parents and their cygnets) that included already identified swans.

Dominance was determined in the following manner: if a family proceeds forward while the other changes direction as two families encounter each other, the former is dominant over the latter. Also, as two families meet, one or more of the dominant family adopts a threatening posture and holds the other in check, or the male actually wins a fight.

Results

The following trends have been found in the hierarchy:

(1) Family groups with larger numbers of members are dominant.
(2) In family groups consisting of the same number of members, a family that has arrived earlier becomes dominant.
(3) A family led by an aggressive male becomes dominant.
(4) There are exceptions to the above. Hierarchies from previous year(s) could be a factor for such exceptions.

During winter, reversals in the order of dominance were often noted. This was the result of challenges made by subordinate families. In several instances, families dominant during the early part of the winter lost their dominance later. Families with cygnets that arrived earlier in winter came to be fed earlier than the later arrivals and stayed longer. However, they later lost their attachment to the feeding station, resulting in a shorter stay there. It seems likely that this in turn causes a decline in the social hierarchy.

Summary

Cygnus cygnus cygnus were observed at close range during artificial feeding at Lake Hyoko. Individual swans were recognized by bill pattern, and family groups by already identified individuals. Trends in hierarchy among family groups could thus be recorded; reversals in dominance were, however, often noted.

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SOCIAL BEHAVIOUR OF WINTERING *CYGNUS COLUMBIANUS BEWICKII*

D K SCOTT

Introduction

Among birds, continued association between parents and their fledged offspring is most typical of co-operatively breeding species, where offspring remain on their natal territory or in a group home range throughout the year (eg Zahavi 1976). However, such relationships also occur in some species that do not breed co-operatively, among waterfowl *Dendrocygnini, Anserinae* and some *Tadornini* (Kear 1970).

In many co-operative breeders, the advantages of extended parent–offspring relationships may lie in the assistance by older offspring in caring for younger offspring. This may increase the inclusive fitness of both parents and offspring: in several species the productivity of groups with 'helpers' is higher than that of a pair alone. In cases where this has not been demonstrated, it has been suggested that 'helpers' provide valuable assistance in defence of the group territory.

With the exception of the seabirds which continue to feed their young during the first winter, the advantages of extended parent—offspring relationships in birds that do not breed co-operatively are not obvious, since these species do not usually defend a territory all year nor do the parents continue to feed or brood the young. It has been suggested that in migratory swans and geese, parents are guiding their young to traditional wintering areas (Ogilvie *in* Scott *et al* 1972). However, this does not explain why migratory ducks do not maintain family bonds nor why parents and offspring continue to associate after fledging in some sedentary species (eg *Cygnus olor, Cygnus atratus).* It has also been suggested that parents are protecting their offspring from predation by keeping watch while the offspring feed (Owen 1972) but this again fails to account for species differences in parent—offspring relationships. Another suggestion, that parents may be protecting their offspring from feeding competition, has arisen from the work of Boyd (1953) and Raveling (1970) who showed that goslings were less successful in aggressive encounters when separated from their parents.

The present paper reviews the results of a detailed study of the behaviour of wintering *Cygnus columbianus bewickii* in the UK (D Scott 1978a), in which the advantages and disadvantages to different individuals of maintaining close proximity to family members were investigated, to determine whether protection from feeding competition was important. The pair bond was also examined to discover if there were any similar advantages to mates of maintaining proximity.

First, however, it was necessary to investigate whether success in competition affected access to food, subsequent survival or reproductive success. Although individual differences in competitive ability or dominance have been demonstrated in flocking birds, eg *Tadorna tadorna* (Patterson 1977), few studies have investigated the relationship between age or presence of associates on dominance or the effect of dominance on access to resources or survival. However, a number of studies have concluded, following Lack (1954), that access to food in winter may be important in regulating population density in birds.

A good opportunity to investigate competition and the advantages of being a member of a group or unit is provided by *C. c. bewickii.* Individuals vary in the pattern of black and yellow on the bill and can be recognized without the necessity for marking (P Scott 1966). Families (mated pairs with their cygnets), pairs without offspring, and single individuals are easily visible as units within winter flocks. Age differences are apparent up to 2½ years and the sexes are distinguishable with 89% accuracy (D Scott 1978a). Finally, a large proportion of individuals return to the same wintering grounds in successive years, including the Welney Wildfowl Refuge, Norfolk, and the Wildfowl Trust, Slimbridge, where there is access for observation at close range (Evans 1978; D Scott 1978a).

Study site

The study was carried out between 1974 and 1976 at the Welney Wildfowl Refuge, Norfolk, on the Ouse Washes, where 200 to 300 swans regularly came for the grain provided at 0930, 1530 and sometimes 1900 hours. Over 1000 were sometimes present during cold weather. Observations were made both from the main hide on the Refuge and on surrounding fenland where the birds often fed during the middle of the day on agricultural crops (winter wheat, sugar beet and waste potatoes). Fen flocks also contained many individuals that were unfamiliar with the grain provided in front of the hide, spending the whole day feeding on crops. Some additional observations were made on flooded meadows in the vicinity (at Swavesey and Earith) where small flocks stayed for short periods.

Observations were made from October when the first swans arrived through to March or April when the last swans left on migration for the Soviet Arctic. Additional observations were made at the Wildfowl Trust, Slimbridge in Gloucestershire, where *C. c. bewickii* has been studied in detail since 1964 (Evans 1978, 1979). Data collected at Slimbridge on weights were also used.

Methods

Methods of recognizing individuals by differences in bill pattern and of recording and filing patterns have been described in detail elsewhere (Rees 1981). In the study described here, 583 different individuals were identified and all regular visitors to the lagoon in front of the hide (200 to 300 individuals) could be identified instantly from memory (see Bateson 1977).

Individuals were also classified according to age, sex, size and paired status. While adult swans are completely white, cygnets (first winter birds) can be distinguished by their grey plumage. Second winter birds can be identified by traces of grey feathering on the head and neck. Beyond this it is not possible to age unknown birds. However, in this study, third winter birds could be identified as those which had been present the previous winter as second winter birds.

Sex was estimated from size, since adult males are 13% heavier than females (Evans and Kear 1978). Evidence from 150 birds at Slimbridge sexed by estimation of size and subsequently caught and sexed cloacally showed that sex had been estimated with 89% accuracy. For paired birds (n = 100) the accuracy was somewhat higher (95%) than for single individuals (n = 50, 78%). The sex of cygnets was probably estimated with lower accuracy, since male cygnets average only 10% heavier than females (Evans and Kear 1978). Of 14 cygnets at Slimbridge whose sex was confirmed cloacally, ten had been correctly sexed by estimation. In this study, nine of the 19 cygnets studied in detail have returned in subsequent years and their sexes confirmed in relation to temporary or permanent mates.

The three main units within the flock, families, pairs and single individuals, were rapidly apparent. White birds associating with pairs were, in all but one case, offspring of previous years associating with their parents. While being obvious on account of the resemblance of parents and offspring, which has now been demonstrated statistically (Bateson *et al* 1980), this has been confirmed at Slimbridge where birds ringed as cygnets have been observed at the ages of two, three and four (and occasionally older) associating with their parents (Evans 1978).

Individuals were also classified as large, medium or small. The accuracy of size estimates was checked by examining the weights of birds caught at Slimbridge whose size had been estimated previously.

Data were collected in three ways:

(a) Systematic observations of particular 'focal' individuals were made during the hour-long periods in which birds loafed in front of the hide awaiting feeds. It was necessary to sample each bird for a short time in a rota, in order to obtain data on different individuals in similar situations. In the sampling rota five individuals were watched, each for one minute every ten minutes. In each hour-long session, focal individuals were of one class (ie all male parents, all female parents, etc) and the class was rotated. Most focal individuals were observed in at least five sessions (ie usually 25 minutes) throughout the winter.

During each sample minute, all signals and interactions were recorded, as well as the identity of the interactant and whether associated birds were present. At the end of each minute, point samples of the following were taken: distance to mate, cygnets or parents, distance and identity of three unrelated nearest neighbours and general activity (feeding, alert, preening, sleeping). Distances were recorded in swan lengths (sl): 1 swan length = 0.67 m.

(b) Flock scan samples of one hour were made after the morning feed from 1030 to 1130 in front of the hide and on the fens on alternate days. During these samples, all instances of aggressive encounters involving display were recorded, including details of their duration and intensity, and the identities of all participants.

(c) In front of the hide, data were also collected on an *ad lib* basis. Aggressive encounters involving display and their outcomes were recorded whenever possible in order to investigate dominance.

Three measures of individual differences in competitive ability or dominance were used: (a) who beat whom; (b) proportion of different opponents (individuals or units) beaten of all encountered; (c) proportion of encounters won. (This measure was considered less satisfactory than (a) and (b) because some individuals and units scored extreme values after interacting with the same opponents several times; it was used only where data were otherwise scanty).

Results are given in detail (with statistics) elsewhere (see D Scott 1978a, 1980a and 1980b), as are details of the analyses involved.

Results

Partners of pairs and family members were together in 90% to 95% of aggressive encounters. For this reason, the dominance relationships of units (families, pairs and single individuals) are considered first. Differences in dominance of individuals within units are investigated afterwards.

Dominance relationships between units within the flock

Both in 1974/75 and 1975/76 it was possible to rank units according to who beat whom so that the top-ranking ones differed greatly in success from the bottom-ranking ones. However, it was not possible to arrange units in a strictly linear hierarchy since circular relationships (ie relationship going up the hierarchy) occurred, but at most in 10% of cases.

Despite circularities, dominance relationships were relatively constant throughout the winter. The mean percentage of a unit's relationships which changed (usually once but very occasionally twice) during a winter was only 4.6 in 1974/75 and 7.1 in 1975/76.

Between years, dominance relationships were again remarkably constant. 81.8% of the dominance relationships of six units were in the same direction in both 1974/75 and 1975/76.

Dominance relationships were also stable in different situations. Observations of known individuals on the fens showed that their success in encounters when feeding on crops was closely related to the proportion of opponents they beat in front of the hide.

Dominance relationships between classes within the flock

The most obvious differences in competitive ability within the flock were between different kinds of unit. As in geese (Boyd 1953; Raveling 1970), families generally dominated pairs without offspring, which dominated single individuals. Thus, in front of the hide at Welney and at Slimbridge, the proportion of encounters in which families beat pairs and pairs beat singles was higher than vice versa. However, in contrast to geese, there was no significant tendency for large families to dominate smaller ones. Furthermore, there were many exceptions to the rule that parents beat pairs which beat singles.

In front of the hide, it became apparent that 'anomalous' relationships in which a particular pair dominated a particular family, or a single individual dominated a pair, could be stable throughout the winter. In 1974/75, two of 14 'anomalous'

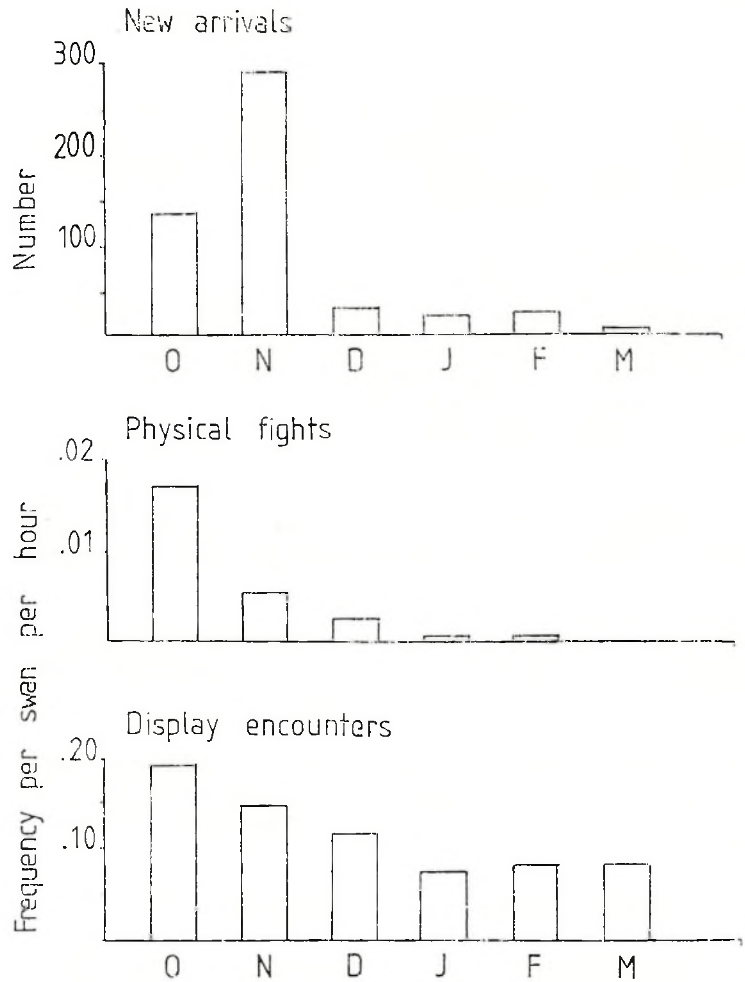

Fig 1. Decline over the winter in the number of newly arrived birds, physical fights and aggressive encounters involving display.

relationships where pairs dominated parents changed during the winter and in 1975/76, 12 of 28 such relationships changed.

Establishment of dominance relationships

When most birds arrived, in October and November, frequencies of display encounters and physical fights were high and subsequently declined during the winter

(Fig 1), except for a small peak in February, corresponding to a small influx of swans apparently passing through on northward migration. It seems likely that the early high frequency is associated with new arrivals for two reasons. First, on landing, 75% of units became involved in aggressive encounters within the first five minutes. Second, units were observed in more encounters on their first day than on subsequent days.

That these encounters on arrival were associated with establishing dominance relationships is also suggested by the following evidence: firstly, the outcomes of encounters with particular opponents on the first day remained the same on subsequent days but they became less intense; secondly, units were involved in display encounters more often with particular opponents on their first day as well as with a greater total number of opponents than on later days.

Units appeared to establish relationships with many birds within the first day. One newly arrived pair with three cygnets interacted with a total of 40 different opponents within 2½ hours. For this family, the number of encounters in each half hour, their duration and intensity all decreased over this period, as did the duration and intensity of encounters with nine opponents encountered more than once.

Maintenance of dominance relationships

The reduced frequency of encounters raises the question of whether individuals are able to recognize each other. Among the swans, there are two observations which are difficult to explain if individuals did not recognize at least some other birds within the flock. First, individuals returning after short absences did not show higher frequencies of encounter than on other days and showed lower frequencies than on their first day in the season (Table 1). Secondly, individuals of similar rank

Table 1. Mean number of encounters on different days.

On first day	6.18 ± 3.4	n = 22 individuals
On return day after absences of any length (mean length was 16 days, n = 75 absences)	0.72 ± 0.47	n = 36 returns
On return day after absences of <10 days	0.46 ± 0.78	n = 13 returns
On return day after absences of >10 days	0.87 ± 0.58	n = 23 returns
On all days except first	0.69 ± 0.15	n = 14 individuals

and similar paired or family status (with equal numbers of cygnets if present) should be less likely to be able to deduce each other's relative dominance from overall physical appearance than individuals dissimilar in these respects. However, individuals were sometimes observed avoiding similar opponents (established as dominant in a previous encounter) without any provocation.

Variables related to dominance

Size, weight and sex were all related to dominance. Large birds tended to dominate a higher proportion of opponents than small birds when the effects of age, sex, paired status and immediate context (presence/absence of associates) were taken into account. There were positive correlations between size and rank for five classes of birds. At Slimbridge 28 of 37 encounters were won by the heavier opponent. Males tended to be more dominant than females according to the proportion of opponents beaten during focal samples. It seems likely that the lower dominance of females is associated with their smaller size and lower weight than males.

Since winners tended to be heavier, it might be expected that age up to 2½ years (when adult weight is probably reached) might be associated with dominance, but there was little evidence that this was so.

Units arriving in October tended to be more dominant than those arriving in November or later. Dominant units also spent more days in the area than subordinate ones and spent a greater proportion of days between arrival and departure in front of the hide. However, it was not possible to determine whether it was the most dominant individuals in each class that arrived first or whether the individuals that arrived first became most dominant.

Observations on the fens indicated that dominant individuals spent more time feeding than subordinates. In addition, differences in dominance were correlated with differences in breeding success the following summer (as measured by the number of cygnets accompanying their parents in the subsequent winter). Moreover, birds that brought cygnets one year but not the next were lower in rank than average for parents in the year before they failed to bring cygnets.

Effects of proximity of associates

The competitive ability of most unit members appeared to decrease when they were separated from the remainder of the unit. On flooded meadows, cygnets won 75% of aggressive encounters when less than four swan lengths from their parents and only 33% of encounters when farther away. In front of the hide, six cygnets observed consistently during the winter 1975/76 dominated a smaller proportion of different opponents when away from their parents than when with them. In addition, offspring of previous years, associating with their parents, were less dominant when away from their parents than in the presence of their parents (Fig 2). Moreover, those arriving earlier in the season than their parents became more dominant once their parents had arrived. There were no apparent differences in effect of proximity of offspring to male or female parent.

Partners of pairs also suffered reduced competitive ability when separated. In front of the observatory, the success in encounters of focal female paired birds without

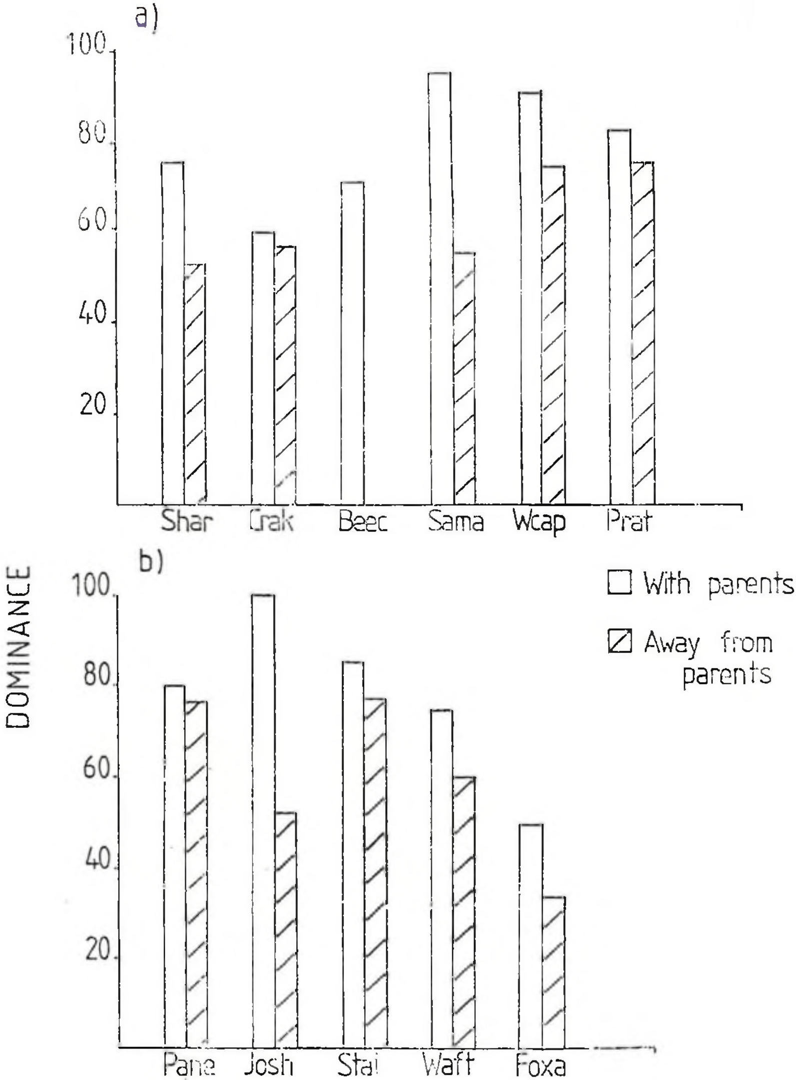

Fig 2. Dominance of second (a) and third (b) winter offspring with (< 4 sl) and away (> 4 sl) from parents.

cygnets showed a significant negative correlation with distance from mate (Fig 3), and the same was true for focal male paired birds. However, there was no evidence that parents suffered decreased ability in the absence of their cygnets.

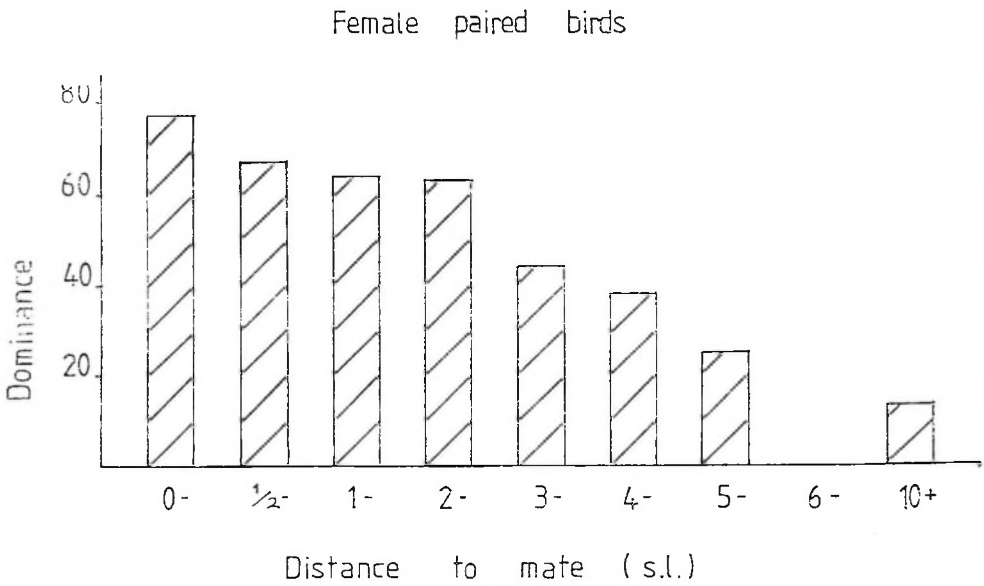

Fig 3. Relationship between dominance and distance to mate for female paired birds.

Proximity to other unit members was also related to the amount of time individuals spent feeding. On flooded meadows, cygnets spent only 52.1% of the time feeding when away from their parents ($>$4 sl) and 81.5% when close to them, and there was a significant negative correlation between time spent feeding and distance to parents. Female paired birds on the fens spent only 61.4% of the time feeding when away from their mates ($>$4 sl) and 80% when with them, again a significant difference. For male paired birds on the fens, this tendency was still apparent: they spent 56% of time feeding when away and 75% when with their mates, but the difference was not quite significant.

Assistance in aggressive encounters

Parents frequently intervened in encounters on behalf of their cygnets when the latter were being threatened by other birds. Such interventions occurred in 34% of all cygnet encounters with others on flooded meadows. The presence of the parents appeared to inhibit other individuals from threatening cygnets. All six focal cygnets were threatened by others more often when away from their parents than when with them. In addition, subordinate individuals usually moved out of the way of family units, often without any visible signs of aggression from the latter. As a result of this inhibitory effect, cygnets in their parents' presence essentially assumed their parents' rank.

In similar ways, partners of pairs assisted each other in encounters. 'Supported' encounters comprised 25.8% of those in which female paired birds were involved and 22.5% of those in which male paired birds were involved. The influence of an inhibitory effect was also apparent in the increased frequency with which partners were threatened when away from their mates. This was more marked for female than for male paired birds: females were threatened four times more often when away from their mates, while males were threatened only twice as often.

Both partners of pairs and members of family units were particularly close to each other during the display encounters which always preceded fights. It is possible that the assistance of the female in these displays (and perhaps the presence of cygnets) reinforced the displays of the male.

However, since dominance relationships depended ultimately on ability to win physical combat, and, since females almost never joined in such fights, it is not clear why the presence of the female enhanced the competitive ability of the male, unless he was more willing to fight when his mate was present than when she was absent.

Variation in proximity

Unit members should maintain greater proximity in dense flocks than in dispersed flocks. In addition, members should be closer when feeding on foods over which competitive interactions are frequent than where interactions are infrequent. Since interactions among swans were more frequent during feeding in front of the hide than on the fens, and on waste potato crops than on winter wheat, unit members should be closer in the former of each of these comparisons than in the latter. Finally, since competitive ability was related to body size, weight and sex, small individuals and females should maintain greater proximity to family members than large individuals or males. These predictions were largely upheld.

There were two results which failed to support the predictions. During the feed in front of the hide, when density was exceptionally high, partners of pairs, and family members were separated for most of the time and reunited afterwards. Partners of pairs also maintained greater distances to each other relative to the distances to other flock neighbours when feeding on waste potatoes than on winter wheat.

Proximity of unit members also varied in a number of other ways. Among families, proximity decreased with the age of the offspring: parent—cygnet proximity decreased over the winter and relationships between parents and previous years' offspring were usually loose. Average distances between third winter offspring and parents were greater than between second winter offspring and parents. In contrast to the peaceful relationship between cygnets and parents, the latter frequently threatened their offspring in later years.

Parent–cygnet proximity was greater among subordinate families than among dominant families. Despite this relationship, the cygnets of dominant parents tended to be more successful in encounters both alone and with their parents than those of subordinate parents.

In contrast to the greater proximity of members of subordinate families, partners of pairs in which the male by himself was high-ranking tended to maintain greater proximity than those where the male was low-ranking. Pairs in which both partners were either very large or very small tended to spend less time together than other pairs.

Proximity of partners was also greater when they had no accompanying offspring than when offspring were present. But since the offspring frequently positioned themselves between their parents, this is an unsurprising result. All unit members maintained greater proximity during roosting than during feeding.

Discussion

The advantages to individuals of maintaining proximity to other unit members were apparent in terms of increased competitive ability and time spent feeding by most individuals in the presence of family members compared with when separated from them. The evidence indicated that differences in competitive ability were important in affecting access to food and subsequent breeding success and that individuals differed in ability according to size, weight and sex. In accordance with this variation in dominance, female cygnets (ie small cygnets) tended to maintain greater proximity to their parents than male cygnets and, as adults, female paired birds benefited more from the proximity of their mates. Correspondingly, cygnets benefited more than their parents from maintaining proximity. In addition, parent–offspring proximity declined as offspring grew older and approached adult size. But since second winter birds are still significantly lighter than adults and third winter birds may also be below adult weight, these birds may continue to gain substantial protection by associating with their parents.

If competition for food occurs in other waterfowl species, these findings may provide an explanation for species differences in the extent of parental care in waterfowl. While evidence suggests that cygnets and goslings do not reach adult weight until they are more than one year old (Owen *et al* 1977; Evans and Kear 1978), immature ducks appear to reach adult weight in their first autumn (Owen and Cook 1977). If competitive ability is determined by relative body size in ducks, first winter individuals may not require parental protection in competition with conspecifics. The difference is essentially a function of body size, since large birds have slower growth rates (Ricklefs 1973) and therefore take longer to reach adult size. This argument is supported by the fact that prolonged parental care occurs in other large, slow-growing waterfowl (eg *Tadornini)* which form flocks in the non-breeding season.

There may be many other benefits associated with parental care, including guiding offspring to traditional wintering grounds or particular feeding sites, or protecting them from predation. However, by themselves these benefits do not account for the differences in parental care between waterfowl species.

The results also provide a possible explanation for the early formation of pair bonds in many duck species. If competition for food is significant and if males are able to protect females (Ashcroft 1976) or partners gain mutual assistance in aggressive encounters, early formation of pair bonds may be advantageous.

In *C. c. bewickii* the evidence also indicated that benefits of proximity could sometimes be counteracted by costs, with the result that unit members separated. This was apparent during the feed in front of the hide, when density was exceptionally high and unit members usually became separated. In this situation it seems likely that the costs of maintaining contact in the confusion of birds jostling for food outweighed any benefits of proximity. Costs of proximity may help to explain why unit members were closer during roosting than during feeding as in *Anser brachyrhynchus* (Lazarus and Inglis 1978) if competition occurs within as well as between units. Such costs could also account for the tendency of mates to be farther apart when feeding on potatoes, where competitive interactions were frequent, than on wheat, where they were infrequent. However, this raises the question of why parents and cygnets should be closer on potatoes than on wheat, unless parents spend more time protecting the cygnets than feeding themselves. This may indeed be the case, since parents spent less time feeding than did pairs without cygnets, especially during the first part of the winter.

Costs of proximity in terms of feeding interference between unit members may also explain variation in proximity of mates and family members in other species and in different situations. Evidence suggests that in some goose species and in some situations, mates and family members are usually each other's nearest neighbours while, in others, they may be at greater distances with other birds between them.

In *C. c. bewickii* the advantages of proximity were particularly great for the offspring of dominant families and females mated to dominant males. The first of these findings parallels the results of a number of studies of primate species, where offspring 'inherit' their mother's rank, giving the offspring of dominant mothers priority of access to resources. As yet it is not known whether the effect continues into adult life among swans as it does among primates. However, there is preliminary evidence that the cygnets of dominant families remained dominant among yearlings in the following winter, even when they were completely alone, ie before their parents had arrived. Long-term consequences of early differences between individuals are being discovered increasingly in other species and further study may reveal their extent in *C. c. bewickii.*

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Summary

Winter flocks of *Cygnus columbianus bewickii* comprise well-defined units: mated pairs with accompanying offspring, unaccompanied pairs and single individuals. Pairs and families feed, preen and sleep together, and are particularly close during aggressive interactions between units, especially those involving conspicuous display. This paper reviews the findings of a detailed study in UK which investigated the possibility that assistance in competition for food is an important advantage of staying close together.

Individuals differed substantially in competitive ability; in the presence of other unit members, most individuals were more dominant and spent more time feeding than when separated from them. Large, heavy birds and males tended to be more dominant, while small lighter birds and females suffered greater decreases in competitive ability when separated from other unit members. Since dominant individuals and units showed a tendency to spend more time feeding and to breed more successfully (as measured by the number of young returning the following winter) than subordinates, the advantages of assistance in competition may be considerable.

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SEASONAL VARIATION, SEX DIFFERENCES AND HABITUATION OF TERRITORIAL BEHAVIOUR IN *CYGNUS OLOR*

J DEMAREST

Introduction

Among Old World immigrants resident around Long Island Sound, none is more striking than *Cygnus olor.* In spring, sometimes upwards of 50 birds gather on the bays, inlets and estuaries. Some will leave their flock to find a pond or secluded cove to breed. Others may disperse to find an area uninhabited by mated swans. In the past few decades, however, this swan has undergone a population explosion and uninhabited areas have become uncommon. As a consequence *C. olor* has spread south to Maryland and New Jersey and north to Massachusetts and Rhode Island.

The reason for this success appears to be the swan's lack of competition with other species, its general aggressiveness and the fact that it is highly territorial. Territories vary in area from 0.2 to more than 4 ha and may be maintained for several seasons or longer (Scott 1972). Flocks of swans intruding on a territory are driven out, frequently by both members of the mated pair and territorial boundary disputes are not uncommon. Generally, threat behaviour is all that is necessary to drive out trespassers.

The threat behaviour has been described in general terms by Heinroth (1910) and Johnsgard (1965). The author has examined the graded nature of the threat display and the sequential order of behavioural postures leading up to and following an attack (Demarest 1980a, 1980b) and in this paper explores several parameters of territorial defence.

General method

The studies were carried out between 1973 and 1977 at sites in eastern New York on the north shore of Long Island in an area known as Setauket Harbour and in New Jersey at Wreck Pond on the Atlantic shore. Territories were defended by four mated pairs at the New York study site, only one mated pair at the New Jersey site. The territorial birds were named after the body of water they inhabited, ie Van Brunt's Cove, Harbour Cove, Little Bay North, Little Bay South and Wreck Pond. All areas were estuarine waters connected to a larger bay, in generally residential neighbourhoods. Each pair of the New York swans shared at least a portion of their territorial boundary with another pair. However, these birds rarely crossed into another's precinct. Trespassers were almost always unfamiliar birds.

The behaviour of the swans was collected by direct observation, recording the observations on protocols with a concurrent time base. Some sessions were recorded on videotape. Models were used to simulate territorial intruders since actual confrontation was infrequent and was typically brief with a quick retreat by the intruder. The models had the added advantage that they could be presented systematically for fixed periods, at specific locations and their 'behaviour' was consistent. The models were white polyethylene imitations of swans, 57 cm in length and 20 cm in diameter. The wings and neck were shaped into a Busk posture (see Fig 1B) and each model was weighted with 7 kg of sand to achieve stability and a natural waterline.

Seasonal variation in the threat display

The threat display of *C. olor* is a graded series of wing and neck postures indicative of different intensities of threat (Demarest 1980a). Five of these postures are

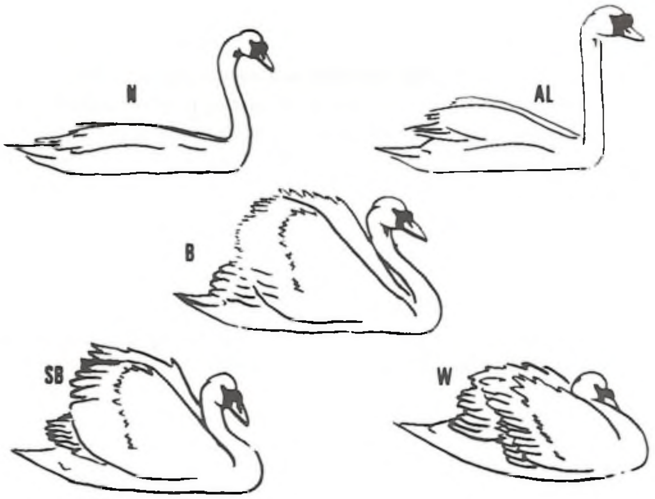

Fig 1. A graded series of postures used to signify increasing intensity of threat in *Cygnus olor.*

(N) Normal posture, (AL) Alert threat, (B) Busk, (SB) Strong Busk and (W) Wedge posture.

shown in Fig 1. The least threatening Normal posture (N) is in the upper left-hand portion of the diagram and the most intense threat, the Wedge (W), is in the lower right-hand corner. Alert threat (AL), Busk (B) and Strong Busk (SB) are intermediate intensity threats. A more intense display, not shown here, is the Zig-Zag Dance (ZZ), most often observed during boundary disputes between territorial males. In general, the most frequent threat display performed is the Busk, and it is usually sufficient to drive away territorial intruders at any time.

Method

In order to assess seasonal variations in the strength of territorial defence, the model was presented to each mated pair in the New York population (N = 4) once a month from March 1973 to March 1974. The model was always anchored 2 m from the shoreline approximately 100 m from the swans. During the incubation period the model was placed 100 m from the nest. Each test lasted ten minutes and every 30 seconds the type of display posture and the distance between each swan and the model was recorded. Since spatial distance between defender and intruder is inversely related to the intensity of the threat display (Demarest 1980a), only threat display data are considered here.

Results and discussion

The number of 30-second intervals in which either the male or female performed a Busk threat or more intense threat display was tabulated for each pair. These data were combined over two-month periods and averaged across pairs of birds. Fig 2 shows the mean amount of time threatening the model during each of the six two-month seasons of the year. Threats were most often observed from March to June, the period of nest building and incubation. The frequency of display dropped off in July and August but increased again in late autumn. The lowest incidence of threat display was found from November to February. In fact, almost all of the displays elicited in the first two months of the year were from the February test and coincided with the first appearance of threat behaviour by first-year juveniles in some of the families. This seasonal onset of display in the young suggests very strongly that the threat display is at least partly under endocrine control.

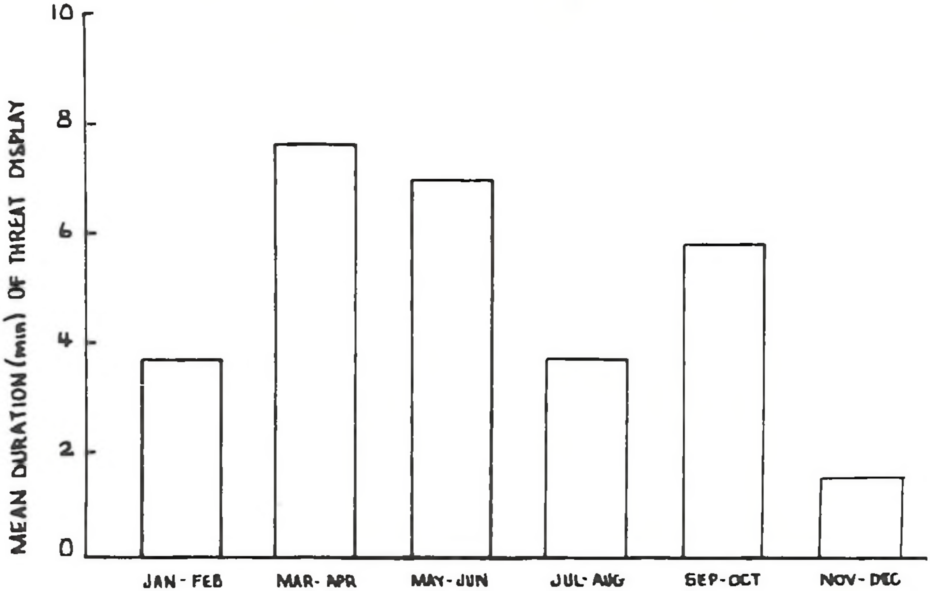

Fig 2. Seasonal variation in the mean duration of the threat display (ie B, SB, W or ZZ) directed to the model.

Independent of the tests with the model, records were kept of the number of intruders observed in each territory each month. These records were not entirely systematic; they were made haphazardly at semi-random times of the day, typically two or three times a week from 1973 to 1974, and emigrant swans most often invaded only two of the four territories studied. The total number of swans observed in all the territories in two-month periods was tabulated and averaged over the number of observations made during each period. This gave the mean

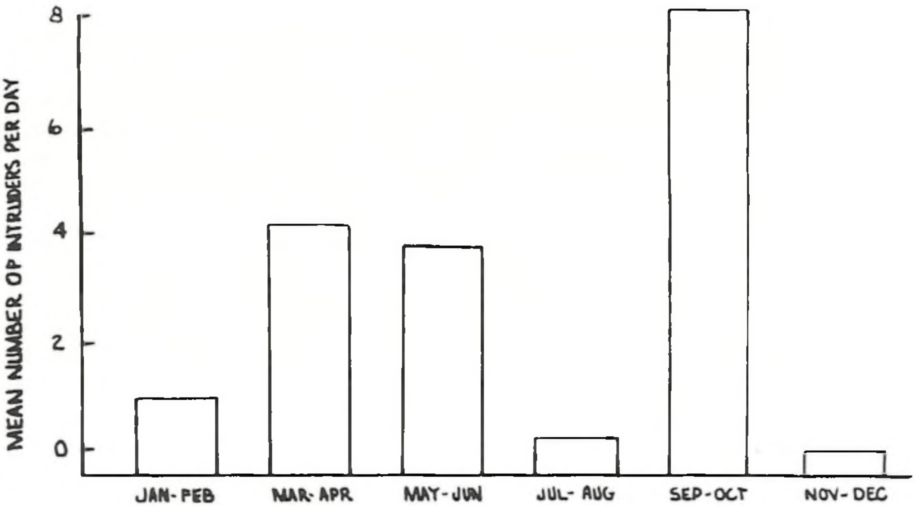

Fig 3. Seasonal variation in the mean number of alien *Cygnus olor* entering the Setauket Harbour area each day.

number of swans in Setauket Harbour each day. Subtracting the number of swans that had territories gives the mean number of intruders a territorial *C. olor* could expect to confront on a given day (Fig 3). The figures undoubtedly underestimate the actual numbers since small groups of three or fewer intruders were typically expelled from an area in ten to 20 minutes, and observation periods were sometimes no more than spot checks lasting from five minutes to half an hour. Despite the deficiencies of the procedure, the results provide an interesting backdrop for the seasonal variation in threat display. Territorial trespassing appeared to peak in early spring and again in late autumn, the periods when the probability of threat display is highest. Interestingly, intrusion was rare during July and August when incubation came to an end and the young cygnets began to hatch and leave the nest. It may be that the original flocks of birds observed in March and April secure a territory or temporary feeding ground for the next few months.

Territorial defence by the male was most evident during the May to June incubation period. This behaviour is undoubtedly under strong selection pressure since a safe and ready access to food and feeding sites would appear necessary to sustain the female who remained on the nest most of the day, occasionally leaving to feed for short intervals only.

Sexual diethism in the threat display

Because of the essential differences between the sexes in parental investment (Trivers 1972), polygamy and promiscuity would seem to be the mating systems most preferred by males. Among birds, however, monogamy is the most common system (Lack 1968) and swans, in particular, are believed to mate for life (Johnsgard 1965). Monogamy usually correlates with near equality in parental investment by both mates and is expected when successful reproduction requires the co-operation of two committed adults (Barash 1977; Orians 1969). In the white swans of the Old and New Worlds the males do not seem to take part in incubation but they may now and then stand over the eggs to guard them (Heinroth and Heinroth 1958; Scott 1972). The male and female do co-operate in nest building, however, and both animals may defend the territory against intruders, especially early in the spring (Boase 1959; Heinroth 1910; Huxley 1947). Threat displays in male and female *C. olor,* however, appear to differ in intensity and the male appears to take the greater risks. This was examined in a series of experiments on model-elicited territorial aggression.

Methods and results

Preincubation test: Model tests were administered prior to incubation in three pairs from the New York population in 1974 and one pair from New Jersey in 1977. All tests were initiated in March. The model was presented once a day for seven days, two hours after high tide at a point 2 m from the shoreline and 100 m from the swans. Each test session lasted 10.5 minutes and every 30 seconds the type of display posture and distance between the swan and the model was recorded. Each bird's behaviour was therefore recorded a total of 147 times. The analysis included the behaviour of both the male and the female.

The total number of recorded threat postures were grouped into four categories representing different intensities of threat display. The complete absence of any display was Level 1. Level 2 included Alert-threat and Busk displays, Level 3 the Strong Busk and Wedge postures, and Level 4 incorporated all episodes of Zig-Zag Dance and Attack. Totals for male and female are shown in Table 1. Males performed the most intense displays more often than any other display, while females failed to threaten almost half the time. Females, in fact, never performed a Zig-Zag Dance and never attacked the model. A Chi-square test performed on the group totals indicated that the sexual diethism is highly significant (X^2 (3) = 317.5, $p < 0.001$).

In addition to intensity of the threat display, the spatial relationship of male and female swans with respect to a territorial intruder appears to differ. Mean distance for the male swans and for the female swans as a function of time from the introduction of the model into the territory is averaged in Fig 4. A repeated measures analysis of variance performed on these data indicated that the birds approached the model more closely as time progressed (F (11, 146) = 63.6, $p < 0.001$), and that the rate of approach for a male was more rapid than for a female (F (11, 146) = 3.57, $p < 0.001$). No female ever got as close as its mate but the females from two territories (Little Bay North and Van Brunt's Cove) each

Table 1. Sexual diethism in the frequency of different intensities of threat display elicited by a model.

		Intensity of threat display			
	Territory	Level 1	Level 2	Level 3	Level 4
Male	Van Brunt's Cove	29	26	49	43
	Harbour Cove	43	38	27	39
	Little Bay North	3	44	33	67
	Wreck Pond	11	30	70	36
	Total	86	138	179	185
Female	Van Brunt's Cove	76	49	22	0
	Harbour Cove	97	41	9	0
	Little Bay North	45	64	38	0
	Wreck Pond	69	36	42	0
	Total	287	190	111	0

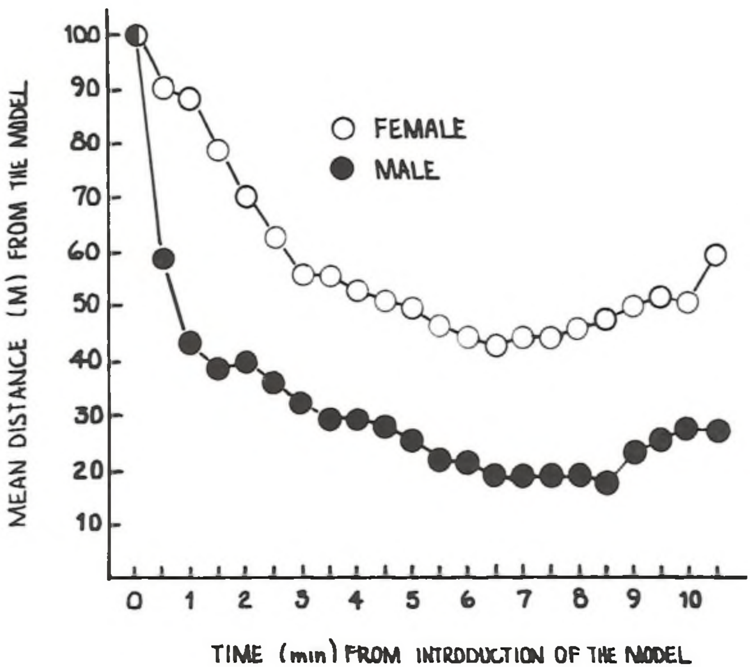

Fig 4. Gender differences in the mean distance between a territorial swan and the model, computed at 30-second intervals from the time the model was placed in a territory.

approached the model more closely than did the males from Harbour Cove and Wreck Pond.

Incubation test: Model tests were resumed seven days after the first egg was found in the nest and were continued every day for 20 days. During incubation the female generally ceased responding to the model. Only three pairs of swans produced successful nests and of these only two continued to respond to the model. The Harbour Cove male failed to react after the fifth day of testing and the experiment was terminated for this bird after five more days.

The testing procedure during the incubation period was the same as in the previous section except that the model was always placed in the same location in the territory, 100 m from the nest. Records were made of the behaviour and distance from the model of each member of a territorial pair. On each trial the observer indicated whether the animal spent most of the test interval on the nest, threatening the model, or engaged in some other activity (eg feeding, preening). If an animal did more than one of these, the activity that was performed most often was counted. Although each trial lasted 10.5 minutes, it was unusual for an animal to change its behavioural response.

The total number of trials on which the animal was scored as threatening, incubating or engaged in some other behaviour is shown in Table 2. Males spent

Table 2. Sex differences in the activities typically performed during the incubation period.

		Activity engaged in					
		Sitting on the nest		Threatening the model		Other	
	Territory	N	%	N	%	N	%
Male	Little Bay North	3	15	17	85	0	0
	Wreck Pond	1	5	19	95	0	0
	Harbour Cove	1	5	4	40	5	50
	Total	5	10%	40	80%	5	10%
Female	Little Bay North	15	85	3	15	2	10
	Wreck Pond	14	70	0	0	6	30
	Harbour Cove	7	70	0	0	3	30
	Total	36	72%	3	6%	11	22%

little time on the nest and most of the time threatening the model. Females spent almost all their time either on the nest or preening nearby. Occasionally the female would threaten the model but, except for one trial, this was always performed as the bird was swimming to feed near the test area. As has been reported previously (Boase 1959; Heinroth 1910; Huxley 1947) males never actually incubated the eggs, rather they stood on the side wall of the nest, usually engaged in preening.

One pair attempted several nests during this season, none of which was successful. The first nest was poorly constructed and completely washed away after 17 days. One egg had been laid but had not been incubated until day 12. On day 20 the pair began building a new nest which was again destroyed by the tide. Over a 25-day period the male threatened the model on 21 sessions and the female displayed on 19 of these sessions. Two of the days on which they ignored the model were times when both birds were engaged in nest building. The female remained on the nest during four of the sessions. Differences in defence motivation between the male and female of this pair are thus not as dramatic as in incubating birds. Indeed, the first two times the model was introduced into the territory both birds threatened and, upon its removal, performed the Triumph Ceremony (Johnsgard 1965). Furthermore, the female in this pair was as likely to threaten the model (76%) as were the males from the nesting pairs of swans (80%). Thus there does not appear to be a significant gender difference in the motivation to defend the territory in non-incubating birds. The male did, however, continue to threaten at a closer distance to the model.

Post-incubation test: After hatching, the tests with the model were resumed for seven days. Two males stopped displaying altogether and stayed with the female and cygnets as they moved from one place to another in the territory. The third male, from Little Bay, did not respond to the model on the first two days after hatching and responded somewhat unevenly over the next five test days (Table 3).

Table 3. Sex differences in the activities typically performed after the young have hatched.

	Sex of the parent			
	Male		Female	
Activity engaged in	N	%	N	%
With the cygnets	11	52	21	100
Threatening the model	4	19	0	0
Other activity	6	29	0	0
Total	21	100	21	100

Territorial defence by the male dropped from 80% of its activities during incubation to 19% after hatching. Male hostility in several species of *Anatidae* has been shown to wane with the hatching of the young (Lorenz 1959; McKinney 1970) and subsequent studies on different territorial pairs of *C. olor* verified the reduction and almost complete lack of response to the model upon hatching of the young and their exodus from the nest.

The female, on the other hand, spent all of her time with the cygnets. This close bond continued throughout the summer and winter months. Indeed, juveniles were still following their mother at eight months of age. The male, in each case, was close to the family group but usually remained spatially distinct and never actually initiated group movement from one place to another.

Discussion

Wilson (1975) has argued that monogamy may serve to facilitate defence of a scarce and valuable resource. This hypothesis is certainly compatible with the *C. olor* situation since the population explosion in the northeast United States has placed a premium on satisfactory nesting habitats. However, while both the male and female engage in territorial behaviour prior to the onset of incubation, after incubation this activity is predominantly the role of the male. Johnsgard (1962) and Kear (1970) have discussed evolutionary trends in waterfowl breeding systems and they suggest that differences in defence motivation favouring the male and/or differences in incubation drive favouring the female could result in gender differences such as those observed in this study. These motivational differences are very probably under the control of a complex interaction between stimulus conditions and endocrine state (Silver 1977; Stokes 1974) and can probably be better understood as threshold differences (Hinde 1966; McKinney 1961). Abundant evidence shows that, in vertebrates, increases in aggression parallel the growth of the testes, are eliminated by castration and can be induced by injections of male gonadal hormone (Beach 1948; Collias 1950; Guhl 1961). Androgens, for example, lower the threshold for aggression in many species. Often this lowered threshold is accompanied by an increase in the distance at which the eliciting stimuli are effective and a tendency for aggressiveness to become linked with environmental references such as a territory. The implication for swans is that females shift from territorial behaviour to nest building and incubation to care of the young with changes in hormonal and contextual stimulation, and in the same sense, males shift from territorial defence to defence of the nest to a strategy of defending the young. Furthermore, defence of the young may shift back to territorial behaviour when environmental and endocrine states are suitably altered. In two consecutive years males with young began to threaten their offspring for the first time at approximately eight months of age, in January and February. In each case the threats resulted in the emigration of the young from the territory several weeks later. Changes in length of day, in the size or plumage colour of the juveniles and possibly other characteristics (Norman 1978) may have influenced this behaviour.

We might also consider these gender differences in terms of current evolutionary theory. Triver's (1972) treatment of parental investment implies that the sexual diethism of swans must be constrained to the extent that monogamous couples should have an equal investment in rearing their young. In the tests described here, both sexes participate in territorial behaviour prior to nesting. When nesting starts, roles begin to differ. Nest building is shared equally but incubation is primarily a female activity. Defence is primarily a male activity. From Table 2 we can determine that males are responsible for about 93% of all territorial defence and only 12% of the incubation activities. Females, on the other hand, are responsible for 88% of the incubation activities and only 7% of the territorial defence. The mean investment for males in these two activities is approximately 53%, while female parental investment is slightly less, 47%.

The female, however, has the greatest energy investment in egg production (Daly and Wilson 1978; Williams 1975). In *C. olor* the average egg weight is 300 g and the average clutch size is six eggs (Scott 1972). Each season a female produces gametes weighing approximately 1800 g, almost 20% of her body weight. Males, however, invest virtually none of their energy resources in egg production. Females also appear to assume most of the rearing activities. Cygnets selectively follow the female and are frequently seen riding on her back. The close mother–infant relationship usually lasts eight or nine months. This asymmetry of parental behaviour is unexpected in a monogamous species, especially one with a prolonged period of infant dependence (Wilson 1975) and may be difficult to reconcile with our expectation of equal investment by the parents. On the other hand, it may be a contributing factor to the evolution of sexual diethism in territorial defence with greater risk to the male during non-reproductive periods of the year.

Habituation of the threat display

Several workers have suggested that habituation is the most fundamental form of adjustment to environmental change available to an organism (Thompson *et al* 1973). It is thought to be the simplest type of learning and a process which is similar in all animals (Thorpe 1963; Wyers *et al* 1973). Studies of habituation in a natural setting indicate that the process is important to adaptation (Petrinovich 1973) and that it probably accounts in part for a number of significant social phenomena (eg the 'dear enemy' phenomenon, Wilson 1975; sexual satiation, Marler and Hamilton 1966; the establishment and maintenance of territories in birds, Falls 1969).

Animals confronted by stimuli and situations which neither facilitate survival and reproduction nor interfere with these processes eventually come to neglect these features. Rouse (1905), for example, reported that pigeons, exposed to what he referred to as 'significant' sounds, continued to attend to these stimuli while habituating to 'meaningless' sounds. Thompson (1969) also demonstrated that male buntings *Passerina* exhibited continued territorial response in the field to playback of their own species song in contrast to song playback of two other species of bunting. Furthermore, stuffed dummies elicited virtually no reaction from territorial birds, whose attention was given to threatening the loudspeaker.

Auditory stimulation does not appear to be an important feature of *C. olor* territorial behaviour (Demarest 1980a). One might expect that reactivity to visual cues in this species is more 'significant' and that these responses ought to be resistant to habituation. However, even species-meaningful stimuli eventually cease to elicit selected responses with repeated presentation (Petrinovich 1973; Petrinovich and Patterson 1979). The September to October 1973 increase in territorial intruders (see Fig 3) was concentrated at the eastern sector of Setauket Harbour, adjacent to Van Brunt's Cove. Over a period of three to four weeks a flock of 12 to 16 birds gradually worked their way into the cove to feed and preen. Initially the mated pair inhabiting the cove threatened and chased any swan that broached the territorial boundary. By mid-October, however, the mated swans were feeding side by side with these trespassers and few threats were seen. It would appear then that habituation of territorial behaviour is possible under natural conditions and that it could play a role in determining which swans will mate and find a place to live.

Method

In order to determine the course of behavioural habituation to territorial encroachment, the males' data from the incubation phase of the 1974 model tests were examined over successive daily presentations. Omitted, however, were the data from the Harbour Cove male, which habituated unusually fast, failing to respond to the model after day 5.

Each bird was administered 20 test trials with the model placed in the water 100 m from the nest. On day 21 a dishabituation test was given in which the model was placed 20 m from the nest. This was followed by three more trials with the model located 100 m from the nest. Testing was discontinued for six days and on day 31 a test for spontaneous recovery was administered. The type of display and distance between the test bird and the model was recorded at 30-second intervals, for ten minutes, at which point the model was removed from the territory. Observations were continued at one-minute intervals for ten minutes after removal of the model.

Results

The first measure, intensity of threat, was found by first grouping each of the 20 daily recorded threat postures of an animal into one of the four levels (see page 215). A daily threat intensity score was calculated by multiplying the frequency of responses in each level by the number value assigned (ie 1 to 4). The daily threat intensity score could thus vary from a low of 20 (ie 20 observations of Level 1 response) to a high of 80. These scores were then divided by 20 to yield the mean daily threat display of each swan and group averages were computed from the products. These data are shown in Fig 5A for each of the 20 days of testing, the dishabituation test on day 21, the following three rehabituation days (ie days 22 to 24) and the spontaneous recovery test on day 31. A repeated measures analysis of

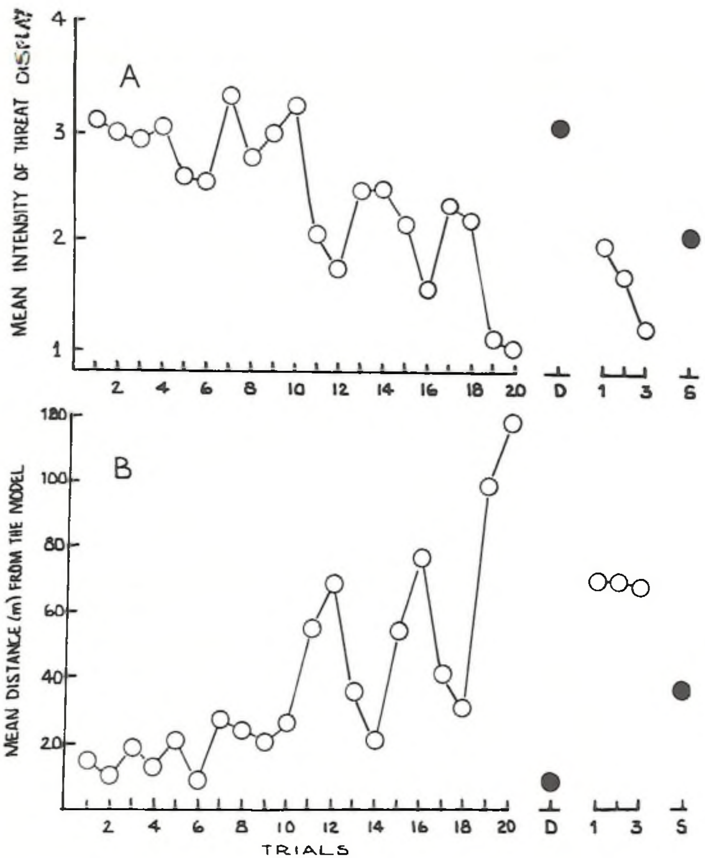

Fig 5. Habituation, dishabituation (D), rehabituation and spontaneous recovery (S) of the *Cygnus olor* threat behaviour over a 31-day period.

The mean intensity of threat display is shown in A and the mean distance between a territorial swan and the model is shown in B. The model was moved to a new location in the territory on the dishabituation trial and spontaneous recovery was assessed after a six-day rest.

variance computed on the first 20 days yielded a significant habituation effect (F (19, 38) = 6.84, $p < 0.001$). At the end of 20 days the swans were no longer reacting to the model. On the dishabituation test, with the model placed only 20 m from the nest, all three birds resumed their threat display activities. In fact, the reactions were as intense as the first day of testing. The male from the Little Bay territory responded even more aggressively on this test than during most days of the habituation test. When the model was reintroduced for three days at the original test site, 100 m from the nest, the threat behaviour rapidly diminished in intensity. On the last test, seven days later, however, all three swans exhibited partial recovery of threat activity. The typical intensity of display was only about half as great as during the initial days of testing or during the dishabituation test, but there was no overlap in the range of scores on the spontaneous recovery test when compared with either the last two days of original habituation or the last day of rehabituation.

The distance measure shown in Fig 5B represents the group average distance between the swan and the model on each day of testing. These data were found by computing mean daily distance scores for each swan from the 20 observation intervals and averaging these individual means together. The resultant figures are somewhat misleading because a test always began with the territorial swan approximately 100 m from the test area and individual scores therefore partly reflect the speed at which each bird approached the model. Much of the variability in the individual scores, in fact, was found in the behaviour from the initial five minutes. Despite this, the data show that swans failed to react and approach the model as testing continued. On the last two days no response occurred at all and only token approach responses occurred on several other days (eg days 11, 12, 15 and 16). A repeated measures analysis of variance performed on these data yielded a highly significant habituation effect ($F (19, 38) = 6.09$, p 0.001). On the dishabituation test, all animals approached the model closely; in fact, two of the three birds spent most of this test performing the Zig-Zag Dance within 1 m of the model. The mean distance scores from days 22 to 24, on the other hand, do not provide clear evidence of a decrement in approach behaviour as might be expected of rehabituation. However, the variability in these data mask one otherwise consistent finding. Two of the three birds consistently remained over 80 m from the model, while the male from the Little Bay area continued to approach the model. His mean daily distance, however, increased from 6.9 m to 12.8 m to 20.6 m over the course of these three days. The large amount of variability in the distance scores for rehabituation should be contrasted with the smaller variability in the intensity of threat display over the same period. Finally, the spontaneous recovery test after a six-day reprieve from testing produced closer spacing to the model in all three swans.

Discussion

Thorpe (1963) defined habituation as 'the relatively permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement. It is specific to the stimulation and relatively enduring' (p 61). Additional characteristics have been outlined by Thompson and Spencer (1966) and include spontaneous recovery as a function of time since stimulation, more rapid habituation with weaker stimulation and dishabituation to a novel stimulus. The present study found evidence for a gradual decrement in approach and intensity of threat display to a model, dishabituation to the same model placed in a new location, and spontaneous recovery after a six-day interval without stimulation. In addition, a more rapid response decrement has been demonstrated with a black model (ie 'weak' stimulus) in comparison to a white model with these birds

(Demarest 1980a). These data, then, provide clear evidence that territorial threat behaviour can undergo habituation under repeated invasion of a territory. This habituation does not result merely from sensory adaptation; if it did, one would not find dishabituation with a novel stimulus. It could be argued, however, that the model placement on the dishabituation test was actually a 'stronger' stimulus since it was closer to the nest. If sensory adaptation means that the threshold for elicitation of a response is raised, then a stronger 'dishabituating' stimulus might be expected to restore the threat response. The present design does not clearly distinguish between these mechanisms.

Petrinovich (1973) has recently reviewed naturalistic studies of habituation concluding that the process is slower to species-significant stimuli but that response decrements do occur, even to territorial invasion (Mulligan and Verner 1971; Petrinovich and Patterson 1979; Petrinovich and Peeke 1973; Thompson 1969). Falls (1969) has suggested that habituation might be involved in the establishment and maintenance of territories in birds and this is consistent with the field observations described here. A persistent mated pair of birds may, through repeated intrusion into another's territory, gain a small area for themselves. With continued habituation on the part of the original territorial bird, this new pair could enlarge their 'safe' area and begin to defend it. Eventually the area will become sufficiently secure for a nest to be built and young fledged. The author has been witness to such a sequence of events over the years in both the Van Brunt's Cove swans and in the Little Bay South swans, although the latter pair have yet to fledge young.

Furthermore, habituation of territorial behaviour would help to account for the dear enemy phenomenon (Fisher 1954; Wilson 1975). When a recording of a neighbouring conspecific is played to any of several songbirds, the birds do not exhibit a reaction. A recording of a stranger's song, however, elicits aggression and territorial defence. This distinction between strangers and neighbours apparently serves to reduce injury and energy expenditure in agonistic encounters at territorial borders and may also serve some mutual stimulation function (Fisher 1954). In *C. olor,* too, habituation of territorial behaviour toward neighbouring or familiar birds would seem to conserve energy and reduce risk. Furthermore, there is reason to believe that at least some territorial neighbours are related to one another (D Norman, pers comm 1978); thus the dear enemy phenomenon may serve to increase inclusive fitness.

General discussion

Previous studies examining the information available in *C. olor* territorial display (Demarest 1980a, 1980b) have shown that the displays are highly predictive of an animal's impending behaviour. Threat displays prior to an attack, for example, have been shown to follow a sequence which is adequately described by a first-order Markov chain model, if repetitions of acts are ignored. The probabalistic relationship of acts after an attack was also found to be dependent upon the animal's immediate preceding display and in some instances was absolutely predictable from the preceding behaviour. Smith (1977) has argued convincingly that this sort of relationship between display posture and future behaviour is a message in animal communication. The message is the information that a signal makes available about its sender. It tells what the signaller is likely to do at any moment and hence what it will probably do in the next instant if the situation does not change.

Among *C. olor* the signal value of a given display provides information about the outcome of future interactions. For an animal that finds itself in unfamiliar waters, even a moderately threatening display by the territory owner ought to signal the possibility of attack and injury. As the present results show, however, the messages vary in frequency and ease of elicitation as a function of the time of the year, the sex and reproductive status of the territory owner and the number of previous encounters with the territory owner.

Habituation may not only lead to a 'taming' effect of one animal upon the other but it may also produce familiarity and, as a result, a finer reading of the message in the other bird's display behaviour. A mild threat display which is actually inhibitive of attack (cf Table 3 in Demarest 1980a) might produce an avoidance response from an intruder unfamiliar with the territory owner but no reaction from an intruder from a neighbouring territory. Furthermore, familiarity tends to produce attraction and attachment (Zajonc 1971) and a lower probability of danger for the birds involved. It makes sense that something that stays around for a long time without causing harm is probably part of the favourable environment (Wilson 1975). Threats to the favourable environment are wasted energy and may, in fact, be counter-adaptive. For example, one invasion of Setauket Harbour by five swans in 1973 resulted in intergroup co-operative defence by the Harbour Cove male and both swans from the Little Bay South area. At one point, all three territorial birds postured three abreast in a Wedge display and together chased a single intruder from the area. Although this was the only time I have witnessed intergroup 'co-operative' defence by territorial swans, individual defence by birds from two or more neighbouring territories would certainly reduce the probability of injury to any one bird (Wilson 1975). Individual recognition of neighbours and an ability to interpret the message of a neighbour's display based on familiarity with this animal's behavioural tendencies in various environmental contexts, including seasonal variation and changes in reproductive status, would serve to enhance the adaptiveness of this behaviour.

Acknowledgements

Preparation of this paper was supported by a Faculty Grant from Monmouth College. The author would like to thank Everett J Wyers for suggesting some of the tests used in the habituation experiment and for commenting on an earlier version of this paper.

Summary

Territorial behaviour was observed in mated pairs of *Cygnus olor* in eastern New York and New Jersey from 1973 to 1977. The frequency of threat display varied seasonally, as a function of the number of territorial intruders. Territorial intrusion reached a peak in early spring and again in late autumn, and was infrequent during the incubation period. Defensive behaviour was studied during the incubation period by the introduction of an artificial model into the territory. The male is almost exclusively responsible for territorial defence. When a female does threaten an 'intruder' (the model), the displays are less intense, of a shorter duration and are performed further from the model. The intensity and duration of display bouts habituated with repeated exposures to the model and decreased abruptly the day that the cygnets left the nest. Introduction of the model into a different part of the territory produced dishabituation. The importance of habituation and familiarization with the threat displays of neighbouring swans is discussed regarding the establishment and maintenance of territories.

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Feeding

ARTIFICIAL FEEDING OF SWANS IN JAPAN

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Introduction

There are 32 places where a considerable number of swans occur in winter or on passage (Fig 1). In addition, there are several places which a small number of swans visit regularly. Twenty places in Fig 1 are coastal lakes and others are inland lakes or marshes. Except for Lake Inawashiro, which is located 514 m above sea level, all sites are in the lowlands.

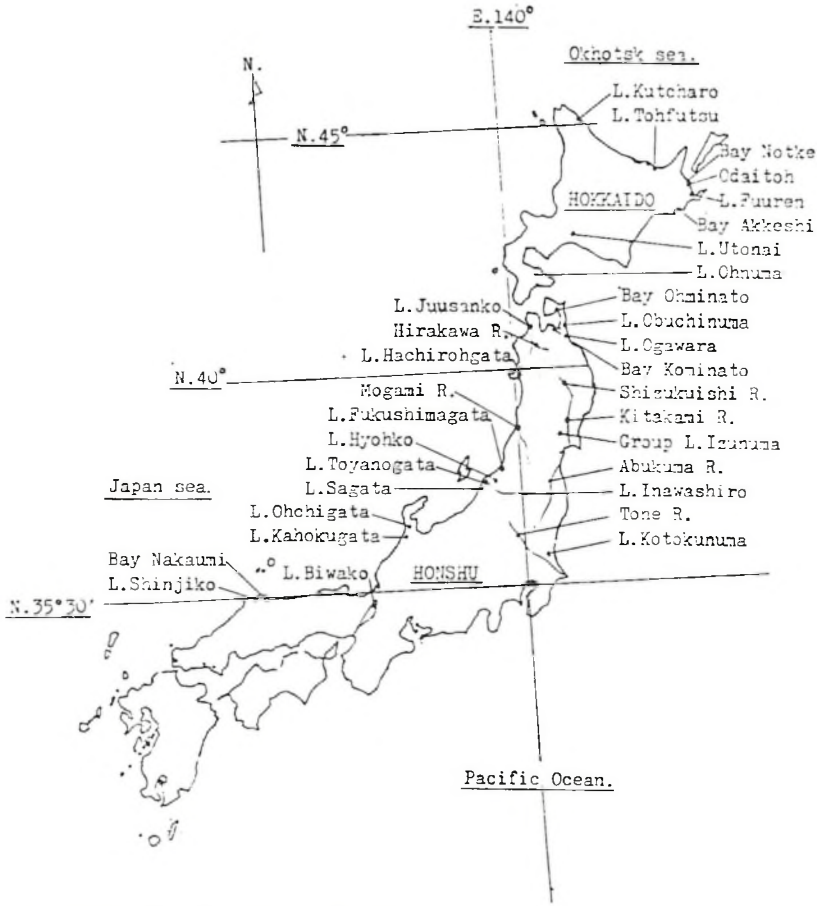

Fig 1. Main sites for swans in Japan.

According to the result of the Annual Count of *Anatidae* in 1979 which was promoted by the Environment Agency, 8416 *Cygnus c. cygnus* and 2550 *Cygnus columbianus bewickii* were observed. The latter winters in areas further to the south.

Table 1. Artificial feeding of swans in Japan.

Area		Type of food
Lake Kutcharo	C	6.7. s
Lake Tohfutsu	C	6.7. s
Lake Furen	–	s
Notke Bay	–	s
Odaito	T	6.7. s
Akkeshi Bay	–	s
Lake Utonai	C	5. w
Lake Onuma	C	4.5. w
Ominato Bay	T	4.5.8. s
Kominato Bay	C	4.5.7. s
Lake Obuchinuma	–	s
Lake Ogawara	–	s
Lake Juusanko	–	w
Hirakawa River	C	4.5.7. w
Lake Hachirogata	–	s
Mogami River (Sakata)	C	1. w
Shizukuishi River	–	w
Kitakami River	–	w
Lake Izunuma	C	1. w
Abukuma River	C	1.2.3.4.5. w
Lake Inawashiro	C	1.2.3.4.5. p.w
Lake Fukushimagata	–	w
Lake Hyoko	C	1.2.3.5. w
Lake Toyanogata	T	1.3.5. w
Lake Sagata	–	s
Tone River	–	w
Lake Kotokunuma	C	5. w
Lake Ohchigata	–	w
Lake Kahokugata	–	w
Lake Biwako	–	w
Nakaumi Bay	C	1.3.5.7. s
Lake Shinjiko	–	w

C = constant feeding; T = temporary feeding. Artificial food: 1 = rice; 2 = cereals; 3 = tea leaves; 4 = fruit rind; 5 = bread; 6 = oats; 7 = maize; 8 = apple. Natural food: p = pasture; s = sea plants; w = freshwater plants.

Artificial feeding

Constant artificial feeding is carried out in 15 places and temporary feeding in several other places (Table 1). The food given to swans is mainly agricultural products of each region. Waste bread is important in the vicinity of cities. About 400 to 500 g (dry weight) per swan is given every day on the assumption that the daily minimum feed requirement of the swan is 10% of its body weight. Besides the food given artificially, swans also take natural food. In a cold northern district such as Lake Inawashiro, where snow and ice prevent natural food from being taken, artificial feeding of some 700 g per day decreased the mortality rate. The motives of artificial feeding are different for each place: some lakes or ponds are too small for swans to get enough food in winter; suburban lakes are valuable for swan watching, but their available natural food is poor; in cold northern places ice and snow cover the natural food.

Artificial feeding does not affect the essentials of migration in swans. They stay in their habitual wintering places even though weather is exceptionally severe and they will not move to warmer southern places they have not visited before, even if people try to induce them by artificial feeding. Artificial feeding is effective only when it is done in sufficient places. In February 1976, Japan was gripped with freezing weather. The cold was especially severe in Hokkaido and some 500 swans were frozen and starved to death in Odaito. At that time, some people insisted that the artificial feeding of swans there had made them give up migrating southward and that was the reason for their death. In fact, the artificial feeding in Odaito was first started at that time to save the dying swans. Similar situations were also seen in Honshu.

Need for wetland conservation

Land reclamation by drainage is going on or planned in ten swan visiting places. We demand the government's reconsideration on such planning. Some people say that swans are not important for industry, but living with nature should not be evaluated only from the economic aspect. It is a barometer of healthy life. Nature-loving minds foster good sentiments, and handing such ideas down to future generations is our duty. Following these ideas, we keep on conserving swans voluntarily.

Summary

Artificial feeding of swans is regularly carried out at a number of sites in Japan, but does not affect traditional migration patterns. Drainage is a major threat to several important swan sites.

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THE FEEDING OF SWANS AND ITS RESULTS

M HATAKEYAMA

Introduction

I had two motives to begin feeding the swans at Asadokoro. One is that I was worried whether there was enough food to feed these big birds in this habitat; the other is that I wanted to know their feeding habits. I had first seen the swans offshore in the Sea of Okhotsk in late September 1926. At that time I had thought they were cranes, not swans. Since then I have been interested in them and have observed their feeding habits, several changes in adaptability to the seasons, and other things.

Natural swan foods

They like to eat certain kinds of sea plants – *Zostera marina, Zostera asiatica, Ulva reticulata, Enteromorpha intestinalis, Ulva pertusa;* some kinds of water insects – *Gonocephalum pubens;* lobsters, squillas; certain kinds of land insects – locusts, dragonflies; grass seeds which float on water – *Poa pratensis, Juncus, Agrostis palustris, Dactylis glomerata, Equisetum arrense;* and the leaves of *Phragmites communis.* When they have no food in the cold season, they even eat pine needles. Because of this, the trees often die. Though I thought they might eat sand, I was surprised to learn that they eat a great deal of soil.

Effects of artificial feeding

In some places, people feed the swans tea leaves (dregs), oats and empty husks of cereal. For my part, I give them powdered shell and sand. In the coldest season, I give them soil, too.

There are four reasons which have been advanced for not feeding the swans:

- various harmful germs might be transmitted;
- they will forget how to feed themselves;
- the supernutrition will have some effect on their breeding;
- unbalanced nutrition also will have an effect on their breeding.

I agree that it is the best protection for the wild animals to return to nature. But when it is impossible for them to feed themselves because of the cold, we cannot desert them. In such cases, the swans easily eat the food given by us. Then they will not perish. At some places where swans live, it seems that people feed them only for the sake of tourist development.

I would like to express my opinion which I have formulated over the past 20 years about the four objections listed above:

- At first I was a little worried about mould but the results of my feeding set me at ease. We have to be careful about fermented soy beans; otherwise mould has not hurt them at all.
- The swans coming from over the sea stay only five or six months. Four years have passed since I started feeding the swans and they do not show any change in their feeding habits, though they rely upon me a little.
- If I give them too much food, they eat only what is necessary. To my surprise, they control themselves.
- During the night, they leave their feeding place and feed themselves offshore, to make up for any food deficiencies.

I think that Asadokoro serves as a training place for feeding. The swans which have experience of being fed are not afraid of humans and soon become used to them. So many of them are loved and given food and it is certain that that has been the reason why the swans break up into groups and live there. We have many other good reasons for feeding them. For example, we can easily catch them to mark them. The swans return here again with their marks and approach us and we can read the numbers. This is quite different from the case of feeding the monkeys and Japanese serows.

I would emphasize that feeding the swans is not injurious but beneficial.

Summary

Food of wild swans in Japan is listed, and possible problems arising from artificial feeding, which the author concludes is not injurious but beneficial.

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WINTER HABITAT AND FOOD OF *CYGNUS CYGNUS BUCCINATOR* IN BRITISH COLUMBIA, CANADA

R W McKELVEY

Introduction

The world population of *Cygnus cygnus buccinator* is thought to number about 5500 birds. One subpopulation of about 500 birds breeds in northwestern Alberta and in the tri-state area of Montana, Wyoming and Idaho and winters in the tri-state area. The larger subpopulation, of about 5000 birds, breeds mainly in Alaska and winters along the Pacific coast from Alaska to northern California.

At least 50% (approximately 2500 birds) of the Alaska subpopulation winters in British Columbia (McKelvey in press). Preferred winter habitats are the estuaries of the many creeks and rivers along the coast, while smaller groups of swans are found on inland water bodies which remain ice-free.

Until recently information on the ecology of swans wintering in British Columbia consisted only of winter surveys (Smith and Blood 1972; Davies in press; McKelvey 1979) and the casual observations of naturalists (Campbell *et al* 1979: 145). The importance of estuaries to wintering swans has long been recognized (Brooks 1923; Smith and Blood 1972) but the grazing of dairy pastures is a recent phenomenon (McKelvey 1979).

Coastal study areas

Comox Harbour: Comox Harbour is situated on the east coast of Vancouver Island (Fig 1). It has a southeast exposure, the direction of the prevailing winds during winter, and is characterized by above-freezing temperatures, frequent precipitation and moderate snowfall (Table 1).

Table 1. Winter climatic information for Comox Harbour and Port Alberni, British Columbia.

	Comox[1]	Port Alberni[2]
Lowest mean daily temperature	2.1°C	0.6°C
Month	January	January
Highest mean monthly precipitation	211.6 mm	313.4 mm
Month	December	November
Average annual snowfall	106.2 cm	81.0 cm
Month of peak snowfall	January	January

[1] Data source: Canada Dept of the Environment, 1971.
[2] Data source: Canada Dept of the Environment, 1972.

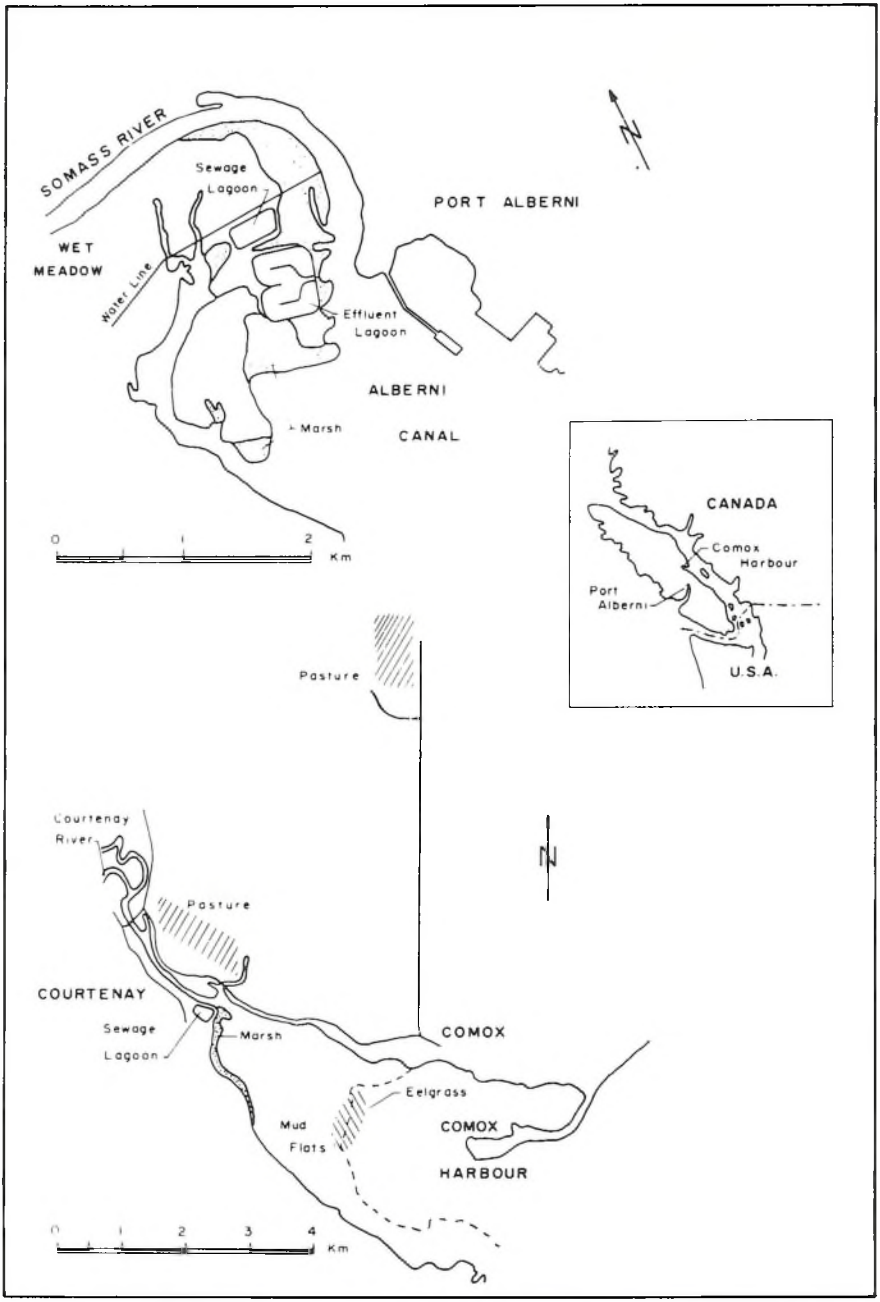

Fig 1. Location of estuarine study areas on Vancouver Island.

There is one major discharge of fresh water into the Harbour, and several smaller creeks. Most of the fresh water comes from the Courtenay River, which flows at a mean annual rate of 57.3 m^3/sec (Morris *et al* 1979). Tides are of the mixed semi-diurnal type (Canadian Hydrographic Service 1979) generally with highest tides in the early morning and lowest tides at midnight, during the winter (Fig 2).

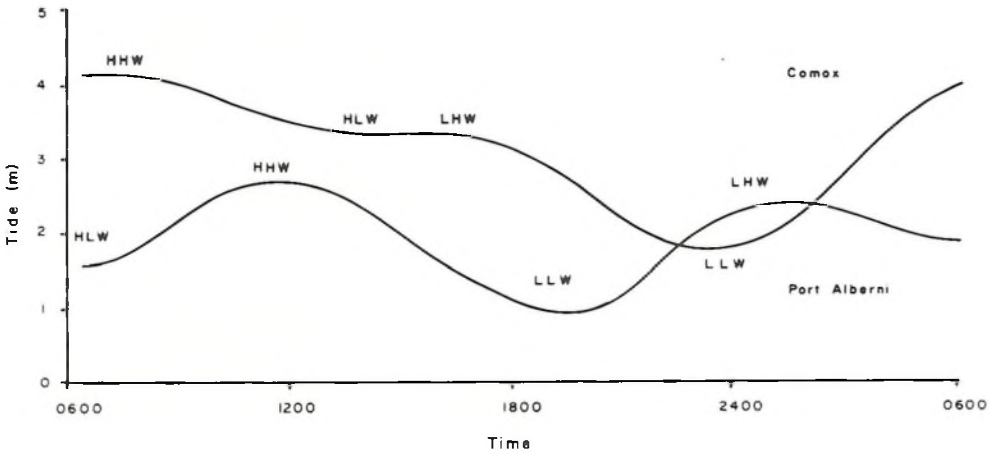

Fig 2. Composite tide cycles at Comox Harbour and Port Alberni, over the period November 1978 to March 1979.

Flood tides cause a counter-clockwise circulation of water, fresh water from the Courtenay River being deflected and mixed along the southeast side of the harbour.

Fields grazed by swans are dairy pastures which become too wet during the winter to be used by cattle. Field feeding occurs only on certain farms, generally the most productive in the area. The agricultural capability of the soil is moderate; high yields of forage crops are obtained only by heavy fertilization (R DeMong, pers comm). The fields most frequently used by swans are dominated by rye grass *Lolium perenne* and orchard grass *Dactylis glomerata.*

Port Alberni: Port Alberni is located at the head of the Alberni Canal, a fjord-like inlet on the west coast of Vancouver Island (Fig 1). The climate is similar to that of Comox Harbour but is slightly drier and cooler in the winter (Table 1).

The Somass River is the only major source of fresh water at the head of the Alberni Canal. Its flow is regulated by a dam on Sproat Lake, with a mean annual discharge of 84 m^3/sec (Canada Dept Fish & Env 1978). The tides during the winter are lowest in the early evening with high tides of similar magnitude at midday and midnight (Fig 2). Freshwater—saltwater mixing occurs near the foot of the delta of the Somass River (Tully 1949), the result being weak tidal currents and very little saltwater influence on the vegetation of the delta (J Pogar, pers comm).

Methods

Vegetation structure, biomass and proximate analysis of potential foods, and food habits were assessed on the estuaries at Port Alberni and Comox Harbour. Food habits were analysed and food value assessed through proximate analysis on dairy pastures adjacent to the estuary at Comox Harbour (Fig 1).

A vegetation description was determined from literature sources for the estuary of the Somass River at Port Alberni and by the Braun-Blanquet plant releve technique (Muller-Dombois and Ellenberg 1974) for the Courtenay River Estuary at Comox Harbour. Biomass of below-ground plant material was estimated by core sampling a volume of 0.001 m^3 in standards of uniformly dense vegetation. Proximate analyses for fibre, fat and gross energy levels followed the methods of Horwitz (1965) and were performed by the Department of Animal Sciences, University of British Columbia, and by the Canadian Wildlife Service. Protein and carbohydrate levels were assessed using a Perkin Elmer Elemental Analyzer by the Department of Biological Sciences, Simon Fraser University.

Apparent food materials were collected from areas in which swans were observed feeding. Microscopical analyses of droppings were based on techniques reported by Baumgartner and Martin (1939), Stewart (1967) and Parker *et al* (1976).

Food habits were assessed visually at Nicomen Slough, 100 km east of Vancouver, (Fig 3) in January and November 1979. Plant materials were collected adjacent to feeding sites and analysed for protein content in November 1979.

Locations of active swan feeding were determined in February 1979 near Vanderhoof, in north central British Columbia (Fig 3). Identification of plants thought to be used as food was made in August 1979.

Results

Vegetation

The vegetation of both estuaries reflects the differences in the degree of mixing of salt and fresh water. At Comox Harbour little or no delta formation occurs; the river is somewhat channelized, and the original delta has been usurped for farmland. Much of the harbour is tidal flats, devoid of macrophytes above the eelgrass *Zostera* beds. Where the saltwater—freshwater mixing occurs, typical estuarine

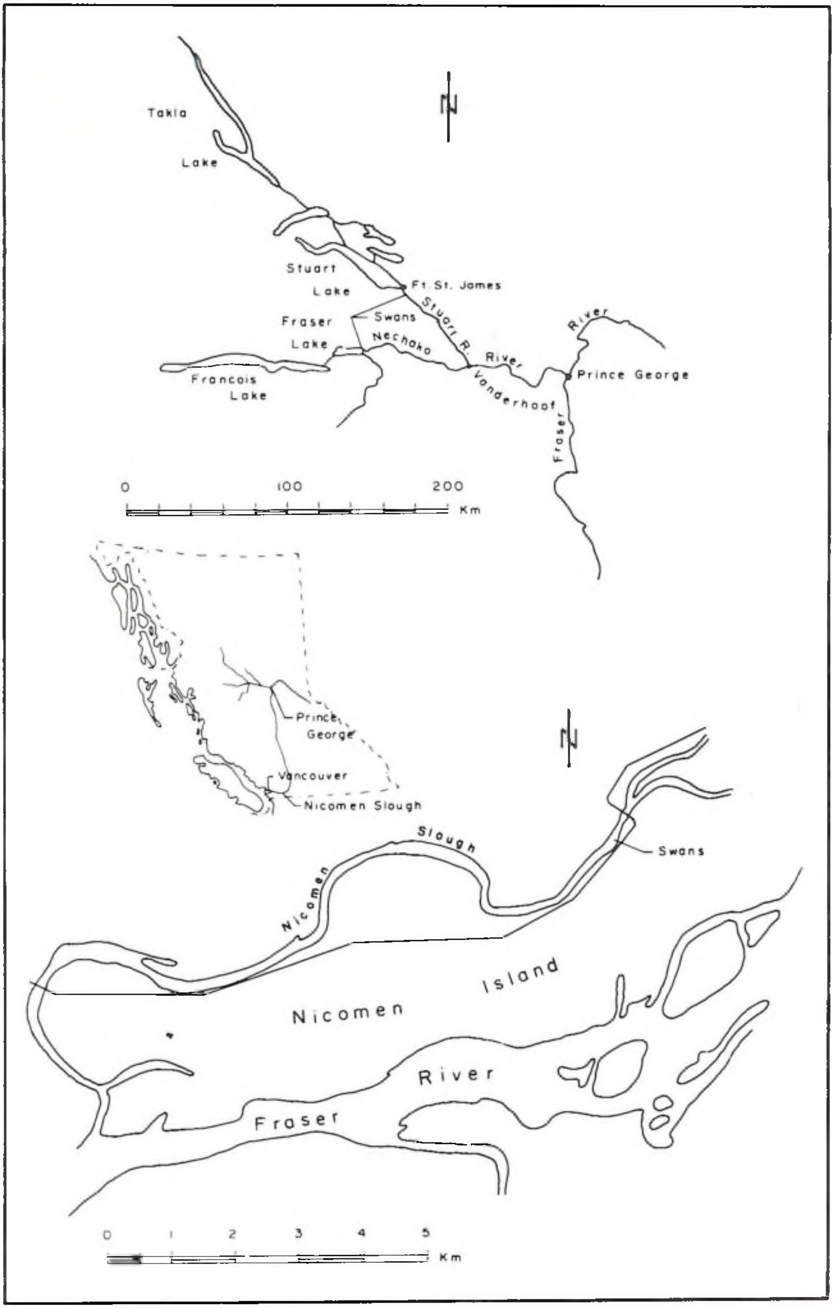

Fig 3. Location of study areas in interior British Columbia.

emergents have developed. They are confined to a narrow strip which tapers away from the Courtenay River mouth towards the southeast (Fig 1). The vegetation is characterized by only two plant associations, composed of 16 species. The associations are a *Scirpus americanus–S. cernuus–Triglochin maritimus* association and a *Carex lyngbyei–Potentilla pacifica–Deschampsia caespitosa* association. The *Scirpus* association is the more widespread, while the *Carex* association occurs between the *Scirpus* and the beach and on elevated portions of the substrate within the *Scirpus* association.

The strong influence of salt water at Comox Harbour is also reflected in plant vigour. The dominant *Scirpus americanus* seldom grows taller than 50 cm, while on estuaries more influenced by fresh water it reaches a height of over 100 cm.

The Somass River estuary at Port Alberni is more typically deltaic. Although parts of it have been developed for industrial use, sedimentation and mixing continue in their original patterns. The strong freshwater influence has resulted in a great diversity of vigorous plants. Over 60 species of emergent plants have been catalogued, and five vegetation types recognized (Paish *et al* 1973): a *Sidalcea canadensis–Fritillaria camschatensis–Solidago canadensis* type; a *Juncus balticus–Deschampsia caespitosa* type; a *Carex lyngbei* type; a *Scirpus acutus* variant of the *Carex* type; and a *Myriophyllum spicatum–Potamogeton natans* type.

Plant growth on the Somass River delta is exceptional. On average the *Carex* grows to a height of at least 100 cm and can be found in some locations over 200 cm high. Similarly *S. acutus* grows to heights above averages reported for the area (Hitchcock and Cronquist 1973).

Proximate analysis and biomass

The proximate analysis of below-ground plant materials showed them to be similar at both estuaries. In general, potential winter foods are moderate in protein (7%) and high in fibre (50% to 60%) (Table 2). The difference in fibre level of plants was highly significant ($p = 0.01$). The biomass per unit volume was significantly higher at Port Alberni ($p = 0.05$). The surface area of the estuary potentially available to swans wintering at Port Alberni was greater than at Comox Harbour with a correspondingly greater amount of food (Table 2). Proximate analysis of pasture grasses showed them to be of much higher food value than potential estuarine foods.

Food habits

C. c. buccinator was observed to feed by extracting the roots and rhizomes of the dominant emergent plants at both estuaries. At Port Alberni most feeding took place over *Carex* beds but also occurred in beds of *Scirpus acutus*. On one occasion, a characteristic swan-feeding crater was found along the edge of a bed of *Typha*

Table 2. Biomass estimate and proximate analysis of potential swan winter foods at Comox Harbour and Port Alberni, and proximate analysis of pasture grasses near Comox Harbour.

Values are ± one standard error; numbers in () are sample sizes.

Factor	Comox Harbour	Port Alberni	Pastures
Biomass ($g/.001/m^3$)	25.9 ± 2.1 (45)	31.9 ± 1.7 (49)	NA
Surface area (h)	8.26	22.94	NA
Food potentially available (m.t.)	115.6	401.4	NA
Protein (%)	7.0 ± .3 (45)	7.1 ± .3 (48)	22.9 ± 1.2 (14)
Fat (%)	1.2 ± .1 (39)	1.0 ± 2.6 (30)	0.4 ± .1 (4)
Carbohydrate (%)	46.8 ± 1.0 (46)	48.0 ± .3 (48)	44.0 ± .5 (14)
Fibre (%)	63.4 ± 1.2 (39)	47.8 ± 1.7 (7)	32.2 ± 1.4 (2.7)
Gross energy (Kcal/g)	4.76 ± .27 (9)	4.82 ± .16 (49)	NA

latifolia though there were no actual observations of the use of that species as food.

At Comox Harbour swan feeding was concentrated over the *Scirpus—Triglochin* association. Smaller numbers of birds were seen feeding on *Carex* beds and occasionally a swan was seen picking up a frond of *Zostera marina* drifted in by the tide. At night feeding activity was observed on *Zostera* beds exposed by low tides.

Animal matter appears to contribute very little to the winter diet of the swans. The dense growth of the plant rhizomes provides habitat only for microscopic animal forms. One source of animal protein, however, which may be used occasionally is to be found in the carcasses of spawned salmon *Oncorhynchus* sp. Butler (1973) recorded a swan picking at a dead salmon at the mouth of the Big Qualicum River, 80 km south of Comox Harbour. I have seen similar activity at the same river by a single family every winter since 1974/75; in January 1979 I saw a juvenile picking at a salmon in Comox Harbour.

The analysis of swan faeces for undigested plant fragments could not be used for quantitative measurements, because the differences between species in epidermal characteristics of roots and rhizomes were too subtle. Samples were analysed only for the presence or absence of four plant types: *Scirpus* sp, *Carex* sp, *Zostera marina* and grasses. Of the 59 droppings analysed, fronds of *Zostera* were seen in 22, *Scirpus* rhizomes in 20, grass parts in 12 and *Carex* rhizomes in 9; two had completely unidentifiable plant remains.

Interior wintering areas

The wintering area east of Vancouver is a small freshwater marsh on a side channel of the Fraser River (Fig 3). Emergent vegetation consists predominantly of a *Carex* sp, probably *C. rostrata,* and horsetail *Equisetum* sp. The water is clear enough to support other aquatic plants as well, *Potamogeton* sp and *Eleocharis* sp being the most obvious. *Equisetum* sp and *Carex* sp, in that order, appear to be the preferred foods. Their protein contents were 5.0% and 4.4% respectively.

The climate in the lower Fraser Valley remains mild throughout the winter. When freezing conditions prevail, the slow river current and the turbulence caused by small creeks entering the marsh keep Nicomen Slough open for feeding.

Though climatic conditions in north central British Columbia are, by contrast, severe during the winter, certain wetland areas remain partially ice-free, particularly fast-flowing rivers and the outflows of large lakes. Their use by swans is traditional. Artifacts from the Hudson Bay Post at Fort St James indicate that swans have been found near the Fort since before settlement (about 1810).

Foods consumed in the northern interior areas are the leaves, tubers and rhizomes of emergent and floating leaved aquatic plants. Species found in areas known to have supported wintering swans included: *Scirpus* sp, *Elodea canadensis, Sagittaria latifolia, Potamogeton* sp and *Myriophyllum* sp.

Discussion

Vegetation

Studies of the vegetation of the numerous estuaries along the British Columbia coast have been confined to the larger and more accessible areas near Vancouver (Lim and Levings 1973; Yamanaka 1975; Dawe 1976). Plant species and associations seem to be similar from one estuary to another, the extent of mixing of salt water and fresh water being most important in determining final vegetation structure.

Vegetation patterns observed during aerial surveys of swans on Vancouver Island (McKelvey 1979) appeared to be similar to those seen at Comox Harbour and Port Alberni and to those reported by Lim and Levings (1973), Yamanaka (1975) and Dawe (1976). The most abundant plants in most estuaries, including estuaries used by swans, are *Carex* sp and *Scirpus* sp. Their importance to swans is undoubtedly as a food source.

Proximate analysis and biomass

Crude protein levels found in this study were similar to those reported in other studies of emergent plants. Burton (1977) measured protein levels of 7% to 14% in rhizomes of *Scirpus* sp consumed by *Anser caerulescens caerulescens* in the Fraser River Estuary. De la Cruz and Hackney (1977) reported crude protein levels in below-ground parts of *Juncus* sp of between 4.0% and 5.4%. Similar ranges of crude protein have been reported for above-ground emergent plant parts by Boyd (1970a and 1970b) and Auclair (1978). Swans wintering on the estuaries at Comox Harbour and Port Alberni have available to them crude protein levels similar to those in many other emergent plant communities. It is difficult to say whether those levels of protein are adequate nutritionally, but as swans have always wintered on estuaries it must be concluded that they are.

High fibre content may reflect a low-quality diet or it may be an artifact of the sampling procedure. Cellulose, the major component of fibre, is not digested by geese (Mattocks 1972) and there is no evidence that swans digest it either. In mammals capable of cellulose digestion, winter diets high in fibre were thought to result in a negative energy balance (Gasaway and Coady 1974). Ingestion of high-fibre foods by birds may similarly lower the efficiency of digestion but high levels (30%) are tolerated by chickens (Bolton 1962).

Swans are probably more selective in their food habits than was the core sampling procedure of this study. Core samples often contained large quantities of roots attached to the rhizomes. The roots generally appeared to be dead; if so, they would be highly fibrous. Swans may be able to extract rhizomes only, leaving much of the root material behind and reducing the fibre levels of the actual diet.

Grazing of pastures

The much higher protein content of the grass on the pastures adjacent to Comox Harbour is the most likely reason for their attractiveness to swans. A popular belief is that when a species changes food habits, eg from emergent plants to pasture grasses, some catastrophe has befallen the natural food resource. My original hypothesis was that over-utilization of the estuary at Comox Harbour was forcing swans onto agricultural fields. However, Port Alberni, where there is abundant food, continues to receive less use while Comox Harbour may soon be over-utilized (McKelvey 1979). Swans attracted to the Comox area for the dairy pastures are still dependent on the estuary at night and during periods of snow when field feeding is not possible.

During the winter the Comox area supports nearly 5% of the world population (250 to 300 birds); it is a critical wintering area. Its popularity with swans is creating some management problems, complaints of depredation being the most obvious. There is direct evidence that limited waterfowl grazing may be beneficial to overwintering crops (Kear 1970; Marriott 1973; Clark and Jarvis 1978) and there is indirect evidence that swan grazing is generally not harmful. The owner of one farm near Comox claims not to have noticed yield changes since swan grazing began in 1974.

The manner in which the swans acquired the field feeding habit is unknown.

Because they are forced onto unfrozen coastal areas in severe weather, it cannot have occurred in response to weather as reported for other swan species (Owen and Kear 1972). The taste for high-nutrient grasses may have been acquired by chance, birds landing on rain-flooded fields then decoying other swans.

Reed (1976) speculated that goose species which have adapted to using agricultural crops may have lowered their reproductive output and shifted the age distribution through increased winter survival. There have been no studies yet of the reproductive success of swans feeding on grass compared with those feeding only on natural foods.

Feeding in fields has resulted in a rapid increase in the number of swans wintering at Comox (McKelvey 1979). The mechanism causing that increase could be a change in productivity or a decrease in winter mortality. Continued yearly observations on the productivity of those swans wintering at Comox would be useful.

Food habits

Winter food habits of *C. c. buccinator* are unlike those reported for other swans (Owen and Kear 1972; Owen and Cadbury 1975), the native foods on wintering areas in British Columbia appearing to be the roots and rhizomes of emergent plants. Other swan species seem to make more use of above-ground plant parts, on wetlands or fields, and of rooted aquatics. The use of *Zostera* has been reported in other swan species, but the extent of its use by *C. c. buccinator* is not known; *Zostera* does not occur at every wintering location, and its use at Comox may have been over-estimated. The rate of passage of food through the gut is unreported in swans but seems to be much slower than in other waterfowl (pers obs). *Zostera* is available only during the lowest daily tide, near midnight, and droppings collected during daylight on intermediate tides may have resulted in an over-estimation of the importance of *Zostera* in the diet.

Interior areas

Habitat and food habits of *C. c. buccinator* wintering in interior parts of British Columbia are similar to those reported for European swans (Owen and Kear 1972). Because there is indirect evidence of a long history of use of some areas, such as Fort St James, those areas may be traditional wintering areas. *C. c. buccinator* does not seem to be a flock bird in the sense that geese and even *Cygnus c. columbianus* are. They winter in small groups and do not migrate, some wintering as far north as Cordova, Alaska. It is possible that at least some of the birds wintering in north central British Columbia are also breeding nearby.

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Summary

During the winter British Columbia supports at least 50% of the world population of *Cygnus cygnus buccinator.* Habitat conditions and food habits are reported from estuaries at Port Alberni and Comox Harbour, from dairy pastures near Comox and from inland areas east of Vancouver and in north central British Columbia.

Vegetation varies between estuaries depending on freshwater influence. The protein content of below-ground plant parts was moderate (7%) and fibre levels were high (50% to 60%). Major food items include the roots and rhizomes of *Carex lyngbei* and *Scirpus americanus* and the leaves of *Zostera marina.*

Pasture grasses were found to be high in protein (23%) and low in fibre (32%). *Lolium* sp is the almost exclusive food item on pastures. The concentration of swans in the Comox area is thought to be the result of the availability of pastures and not the disappearance of the native estuarine food resource.

Food consumed on inland wintering areas include roots and rhizomes of *Carex* sp, *Equisetum* sp, *Scirpus* sp and roots or leaves of *Elodea canadensis, Sagittaria latifolia, Potamogeton* sp and *Myriophyllum* sp.

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FIELD FEEDING BY *CYGNUS COLUMBIANUS COLUMBIANUS* IN MARYLAND

R E MUNRO

Introduction

Cygnus cygnus cygnus, Cygnus columbianus bewickii and *Cygnus olor,* all Eurasian, are known to utilize agricultural fields for feeding (Owen and Kear 1972). The spread of potato eating by *C. c. cygnus* in England (Pilcher and Kear 1966) apparently began in the 1940s in response to severe winters. According to Anderson (1944), heavy rainstorms during February 1943 raised water levels such that *C. c. cygnus* could not reach aquatic vegetation, its normal food resource. It subsequently moved to flooded grass fields but remained there after all traces of floodwaters disappeared.

Cygnus columbianus columbianus of North America was found to be generally herbivorous in Utah waters (Sherwood 1960) and in fresh estuarine areas of Chesapeake Bay (Stewart and Manning 1958), although the latter authors found it to be omnivorous in brackish waters of the Bay. Sincock and Kerwin (unpubl data 1969) reported similar results in their study of swan food habits in the Back Bay, Virginia/Currituck Sound, North Carolina area.

In western areas of the United States, swans use agricultural fields as well as aquatic areas for feeding. Moffitt (1939) indicated that swans in California were rarely responsible for crop depredations on rice and barley. Nagel (1965) described as 'atypical' a movement of swans into harvested corn fields during the spring of 1964 in northern Utah. Field feeding by swans was considered rare and localized in Washington (C A Rieck pers com) and Oregon (R U Mace pers com), and emergency-oriented in parts of Montana (D Witt pers com).

Swans on spring migration from the Atlantic Flyway have been using agricultural fields in some areas since the early 1950s. Gunn (1973) reported that half the eastern population of swans had begun using corn fields east of Lake St Claire in southern Ontario 'within the past five years'. Field feeding by all swans migrating through Ohio began about 1962 (J R Frye pers com). Up to 70% of swans migrating in spring through Saginaw County, Michigan, utilized fields for resting and feeding since the early 1960s (E J Mikula pers com). Spring field feeding has involved 50% of swans in Wisconsin since the early 1950s (J R March pers com), but is uncommon among swans in North Dakota (R E Stewart pers com).

Branta canadensis wintering in Maryland began field feeding 25 to 30 years ago. These populations have continued to increase and during the 1970s averaged over half a million birds, nearly twice the previous long-term average (unpubl data, USFWS Migratory Bird Management Office MBMO, Laurel, Maryland). Their movement to fields was largely responsible for most of this increase.

There are no published accounts of swan field feeding in wintering areas of the Atlantic Flyway or records of this behaviour until the late 1960s. According to V D Stotts (pers com), significant numbers of swans began utilizing agricultural fields in Maryland during the late winter of 1969/70. Field feeding was noted in Delaware in 1972 (C A Lesser pers com), Virginia in 1968 (C P Gilchrist pers com) and North Carolina in 1971 (D M Connelly pers com). Although not necessarily representing the initiation of field feeding in these areas, the years cited represent noticeable or significant field feeding by *C. c. columbianus.*

From 1955 until 1971 swans wintering in Maryland, Virginia and North Carolina comprised 99.8% of the Atlantic Flyway population, which averaged about 53 000 birds or 54% of the continental population (unpubl data, MBMO, Laurel, Maryland). During this period, Maryland wintered 65% of the Atlantic Flyway swan population.

The primary objective of the present study was to document the increase of field feeding by swans in Maryland. Field work began in November 1969 and continued through March 1972. Subsequent observations of neck-banded birds that accumulated through the 1975/76 winter have been included in this report.

Description of the Chesapeake Bay and specific study areas

The Chesapeake Bay is the largest estuarine system along the Atlantic coast of North America. The upper Bay (that portion of the Bay north of the Maryland-Virginia state line and including the Potomac River) is or was one of the most important wintering areas in the Atlantic Flyway for up to 30 species of waterfowl.

Habitat quality

Although data are scarce, aquatic habitat quality has deteriorated in the Chesapeake Bay. Submerged aquatic vegetation, the most important aquatic food resource for waterfowl, has decreased in the upper Bay since 1971, according to Kerwin *et al* (1976). Over the upper Bay, frequency occurrence of submerged aquatic vegetation decreased from about 28% to about 15% of sampled stations from 1971 through 1974. Additional data (unpubl, USFWS Migratory Bird and Habitat Research Laboratory, Laurel, Maryland) indicate a continued reduction in submerged aquatic vegetation through 1979.

Many invertebrate species used by waterfowl for food are associated with submerged aquatic vegetation. Unfortunately, no data comparable to those on vegetation are available for invertebrate populations.

Nevertheless, some changes in invertebrate numbers have been recorded. In 1971 the soft-shelled clam *Mya arenaria,* a species of considerable commercial importance to Atlantic coastal states, was estimated to occupy less than 20% of its 1957 distribution in Maryland waters (F Hammons pers com). There is evidence, therefore, that both plant and animal aquatic food resources for waterfowl were less abundant in the upper Bay by the mid-1970s.

Recent agricultural trends

A general crop summary is provided annually by the Maryland Crop Reporting Service, as well as county statistics on crops planted and harvested. Agricultural plantings in Kent, Queen Anne's, Talbot and Dorchester Counties on Maryland's Eastern Shore have not changed over the ten year period ending in 1973. There was also no change in total land cultivated. Corn was the major crop planted, followed by soybeans.

Specific study areas

Primary criteria for selection of five study areas were the general distribution of swans in Maryland (Stewart 1962), landowner co-operation and accessibility to swans. The areas (Fig 1) are briefly described in Munro (1981). All are within slight to moderately brackish areas of the Bay in the 5—15 parts per thousand salinity range. For a thorough description of Maryland's Chesapeake Bay, see Lippson (1973).

Methods and materials

Plastic neck-bands were used as the principal marker. A standard USFWS band was placed on one tarsus and a plastic band, engraved with the same numerals as the neck-band, was placed on the other tarsus. Unless otherwise specified, all records of individually marked swans reported in this study were based on observations of neck-banded birds. For methods of construction, application and a description of the marking protocol, see Sladen (1973).

Swans were baited with corn and captured in either topless funnel traps set in water or under cannon nets in fields. Three hundred and forty swans were captured and marked at Bay study areas during the winter of 1969/70.

Birds were observed with 15 to 60x spotting scopes that enabled positive identification up to 150 m under ideal conditions. Banding records and subsequent sightings of members of the original marked sample were coded and punched on cards or keyed on magnetic tape either by the author or personnel of the USFWS Migratory Bird Management Office. Data reduction and summarization procedures were also provided by that Office. Statistical analysis was as detailed in Munro (1981).

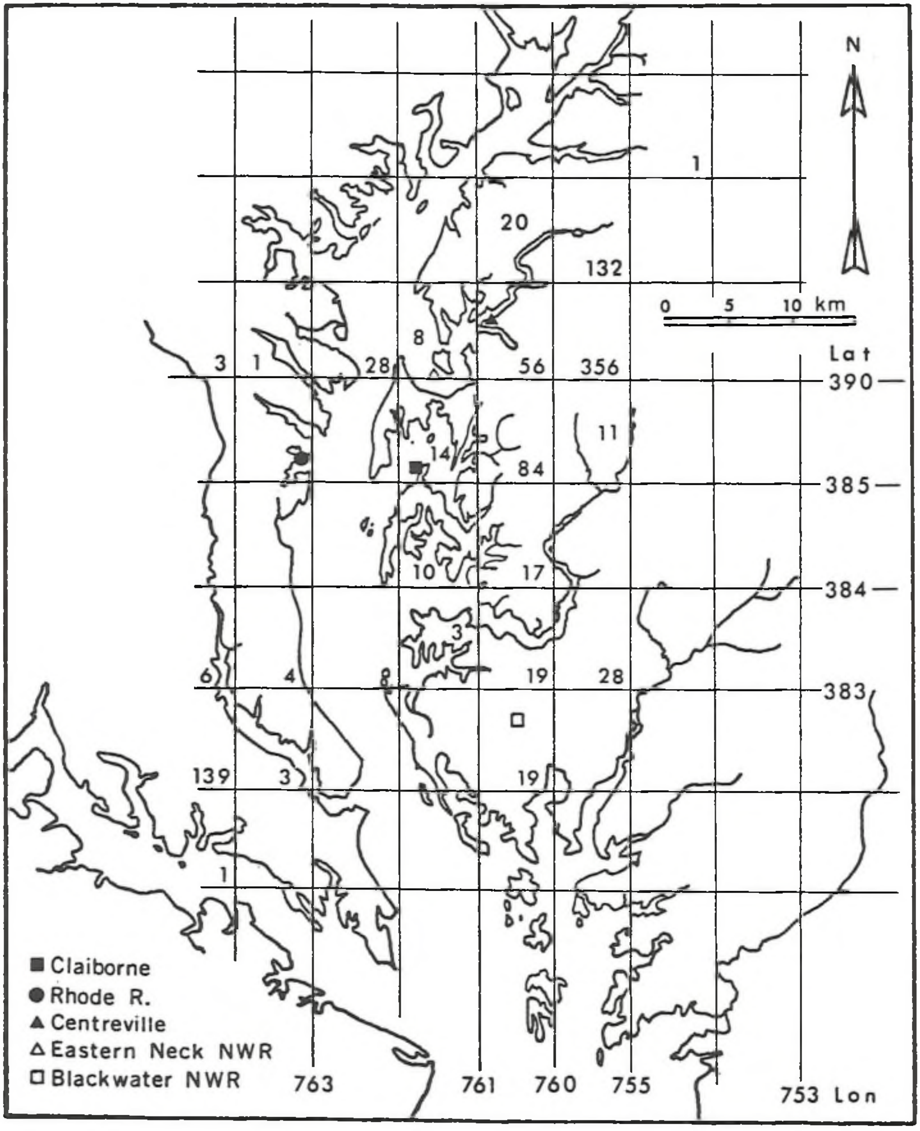

Fig 1. Locations of study areas in the upper Chesapeake Bay of Maryland, and ten-minute block locations of field feeding by neck-banded swans, winters 1970/71 to 1975/76 and study areas combined. (Multiple observations (different days) per individual included).

Results

The recent increase in field feeding

According to V D Stotts (pers com), the movement of swans into agricultural fields in Maryland during the late winter of 1969/70 was in response to six weeks of freezing weather. Concern was also expressed for apparent decreases in submerged aquatic plants and some shellfish in recent years. The decrease in submerged aquatic vegetation (Kerwin *et al* 1976) was followed by a smaller proportion of the Atlantic Flyway swans wintering in Maryland (Fig 2); see also Munro (1981). Although swans had been observed in Maryland fields prior to 1969, their numbers were probably under some stress such as disease.

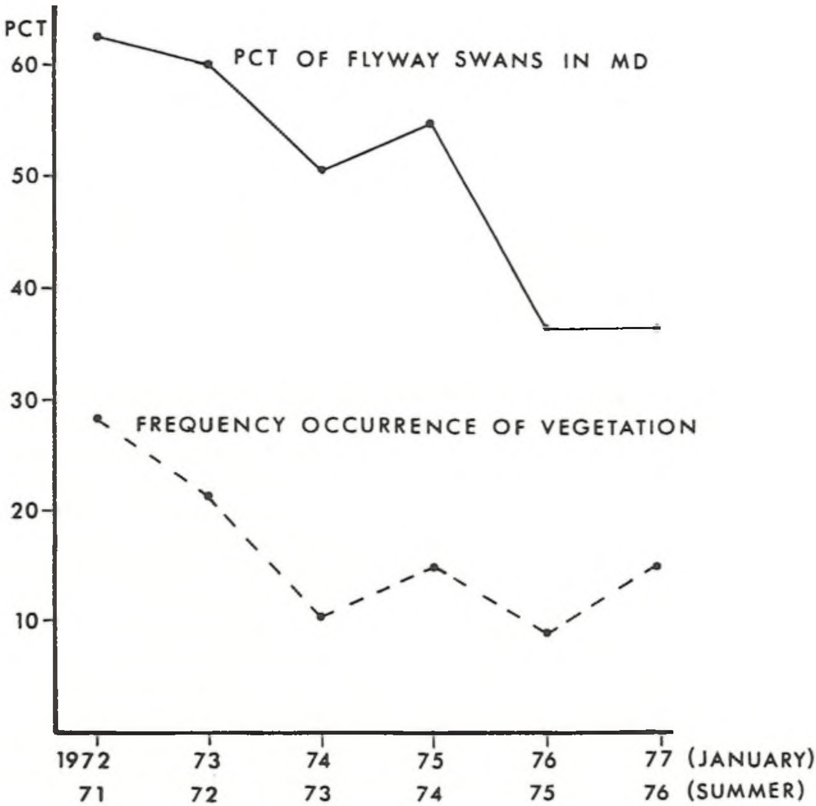

Fig 2. Percentage of Atlantic Flyway swans in Maryland and frequency of occurrence of vegetation.

No survey data have been published on numbers of swans using fields. Although boundaries of areas surveyed during co-operative State-USFWS January inventories are generally oriented around river systems, they include vast tracts of agricultural land. Current procedures continue to combine survey results (except for swans during recent years — V D Stotts pers com) from estuarine and agricultural habitats.

Observations from the original sample of 340 neck-banded swans were examined to determine numbers that returned to the Bay area each winter (Munro 1981). Numbers and proportions of these birds that were observed field feeding were tabulated and analysed by study area of banding (Table 1). The analysis was con-

Table 1. Numbers of neck-banded swans, by area of banding, field feeding around Chesapeake Bay, expressed as the percentage of the number available (see Munro 1981).

RHO = Rhode River, ENR = Eastern Neck, CEN = Centreville, BLK = Blackwater, CLA = Claiborne

Banded	1969/70	1970/71		1971/72		1972/73		1973/74		1974/75		1975/76	
Area		N	%	N	%	N	%	N	%	N	%	N	%
RHO	48	2	6	11	46	1	8	2	25	3	60	3	60
ENR	42	10	36	14	70	7	70	7	70	4	100	1	60
CEN	19	11	85	12	92	2	67	3	100	1	50	2	100
BLK	168	17	24	29	64	8	31	4	44	4	44	3	37
CLA	63	7	19	14	61	6	35	4	40	3	75	4	100
Total	340	47	26.0	80	64.0	24	35.3	20	50.0	15	62.5	13	61.9

structed to test for differences in the combined data and between the proportions of birds field feeding from each study area population, both at the start of the study period (intercept) and across years (slope or trend). Differences among area intercepts were indicated ($p = 0.0057$), as well as an overall trend ($p = 0.0194$). Study areas were compared by testing one arbitrarily chosen sample, Rhode River (RHO), for zero intercept and slope, followed by tests between this and each of the remaining areas. The estimated proportion of Rhode River birds that were field feeding during the band year was 1.5%, which was not different from zero. A large difference (82.5%) was found between the estimated proportions of Rhode River and Centreville (CEN) birds that were field feeding during the band year. That this difference was easily detected ($p = 0.005$) was comforting, since all Centreville birds were captured while feeding in a corn field. The estimated trend in field feeding by Rhode River birds was an increase of 9.4 percentage points per year, which was marginally significant ($p = 0.0629$); nevertheless, it was an indication of a yearly increase in swan field feeding. Tests for slope or trend differences between study area populations were all non-significant.

A similar analysis by age and sex class of percentages or proportions of neck-banded swans feeding in fields yielded uniformly non-significant results. This was affected by the initially high percentage of Centreville birds that were field feeding and the six-year study.

To examine better the extent and trend in field feeding by swans, the Centreville birds were removed from the data set, as were young birds and those of unknown age or sex (Table 2). Using a similar model, an analysis of variance indicated no

Table 2. Numbers of adult male (AM) and female (AF) neck-banded swans field feeding around Chesapeake Bay, expressed as the percentage of the number available.

Banded	1969/70	1970/71		1971/72		1972/73		1973/74		1974/75		1975/76	
		N	%	N	%	N	%	N	%	N	%	N	%
AM	118	9	15	20	62	6	37	5	42	1	50	2	50
AF	138	18	23	37	61	11	30	9	43	10	71	8	73
Total	256	27	19.4	57	61.3	17	32.1	14	42.4	11	68.8	10	66.7

intercept or slope differences among adults; however, the year effect in the combined data was significant ($p = 0.0504$). The estimated intercept or proportion of birds feeding in fields during the band year was 20.8% for adult females, which was not significantly different from zero ($p > 0.2$). Of greater importance, the estimated slope for adult females was +8.4 percentage points per year, which was marginally significant ($p = 0.0529$). Therefore, observations of neck-banded swans indicate the incidence of field feeding among birds banded as adults was between 0 and 21% during the 1969/70 winter, and increased to between 50.4% and 71.2% (0 or 20.8% + [8.4%/year * 6 years]) by the 1975/76 winter.

Within-season changes in field feeding

The movement of swans to fields during the 1969 winter occurred in late January and February 1970, the marking period. Data therefore were arranged by 15-day periods beginning with 1970/71 (Table 3) to investigate changes in timing of field feeding within seasons. Birds from all study areas were combined, as were multiple observations (different days) of individuals. Most swans usually arrived in the Bay area during early to mid-November. Of 125 observations of neck-banded swans in fields during the 1970/71 winter, less than 5% occurred before February; this was consistent with the previous winter. However, almost 10% of 544 field feeding observations during the next winter (1971/72) occurred during November 1971 immediately upon the swans' arrival in the Bay area. Although numbers of observations during later years were small, a season-long pattern of field feeding was suggested.

Table 3. Winter time periods during which agricultural field feeding by neck-banded swans was recorded in the Chesapeake Bay area, all study areas combined.

Season (N. obs.)		Percent frequency by 15-day time period									
		1 Nov– 15 Nov	16 Nov– 30 Nov	1 Dec– 15 Dec	16 Dec– 30 Dec	31 Dec– 14 Jan	15 Jan– 29 Jan	30 Jan– 13 Feb	14 Feb– 28 Feb	1 Mar– 15 Mar	16 Mar– 30 Mar
1970/71	(125)	0.0	1.6	0.0	1.6	0.0	1.6	16.0	23.2	29.6	26.4
1971/72	(544)	1.1	8.5	14.5	1.5	20.2	20.2	4.2	10.9	17.8	1.1
1972/73	(68)	1.5	2.9	23.5	0.0	2.9	29.4	5.9	17.6	16.2	0.0
1973/74	(94)	1.1	1.1	0.0	6.4	10.6	25.5	25.5	23.4	6.4	0.0
1974/75	(81)	0.0	16.1	12.3	4.9	12.3	14.8	9.9	14.8	12.3	2.5
1975/76	(56)	0.0	0.0	16.1	7.1	17.9	19.6	14.3	8.9	14.3	1.8

Multiple observations (different days) per individual included.

Locations of field feeding

Locations of field feeding by neck-banded swans were summarized by 10 minute block of latitude-longitude (Fig 1). Observer effort was concentrated in the Chester River area in Kent and Queen Anne's Counties on Maryland's Eastern Shore. Within that area, attempts were made to observe all field feeding locations without regard to flock size. Three study areas (Centreville, Claiborne and Eastern Neck) are within 25 km of that area. Intensity of field feeding there, when compared with other Bay areas, is over-emphasized when based on observations of neck-banded swans. Nevertheless, about 37% of all field feeding by marked swans was observed in one 10 minute block (390—0755) in Queen Anne's County. That block and the one to the north comprised 50% of over 900 observations of neck-banded swans feeding in fields.

Swans tended to fly farther inland than *B. canadensis.* Since large numbers of geese arrive in the Bay area four to six weeks earlier than swans, perhaps geese deplete food resources in fields closer to water.

Daily patterns of field feeding

About 1800 swans in the Sassafras River area of Kent County on Maryland's Eastern Shore were intensively observed during late January and February 1972. Ice was an insignificant environmental factor in the Sassafras River area when observations began on 27 January. In 30 days, none of these birds was observed feeding in the river or adjoining creeks during daylight hours. Although night-time feeding in the river cannot be discounted, it was improbable since little vegetation was found in the river the previous summer (Kerwin *et al* 1976).

Daily movements by the entire flock to fields about 8 km south of the river commenced not earlier than half an hour after sunrise (about 0710 local time). It was usually 0800 before the first swans left the river, but after 1200 before the last swans departed. Observations of one swan (C955) equipped with a small radio transmitter suggested that temperature affected the timing of daily movement to fields. On seven mornings between 27 January and 11 February this bird left Turner Creek, a Sassafras River tributary, between 0814 and 1022. On four mornings when ice had formed in the creek overnight, departure times were between 1546 and 1733.

The flock's evening flight to water was usually triggered by approaching sunset (when the sun appeared to touch the horizon) and ended not later than one hour after sunset. Although adverse weather conditions such as high winds (>30 km/hr) or fog delayed the evening flight, no swans stayed in fields long after sunset when normal weather prevailed. The absence of nocturnal field feeding by swans was further demonstrated by the movements of C955. On the afternoon of 10 February, after resting on ice most of the day, this bird left water at 1733 to feed in fields even though sunset was at 1738; he returned to water at 1809 after only 20 minutes of field feeding.

Undisturbed swans used the same fields and portions of fields day after day until food resources were apparently exhausted. For example, C955 was observed over the 30-day period in only five fields, all within a 3 km radius; his movements reflected those of the majority of birds in the flock.

Types of fields used

During the winters of 1970 and 1971, swans were observed feeding in 78 fields in Kent, Queen Anne's and Talbot Counties. Fifty-nine of these (75.6%) were harvested corn fields, 13 (16.7%) were other cereal grains (winter wheat, rye or barley) and 6 (7.7%) were harvested soybean fields. During the 1971 winter, availability of Eastern Shore crops was 52.0% corn, 15.4% wheat/barley and 32.6% soybeans (Maryland Crop Reporting Service 1974: Tables 29 to 32). These data indicated a definite preference for corn over soybeans, and a use of wheat/barley cropland in relation to abundance. Aside from crop preferences, swans tended to select large, poorly-drained fields located farther inland than those utilized by *B. canadensis.*

Likely future developments

That Maryland's Chesapeake Bay was less suitable as a wintering area for swans (and non-terrestrial waterfowl) from 1972 to 1977 was indicated by significant shifts in populations from Maryland to North Carolina and reductions in Bay aquatic food resources. Birds that moved to North Carolina, traditionally the southern end of the winter range, must have initially done so to obtain preferred foods, primarily submerged aquatic vegetation. Nevertheless, field feeding increased there as well. This is a strong indication that the flyway distribution of swans will return to the traditional pattern regardless of the abundance of Bay vegetation. Fewer swans will continue to add 350 km to their migration to winter in North Carolina only to feed in fields when Maryland's Chesapeake Bay area offers the same opportunity.

The eastern swan population will in all certainty increase in the future as a result of its adaptation to field feeding in flyway wintering areas. Such has been the result of adaptation to field feeding by other waterfowl species.

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Summary

Historically, field feeding by large numbers of swans while on spring migration from Atlantic Flyway wintering areas began in the early 1950s. But in all wintering areas of the Flyway, swan field feeding was insignificant until the early 1970s. In contrast, *B. canadensis* in these same areas began field feeding perhaps 25 to 30 years earlier.

The initial movement of a substantial number of swans into agricultural fields during the late winter of 1969/70 apparently was stimulated by six weeks of cold weather that froze over most shallow water areas in Maryland's portion of the Chesapeake Bay. Field feeding during the 1970/71 winter was again prevalent in February. However, swans moved into fields upon arrival in the Bay area in November 1971. Thus began a season-long pattern of field feeding that continues to date.

Analysis of observations of swans neck-banded from January to March 1970 indicated a positive trend in field feeding. Although the proportion of Flyway swans wintering in Maryland decreased substantially over the 1972 to 1977 period, field feeding by swans increased at an estimated rate of 8% per year. Between 50% and 70% of the Maryland swan population were feeding in fields by the winter of 1975/76.

Swans fed in fields on a daily basis with movement beginning within one to three hours after sunrise. Unless disturbed, swans usually remained in fields until sunset when they returned to water. Swans were not observed in fields after sunset except during inclement weather. The same fields were used on successive days until food resources were apparently exhausted.

During the winters of 1970/71 and 1971/72, 75% of fields utilized by swans were harvested corn fields. Harvested soybean fields were infrequently used by swans. Winter wheat and barley crops, which are normally harvested in late spring, were used more in relation to their availability than the other crops.

It is suggested that reductions in Bay submersed aquatic vegetation are responsible for continued field feeding and recent changes in winter distribution of swans. It is predicted that Maryland will remain the primary wintering area and that, as a result of expansion into agricultural habitats, the Atlantic Flyway population will increase regardless of trends in Bay vegetation.

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SUMMER BEHAVIOUR OF *CYGNUS CYGNUS CYGNUS* IN ICELAND

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A comparative study was made of breeding and non-breeding *Cygnus cygnus cygnus* in the Myvatn area of northeast Iceland.

Birds arrive in north Iceland, possibly via staging posts on the south coast. Breeders probably migrate paired, or may pair at staging posts, then move into the vicinity of breeding sites to commence nesting when waters become ice-free. Non-breeders first move to areas of spring grazing, then change to aquatic habitats.

Successful breeders moult at the breeding site. However, the remaining moulters can be found in two distinct flocks. Aspects of pairing and of quasi-territorial behaviour, and the time of build-up of the flocks suggest that the first flock, feeding on blanket weed *Cladophora,* is comprised of non-breeders. The second flock, feeding on pondweeds *Potamogeton spp,* is comprised of failed breeders and birds which have occupied breeding sites but have not produced eggs or young.

Detailed aspects of time-budgeting, feeding and reproductive behaviour of breeding and non-breeding birds were also investigated.

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THE BEHAVIOURAL ECOLOGY OF *CYGNUS CYGNUS CYGNUS* IN CENTRAL SCOTLAND

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Observation areas

Area 1 (see Fig 1), to the east, lies between the A91 road to the north and the A905 road to the south and extends to Monument Hill in the west and to Alva and Alloa in the east. Area 2, to the west, lies between the A84 and the A811 as far west as the B8075 and extending to Stirling in the east. All observations were made from a vehicle, mostly at a range of 100 m or more.

The distribution and size of flocks

During the period from 31 October 1977 to 7 May 1979, 142 flocks were recorded from the study areas, the term 'flock' being used for all numbers including singletons. Each flock is given an identification number. This number is retained if the flock remains the same size during consecutive observations, although it may move to a different locality.

During the same period, birds were present for a total of 5123 bird-days, 40.5% (2075 bird-days) in winter 1977/78 and 59.5% (3048 bird-days) in 1978/79. Of a total of 26 localities used, only nine contributed more than 200 bird-days each, only four of which received similar usage over two winters. The remainder each contributed fewer than 100 bird-days (see Table 1 and Fig 1).

Flocks ranged in size from 1 to 134, the mean being 26.9 (24.8 winter 1, 27.3 winter 2). However, if localities contributing more than 200 bird-days are considered separately, the mean flock size is 40 (n = 119: 40.8 winter 1, 39.5 winter 2) while for the remaining localities it is 18.2 (18.6 winter 1, 17.6 winter 2). Over two thirds (70.4%) of all flocks are of fewer than 50 birds (Fig 2). Large

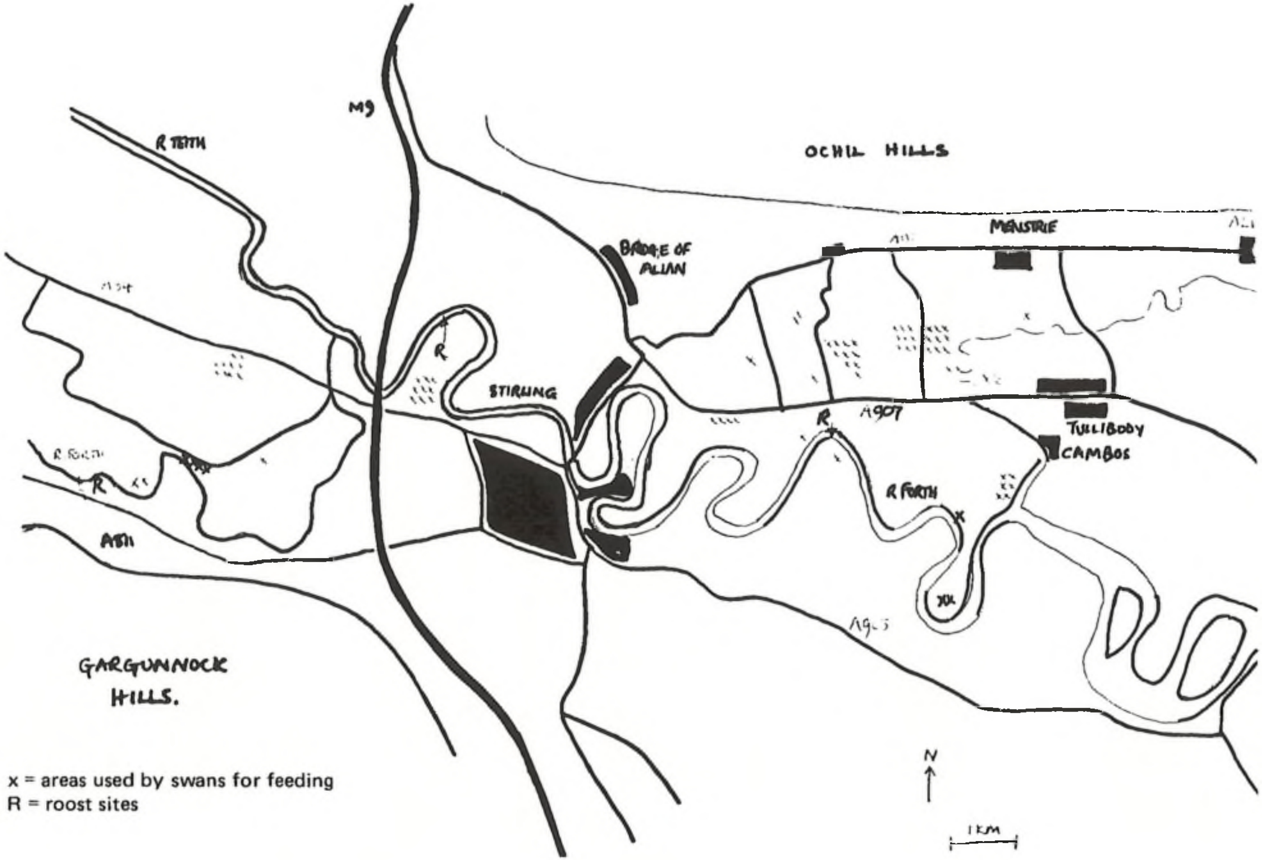

Fig 1. The study areas east and west of Stirling.

Table 1. Habitat use (expressed in bird-days) by *Cygnus cygnus cygnus* in the Stirling area.

	1977/78			1978/79	
Month	Stubble	Grass	Flood water	Stubble	Grass
October				6	
November	671		2.25	1372	
December	506			284	317
January	138	65	45.25	174	
February	31	71	215	69	412.5
March		207.25			43
April		85.75			356.75
May					14
Total	1346	429	262.5	1905	1143.25

flocks of over 30 birds are much more common between October and the end of the year, while small flocks of fewer than 20 are much more common between the beginning of the year and departure in the spring. Central Scotland is a stop-over area; there is good feeding but birds readily move on, especially during hard weather. Autumn arrivals are large but gradually larger flocks move on or split up into smaller units. The advantages of larger flock sizes are discussed later. Sites with higher usage support a larger mean flock size. During the second winter there was an increase of 1000 bird-days, yet mean flock size did not increase.

Flock structure

The number of swans using or passing through the Stirling area is only a small part of the Scottish wintering population, so the proportion of young present in flocks in this area does not necessarily indicate the general level of breeding success.

Including flocks both from the study area and the immediate vicinity, 160 flocks were recorded, of which 93 contained first-year birds. The number of yearlings was determined accurately for 85 of these flocks, the mean number per flock being 5 and the mean percentage 20.2. A total of 153 broods was counted for 26 flocks. Since all broods of zero are missed, it is not possible to calculate the proportion of adults which bred. Poor breeding success is as likely to be due to failure to hatch or rear any young (Boyd and Eltringham 1962) as to reduced brood size. The mean brood size was 1.86 in winter 1977/78 and 2.77 in winter 1978/79. Although the most frequent brood size was 2 in both winters, larger broods were commoner in winter 1978/79. Bell (1979) made a similar observation for northeast Scotland. Bulstrode *et al* (1973) found that 56% of pairs had young with a mean brood size of 3 and Hewson (1964) found that in large flocks the mean percentage of first-year birds was 15.1 and 26.4 in smaller flocks. Both these previous studies showed

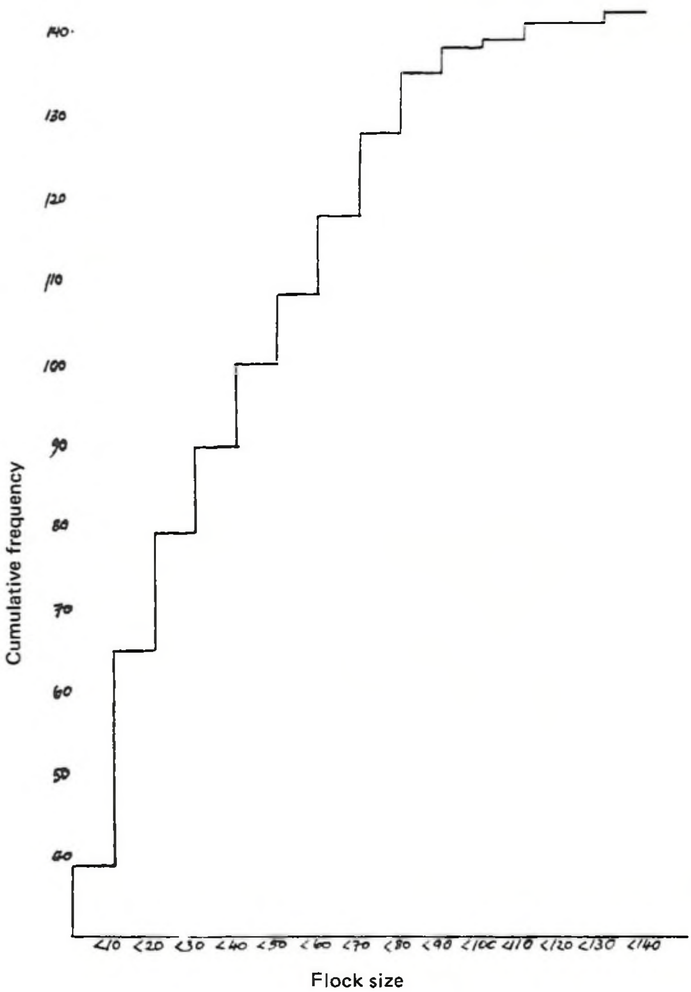

Fig 2. Cumulative frequency distribution of *Cygnus cygnus cygnus* flocks.

a similar breeding success to the present study. The weather in Iceland in summer 1979 was very bad and a census of *Cygnus cygnus cygnus* in Britain that winter showed that over large areas the percentage of young was less than 5% (J Kirk pers comm).

The pattern of behaviour in winter

C. c. cygnus began to use agricultural land for foraging after the series of hard winters in the 1940s (Owen and Kear 1972). In adapting to a new feeding habitat it has adopted a similar daily pattern to that traditionally shown by geese, ie it commutes between a night roost and a day foraging site. Unlike geese, swans do not normally feed by moonlight. In the first half of the winter, from late October until January/February, the swans feed at stubble fields on waste grain and some late-growing grass. In January or February they switch to feeding on grass (Table 1). When the swans are feeding on stubble fields they use the area east of Stirling and roost on the tidal Forth near Manorneuk. When eating grass, they change foraging area, moving to the west, and roost on a stretch of the River Forth near Kildean (Fig 1).

The area west of Stirling has about 10% more stubble than that to the east. In spite of the inevitable decline due to ploughing, by April the proportion of stubble to the west was still two thirds of that to the east in October. The swans could thus feed on stubble all winter. Feare *et al* (1974) found that in stubble fields used by *Corvus frugilegus* grain density declines rapidly from September until November and thereafter more slowly until March. Murton (1965) found that, for *Columba palumbus,* stubble fields became exhausted 'some time between November and early January'.

In October and December, over 40% of both areas was down to grass, whereas stubble at its maximum in October contributes only 24.3% of the western area and 15.3% of the eastern area. Birds are therefore active in their selection of stubble in the autumn and of grass in the spring. Root crops are not common in this area and the use of them by swans is rare and confined to potatoes. Many species, eg geese and sheep (Owen 1971), are capable of selecting those foods with a higher nutritional value.

The availability of grassy vegetation declines only slightly during the winter, from 42.2% to 39.5% between October and April in the west and from 45.9% to 39.8% in the east area. Some is lost to ploughing and some gained owing to the sprouting of winter wheat. Winter wheat and the early spring growth of grass leys is of greater nutritional value than old grass, which becomes less palatable as it gets longer. Autumn grass is presumably of less value than grain, while in late winter new grass is growing as grain densities are being depleted, hence the switch for feeding.

The overall preference for stubbles in autumn and grass in spring has been observed in Aberdeenshire and Dumfriesshire (J Kirk pers comm).

Weather conditions

Prolonged cold weather reduces the areas of fresh water available to swans while snow cover prevents them from grazing. For instance, the extremely cold weather of January 1979 drove birds from the study area. The weather was severe throughout Scotland and most inland waters were frozen for long periods. Swans became scarce in central areas while larger numbers were reported in the southwest. A sighting of swans there flying out to sea (G Sheppard pers comm) on 19 January 1979 suggests that some moved through to Ireland.

Winter movements

Previous observations by Henty (1977) suggested that swan flocks utilizing the area east of Stirling were small, moved regularly between fields and sometimes used separate roost sites. Since 1977, however, it has been rare to find swans other than in a single flock and this tended to use a single field over a period of several days and also a single roost site.

Swans leaving a roost, either river or loch, must climb above tree and powerline height before flying out to the fields. From this height (circa 30 m) they are able to see the variety of fields available to them, as well as where earlier departing birds have landed. Abandonment of previously favoured fields may be due to disturbance or reduced food density. Where birds have been seen to be disturbed, they have moved to another field of the same type.

Diurnal behaviour

Where light intensity is the controlling factor, weather factors such as cloud, mist and frost (Owen 1977) would be expected to delay morning flight and advance evening flight. Seibert (1951) working on Ardeidae found that they left the roost at a lower light intensity than that at which they arrived, while Siegfried (1971) suggested that with *Bubulcus ibis* a specific light intensity threshold for roosting is modified by environmental constraints and physiological needs. Hein and Haugen (1966) found that there was least change in the start of morning flight and the end of evening flight. The end of morning flight and the duration of evening flight changed most. They also found that on dark or foggy days morning flights were delayed and evening flights were prolonged.

Departure time

The time of departure for each subflock and the light reading at that time were recorded. A standard Weston light meter was used in the field. This was later calibrated against a 40x opto-meter to convert light readings into foot-candles. Light readings (zenith) were also taken at regular intervals in the final half hour of daylight. Times GMT were converted to minutes after local sunset (Glasgow minus 2 minutes) and a 50% departure time (shown by Davis (1956) with *Sturnus vulgaris* to be the endpoint least influenced by chance variation) was used. Data are available for 39 evenings for day-lengths from 7 hours to 15½ hours (time between sunrise and sunset).

There is a wide scatter of post-sunset departure times for days of similar length and any relationship is masked. Examining the data from midwinter alone shows a tendency towards earlier departure relative to sunset on longer days.

Some other waterfowl have also been shown to exhibit this relationship, eg Hein and Haugen (1966) found both light intensity and season to be important to *Aix sponsa*. Morning flight began when illumination reached 1 foot-candle in August, whereas by November it began at illumination levels of less than ¼ foot-candle. Evening flights were similarly affected, birds arriving at the roost between 70 and 2 foot-candles in August and between 4 and ¼ foot-candles by late October. Martin (1957), also working on *A. sponsa*, found that flight times were linked with sunset and sunrise (seasonally variable). Morning flights began about half an hour before sunrise and evening arrivals concentrated mostly between 15 and 30 minutes after sunset. Siegfried *et al* (1977) found marked seasonal variation in arrival time at the roost in *Anas sparsa*.

In the present study, frequency of departures increases markedly with falling light intensities (Fig 3). Few departures occur above 0.1 to 0.25 foot-candles, the majority at less than 0.08 foot-candles. Very heavy cloud reduces illumination levels. It was expected that at low temperatures the birds would feed for longer to make up for greater energy loss but the present study does not support this. The swans sometimes remain well after sunset at any time during the winter. Assuming that there is enough light for them to see to fly safely even below the sensitivity of the light meter, the question still remains: why do they remain on the fields after dark? On most evenings, often the last ten minutes are not spent feeding. Waves of 'head-up' positioning pass through the flock and wing-flapping becomes more frequent. Some birds begin head-bobbing and calling and frequently form small groups walking about through the flock. Eventually all members of the flock will stop preening or feeding and adopt the 'head-up' position. Then, finally, departure will occur. Where subgroups depart separately, it is normally the birds which have recently been head-bobbing that leave first. In the time that all this takes place, visibility often becomes very poor. Unless such social behaviour is crucial to the flock members in some way, it seems a dangerous and unnecessary delay, in view of flight obstacles and the risk from flight predators.

It is possible that, for much of the winter, swans feeding and roosting in such an area are not under extreme energetic stress and can afford to spend time on the foraging grounds not feeding. Henty (1977) found 'no noticeable effect of frost during the preceding 24 hours although continued hard weather disrupted the whole commuting system'. If the swans were already under physiological stress, cold weather would be expected to exacerbate this. The effects of low temperatures at night, the critical period at high latitudes (Kendeigh 1961), can be ameliorated in several ways. Communal roosting in *C. c. cygnus* may serve several functions such as both an anti-disturbance strategy and as an information centre but it could well aid in thermo-regulation. Aquatic species roosting on a river will receive some wind shelter from river banks and vegetation. Even when the wind direction is

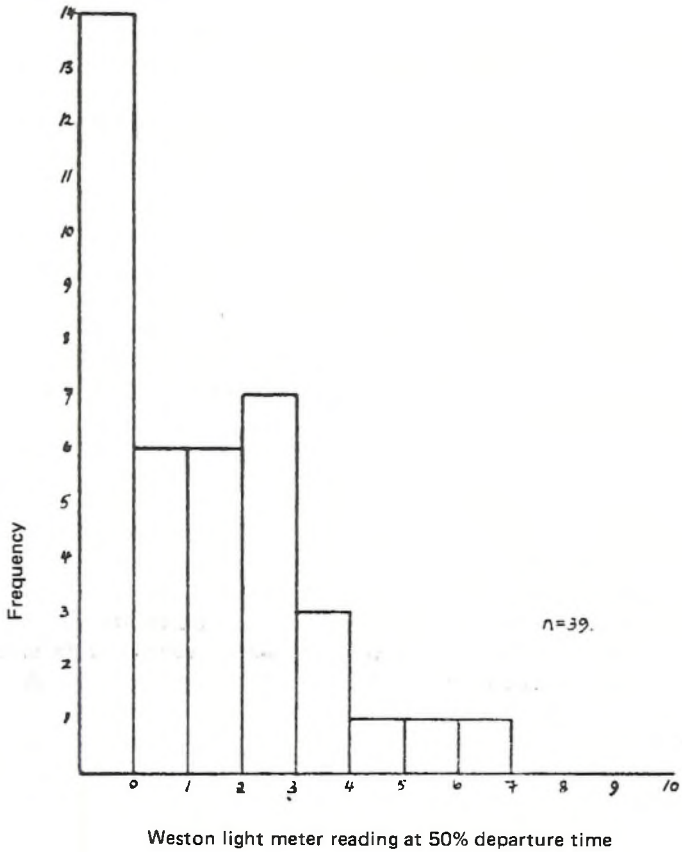

Fig 3. Departure of *Cygnus cygnus cygnus* to the roost in relation to light intensity.

parallel to the section of the river, roosting in a flock will aid thermo-regulation by decreasing wind speed. Some members of the flock will always be in the lee of others. Wind velocity has been shown by many studies directly to affect heat loss and hence energy uptake.

Feeding regime

It is assumed that swans do not feed at night. Casual observations at the roost site after dark and at dawn showed that, when it was possible to make out the birds, drinking and preening are important activities in the evenings. In the mornings head-up and calling are most common.

Monthly activity budgets were compiled for winter 1977/78. Scans were made every 15 minutes and the proportion of the flock engaged in feeding, preening, roosting and head-up was recorded. The term 'feeding' includes birds obviously pecking and those between pecks, ie with the head below the level of the body and close to the ground. 'Preening' is used for all comfort movements including wing-flapping and defaecation. 'Roosting' includes birds standing or sitting with the head resting on the back and tucked into the feathers, whether the eyes are open or closed, and also birds with the neck curved so that the head lies almost horizontally on the lower neck. 'Head-up' includes birds standing or sitting with the head and neck raised above the level of the body. Subjectively, 'head-up' is used by birds which are generally 'vigilant', as opposed to 'extreme head-up', which occurs when a specific stimulus has been perceived and is directed towards it, such as a disturbance or birds joining or leaving the flock. Mean activity level and hence the proportion of time spent in these activities are calculated from the sample scans (Table 2).

Table 2. The activity budget of *Cygnus cygnus cygnus* in the Stirling area 1977/78.

		November	December	Fields January/ February	Water January/ February	March
Feeding	mean per daylight hour (%)	70.8	72.7	61.6	31.5	75.3
	mean per hour (%)	26.5	27.3	28.2	14.4	40.8
Preening	mean per daylight hour (%)	2.1	1.7	3.7	8.7	4.4
	mean per hour (%)	0.8	0.7	1.7	4.0	2.6
Roosting	mean per daylight hour (%)	12.7	9.0	18.8	29.6	4.1
	mean per hour (%)	67.3	65.9	62.7	67.8	47.9
Head-up	mean per daylight hour (%)	14.5	16.5	16.1	30.0	16.1
	mean per hour (%)	5.4	6.2	7.4	13.7	8.7

As is to be expected, feeding is the most time-consuming activity (between 60% and 75% of time). Ecologically, foraging is the most important behavioural component of the time/activity budget and non-foraging daytime activities are influenced by feeding intensity, except head-up, the second most important behaviour in terms of time investment (14.5% to 16.5%).

Many animals show a bimodal pattern of activity, with morning and afternoon peaks. This is true of geese, eg Owen (1972) and Ebbinge *et al* (1975), and of dabbling ducks (Henty 1975).

There is a marked feeding pattern between November and February (Fig 4), with

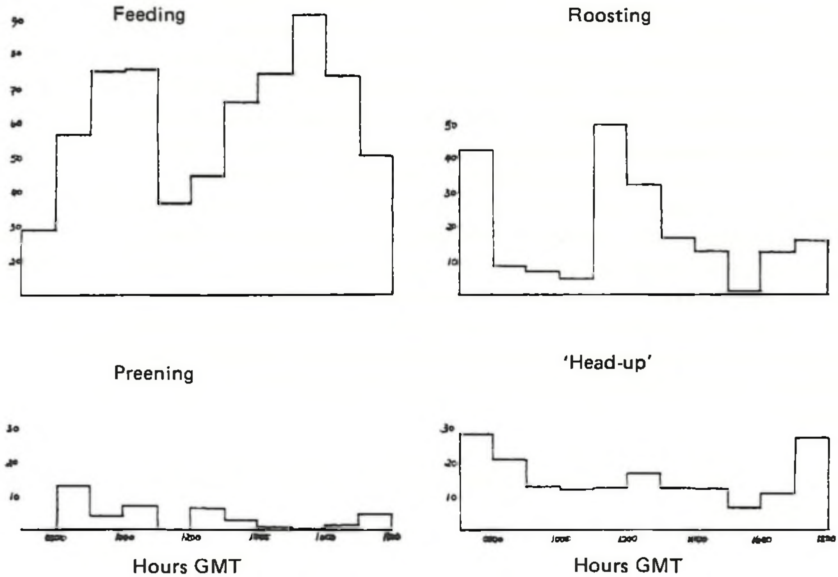

Fig 4. Activity budget: January/February 1978. Grass.

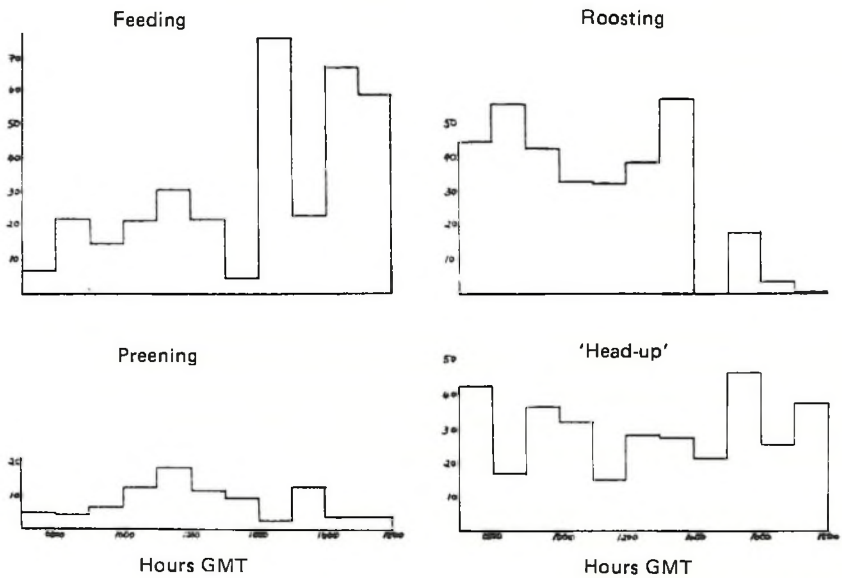

Fig 5. Activity budget: January/February 1978. Water.

high morning and afternoon peaks. By March (Fig 6) this pattern has changed somewhat, with birds feeding at a higher rate for longer and the midday lull has almost disappeared. Excepting March, roosting peaked during the feeding lull and was otherwise at a very low level. Some head-up occurs throughout the day but with noticeable increases occurring usually at the beginning and towards the end of the day. Preening occupies least time and occurs at low levels throughout the day.

The pattern observed for swans feeding on land is distinctly different from that of birds feeding on water (see Figs 4 and 5). Owen and Cadbury (1975) found that for both *C. olor* and *C. columbianus bewickii* the basic pattern of activity was for feeding to begin at a low level at sunrise, for it to increase steadily, reaching a plateau three hours after sunrise in *C. olor* and six hours after in *C. c. bewickii,* and continuing until dark. Intensive feeding continued for one hour after dark in *C. c. bewickii.* For the latter half of January and the first week of February 1978, the *C. c. cygnus* flock within the study area spent its time on flooded meadows by the River Forth near Cambus. The meadows drained between 8 and 15 February owing to a breach in the retaining bank and the flock moved back to the fields. The pattern observed for aquatically feeding swans was very similar to that seen by Owen and Cadbury (1975). There was a steady rise in feeding until between seven and eight hours after sunrise, ie an hour later than that for *C. c. bewickii.* Roosting is the dominant activity in the morning, preening reaches its maximum (18%) between 1100 and 1200 hours, while head-up occurs throughout the daylight period at between 18% and 47%.

This major difference in feeding activity pattern is attributable to the fact that birds feeding on fields must fly to and from the roost and are unable to feed during the hours of darkness. Birds on water, on the other hand, do not have the extra energy requirements of flight and can continue to feed after dark.

The requirements immediately before the spring migration, when fat reserves must be laid down for the migration and, in the case of females, for egg production and the incubation period, are likely to be greatest. Any differences in feeding between the sexes should be most marked at this time.

C. c. cygnus being herbivorous is limited by a low energy diet. As far as is known, there is no cellulose digestion by geese (Marriott and Forbes 1970; Mattocks 1972) and it is reasonable to assume the same for swans. Swans, like geese, counter these factors by a rapid throughput of a large volume of food. Grazing is limited by the gizzard's capacity to process food. For any given energy requirement, therefore, there is a fixed lower time in which the necessary food quantity can be processed. When daylight is equal to this minimum necessary foraging time, the birds will be at starvation level and will lose weight. Such weight loss can be accepted if the overall energy budget is balanced in the long term.

Feeding rate

Time spent foraging is dependent on several proximate factors such as: a) energy requirements, in turn dependent on each individual's weight and metabolic rate, b) daylength, c) weather factors such as low temperature. The ultimate factors involved may be the risk of mortality from predators or from collision during flight due to remaining on the fields after dark. Without changing to a higher energy food supply swans under physiological or environmental stress could: a) feed faster, b) feed longer, c) feed faster and longer. As can be seen from the winter time budget data (Table 2), the time spent feeding increases even though daylength is also increasing. In November and December the feeding day is of approximately nine hours. This increases to 11 hours by February and 13 by March. The cumulative percent of time feeding for any given number of hours after dawn is generally similar except in January/February, eg nine hours after dawn the cumulative percent feeding is 636.4 in November, 654.12 in December, 551.96 in January/February and 696.96 in March. However, the cumulative totals for each month increase progressively. As daylength increases, more time is spent feeding (Table 3).

Table 3. Cumulative percent of time feeding, winter 1977/78.

Time	November	December	January/ February	March
06^{00}–07^{00}				85.91
07^{00}–08^{00}			29.1	170.41
08^{00}–09^{00}	72.27	82.65	86.25	246.86
09^{00}–10^{00}	139.62	170.33	161.95	321.86
10^{00}–11^{00}	225.47	247.47	237.78	391.06
11^{00}–12^{00}	311.14	312.69	274.55	461.98
12^{00}–13^{00}	340.04	367.29	318.75	534.48
13^{00}–14^{00}	398.49	433.64	385.34	619.76
14^{00}–15^{00}	481.12	523.25	459.9	696.96
15^{00}–16^{00}	562.82	605.95	551.96	769.31
16^{00}–17^{00}	636.4	654.12	626.12	845.56
17^{00}–18^{00}			677.42	907.44
18^{00}–19^{00}				979.23

Not only is the length of the feeding day extended by March but the mean hourly level of feeding is also highest. Time spent feeding is only a relative measure of feeding intensity. The quantity of food ingested and hence the energy gained during a day is also dependent on the rate of feeding. The pecking rate of adults, yearlings and parents was measured whenever possible by the method used by Owen (1971). Birds were selected randomly and the number of pecks made during one minute was measured directly between 1977 and 1979. A different method was used in 1979/80 because within a minute's sample there was a high chance that another behaviour would interrupt feeding. This involved measuring the time taken to make 20 pecks. Pecks per minute were then calculated.

The increase in time spent feeding in March 1978 was not correlated with a

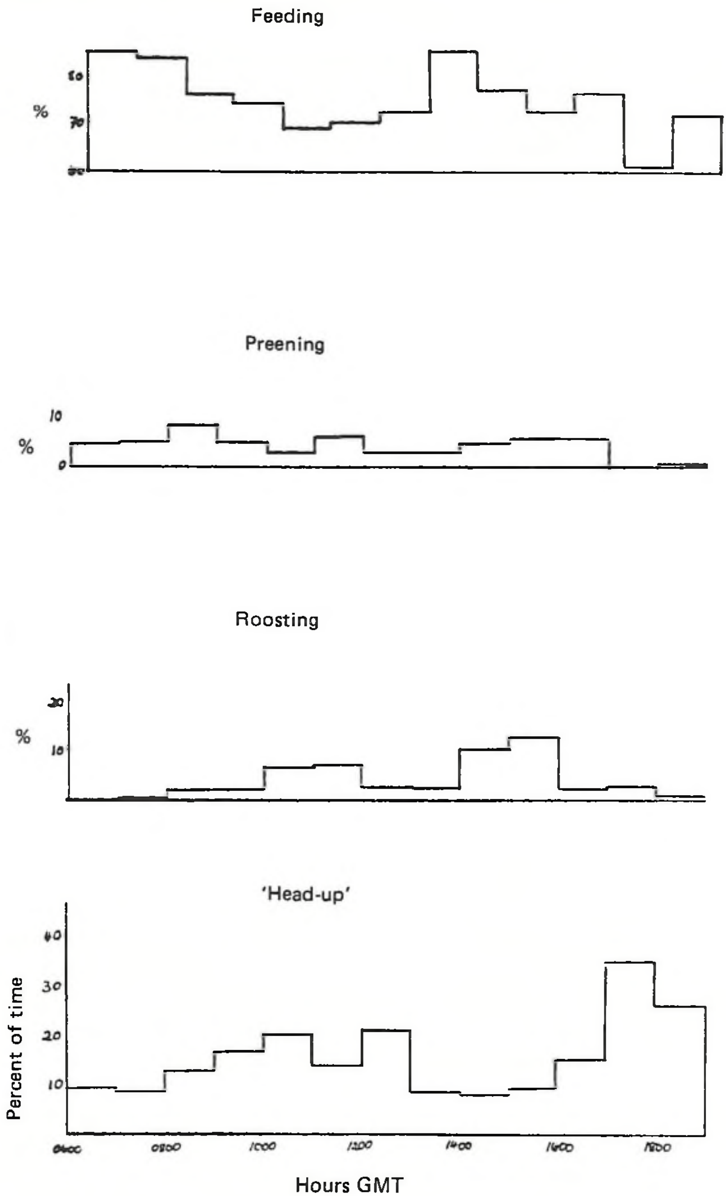

Fig 6. Activity budget: March 1978.

decrease in peck rate. The latter is assumed to be equivalent to ingestion rate as no peck should be unsuccessful. This suggests that, overall, more food is ingested per day in late winter, because the birds' physiological requirements have changed.

The effect of time of day on pecking rate was also studied. Several observations were usually made within a period of ten to 15 minutes. In three consecutive winters the relationship was very similar. Peck rate increased linearly throughout the day, eg January 1980 ($r = 0.5$, $p < 0.01$) to a maximum of over 65 pecks per minute (Fig 7). This is exactly the same relationship as that found by Owen (1972)

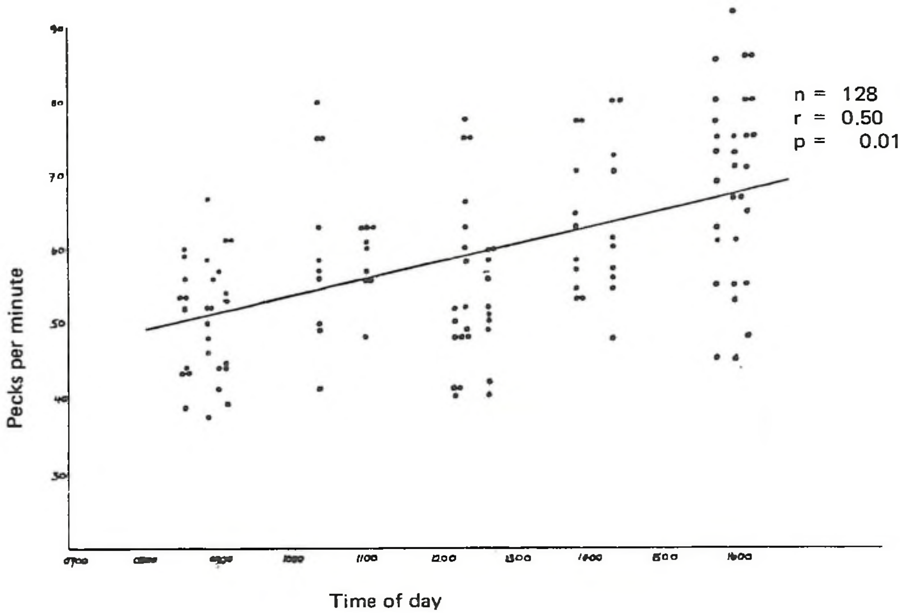

Fig 7. Peck rate of adults, January 1980.

for *Anser albifrons,* although its pecking rate was over twice as high. In *A. albifrons* there is evidence that the increased rate of feeding towards evening leads to an accumulation of grass in the long elastic oesophagus because the gizzard is unable to process it fast enough. It seemed very likely that this would occur in field feeding *C. c. cygnus,* and a yearling bird which flew into powerlines on its way to the roost had an oesophagus full of small pieces of grass.

In March 1978 both adults and yearlings showed the same linear increase through the day in pecking rate. The slope of the regression lines is very similar ($r = 0.318$ adult, $r = 0.321$ yearlings) but that of the yearlings lies above that of the adults. Adult peck rate begins in the morning at about 45 ppm and increases to about 55 ppm, while yearling peck rate begins at about 55 ppm and rises to about 65 ppm.

In contrast to *A. albifrons* which rests more on the longer days, *C. c. cygnus* uses the latter to feed for longer. There is a slight increase in preening, time spent roosting during the day is reduced and head-up remains constant.

Vigilant behaviour

At any one time there is usually at least one flock member in head-up position and looking around. Since a flock is a heterogeneous mixture of birds of different reproductive status and since birds of different status will have differing motivation for feeding and 'vigilance', then it is to be expected, that there should be some behavioural differences between such classes.

Parents, having expended a great deal of energy during the summer in terms of egg production, nest building, incubation, nest and territorial defence and attention to the young, will be in relatively poor condition by the autumn. Non-breeders, having expended no energy in reproductive effort, should be in good condition. Young birds of the year are still growing and have recently migrated and have a great deal of weight to gain. Therefore, parents should ingest more food than non-breeding adults. Young should ingest more food than adults. However, these expectations will be confounded by the conflicting requirements of vigilant behaviour. There is likely to be some behavioural investment by parents in their offspring and this is likely to take the form of vigilance directed towards those offspring and more time generally alert for potential dangers to them. Adults without offspring should spend less time in head-up position than parents. There is no evidence that second-year birds rejoin or nelp their parents. Young birds may not have fully developed the normal pattern of vigilant behaviour. They can rely on their parents being vigilant but can feed only by their own efforts, hence they will spend less time head-up than either their parents or adults.

If parents have both the greatest energy requirements and the greatest motivation for head-up of the three classes, then they may feed faster in between bouts of head-up. Young birds, on the other hand, may spend longer feeding and less time alert or longer feeding and feed faster.

Birds were chosen at random and followed until they became vigilant. The interval between this first bout of head-up and the next was timed with one stop-watch and the length of the following bout of head-up was timed with a second. Parents raise their heads for a mean time of 10.1 sec, adults for a mean time of 9.2 sec and young birds for 7.2 sec. Although the differences between the bout lengths of head-up for the different reproductive classes are not significant (using the Mann Whitney U test), the trend of the means, with parents spending longest and young birds spending shortest times head-up, is, as was expected, when considering the likely relative motivation for this behaviour.

Although the lengths of bouts of head-up do not differ significantly between the three classes, the period from one bout of head-up to the next does. The inter head-up period for parents had a mean length of 40 sec, for adults 77 sec and for young birds 175 sec. The differences between parents and adult and between parent and young were significant ($p = 0.002$, $p = 0.00003$, Mann Whitney U test) but not that between adults and young ($p = 0.389$). Parents, then, are head-up more frequently than either adults or young, although not for longer, again as anticipated.

Frequency and length of bouts of head-up are factors having direct effects on feeding, since these behaviours are mutually exclusive. It follows that parents have less time to feed than either adults or young. If they have to make up condition lost during the breeding season, then they must feed faster or select foods of higher energy values. As yet, there is no evidence on these points. Immatures spend less time head-up less frequently than other birds, thus providing extra feeding time, but they also feed faster than adults. This would enable them to increase in weight rapidly during the winter. Feeding time might also be extended in young birds because they may be less efficient feeders than adults.

It is expected that parental vigilance will decline during the winter as their offspring become larger and older. During winter 1977/78 for all months except November and January there was no significant difference between the lengths of bouts of head-up for the three classes but in November, just after arrival when young birds are relatively small, parents spent longer head-up than they did ($p < 0.01$, Mann Whitney U test). In January young spent longer alert than adults ($p < 0.05$, Mann Whitney U test). It is not known why. The longer bout lengths of head-up in November shown by parents agree with the assumption that parental investment is in the form of vigilance and this declines through the winter. The difference may be increased at this time since the young will need to feed more at this stage and will not have fully developed the adult behavioural sequence of regular head-up interspersed with feeding.

By March all birds spend longer on the foraging grounds and spend longer feeding. This increase in feeding prior to the migration leads to the disappearance of any differences in the inter head-up bouts between the three classes.

Flock size and behaviour

It is evident that flock size affects some aspects of individual behaviour, especially vigilance. Where vigilance increases, other behaviours must decrease and there will be some reduction in feeding time which might be compensated for by a faster feeding rate. The levels of vigilance for a range of flock sizes from 1 to 150 was measured to test for *C. c. cygnus* the hypothesis as stated by Lazarus (1978): 'If flocking reduces the individual's risk of capture by a predator, then the time spent by individuals in vigilance will decline as flock size increases, since the benefit to be gained from such vigilance also declines'.

Scans of the flocks were made, one every minute. At each scan the proportion of birds head-up was recorded and after ten scans the results were combined to produce a mean proportion of head-up. The number of birds vigilant was significantly correlated with flock size ($r = +0.85$, $n = 86$, $p < 0.001$). The percentage of birds vigilant declined significantly as flock size increased ($r = -0.40$, $n = 89$, $p < 0.001$), declining rapidly at first before levelling out at a flock size between ten and 20 (Fig 8). Individuals in larger flocks thus spend less time in vigilant behaviour and therefore have more time available for other activities such as feeding.

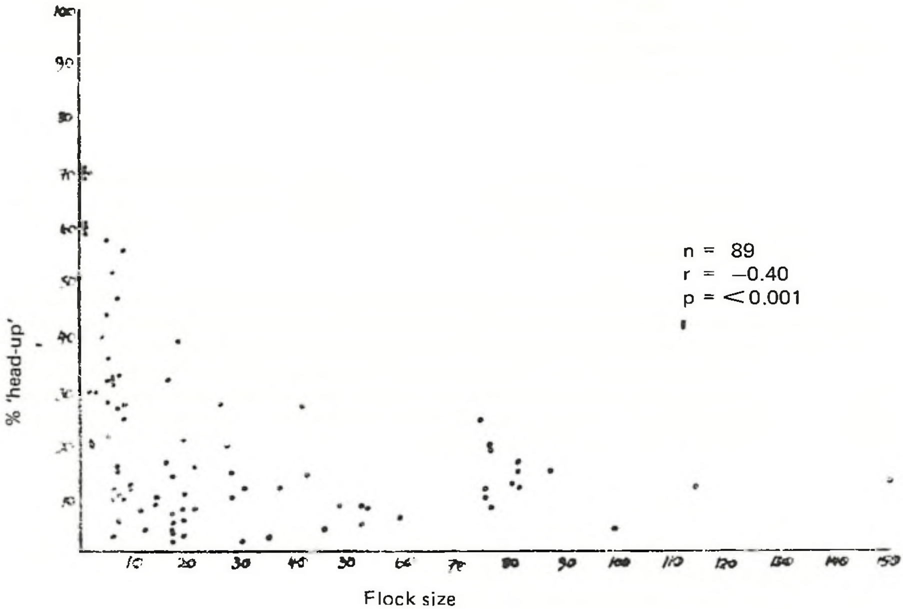

Fig 8. The relationship between flock size and the proportion of the flock which is 'head-up'.

It could be that individuals assess the size of the flock they are in and adjust their behaviour accordingly or that, because of the 'peripheral predation' phenomenon (Lazarus 1978), individuals on the edge would be expected to be more vigilant, as suggested by Drent and Swierstra (1977). As flock size increases, the periphery will represent a reduced proportion of the flock. The structure of swan flocks is different from that of geese. The flocks are usually smaller and flock shape is far less regular. It is not possible, therefore, to assess whether individuals are peripheral or central and in small flocks it seems unlikely that this factor would be important. Nearest neighbour distance could well be an important factor in regulating vigilant behaviour.

The important implication of reduced vigilance by individuals in larger flocks is that more time is available for feeding. This was conclusively demonstrated by Abramson (1979) working on *Numenius arquata.* He showed that look-up decreased significantly as the number of birds increased, while the number of prey captured per individual increased.

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This study was carried out while I held a Stirling University studentship. I am grateful to the Department of Psychology for the use of facilities, to my supervisor Dr C J Henty for his support and to the technical staff for their practical help. I thank John Kirk for many enjoyable and invaluable hours spent discussing the swans. My greatest thanks go to the Vincent Wildlife Trust for their encouragement and for providing transport.

Summary

In central Scotland the size and structure of flocks and their use of agricultural land and patterns of movements between roosting and foraging sites are examined. Birds in autumn feed on waste grain from stubble fields and switch to young grass in January/February. This switch also involves a change in roost site.

Feeding occupies between 62% and 73% of time during autumn and midwinter. Diurnal and seasonal feeding patterns are described and comparisons drawn between aquatic and terrestrially feeding swans. The former slowly increase the proportion of time spent during the day, the latter have distinct morning and afternoon peaks. Feeding as a proportion of the daylight hours increases prior to the spring migration and feeding rate increases prior to evening roost flights. Their behaviour in winter is discussed with reference to environmental and physiological stresses imposed upon them throughout the year.

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FOOD SELECTION BY *CYGNUS OLOR* IN CHESAPEAKE BAY, MARYLAND

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The food habits of non-native *Cygnus olor* in Chesapeake Bay were examined between 1975 and 1978 to determine their effects on the aquatic food supply of native wintering waterfowl. Swan food preferences and daily intake were determined by faecal and gizzard analysis, floral analysis of swan nesting and moulting areas and testing with captive birds.

Preference for submerged vascular vegetation by *C. olor* was demonstrated by

5 gizzard and 92 faecal analyses. In summer, approximately 83% of identifiable faecal matter was submerged vascular flora as opposed to 44% in winter. In pen tests with captive birds, freshwater species such as *Elodea canadensis* and *Valisneria americana* were preferred over the more common brackish water species such as *Ruppia maritima* and the pondweeds *Potamogeton.* However, only *Myriophyllum spicatum* among common submerged aquatics was not selected regularly.

Proximal analysis of these food species demonstrated a wider variability of nutritional content within than between species. Food selection may result from factors other than nutritional quality.

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Hunting and Management

MANAGEMENT OF SWANS IN THE UNITED STATES

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Management plans

The US Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) are independently developing national plans for managing waterfowl and will eventually work together with Mexico towards development of a plan for North America. Apart from these national and continental plans for waterfowl in general are those for particular species and populations within the flyways. Initially in the Pacific and Central Flyways, to be followed in the Mississippi and Atlantic Flyways, biologists from state wildlife agencies and USFWS, aided by those from Canada, Mexico and USSR, have drafted guidelines for managing swans, geese, *Branta bernicla* and cranes. These plans identify goals, objectives, information and habitat requirements, and assign priorities, responsibilities and schedules for accomplishing necessary tasks. The draft plans will be changed where deemed advisable after review and comment by participating agencies and the public. The formal agreements stemming from these plans will provide long-term benefits to both swans and people who enjoy them.

Hunting

In the fall of 1962, Utah became the first state where *C. c. columbianus* could be legally hunted since enactment of the Migratory Bird Treaty Act of 1918. Nearly 1000 hunters, who were authorized by special permit, bagged 320 swans. Utah is now authorized to issue 2500 permits free of charge to hunters for the taking of one swan during the season. Interest in hunting swans is high, with applicants numbering more than three times the number of permits issued. The only other states where swan hunting is permitted are Montana and Nevada, each of which is authorized to issue 500 permits. Swan hunting is permitted only in Churchill County in Nevada and in Teton County in Montana. Statewide hunting is not allowed in these two states, to lessen the chance killing of *C. c. buccinator.* Seasons may be of the same length as, and must be concurrent with, those for ducks.

During the past nine years (1970–78) when the three states were authorized to issue 3500 permits, hunters bagged an average of 1234 swans per season (Regenthal and Provan 1979, Barngrover 1979, D Childress pers comm). Utah hunters reported knocking down but not retrieving 22% of the number bagged (Regenthal and Provan 1979) or almost twice the percentage of unretrieved geese. Hunters may use only shotguns of 10 gauge or smaller bore for hunting waterfowl. However, shotshell loads and gauge size are selected at the hunter's discretion. We believe that some crippling can be attributed to duck hunters who shoot opportunistically at

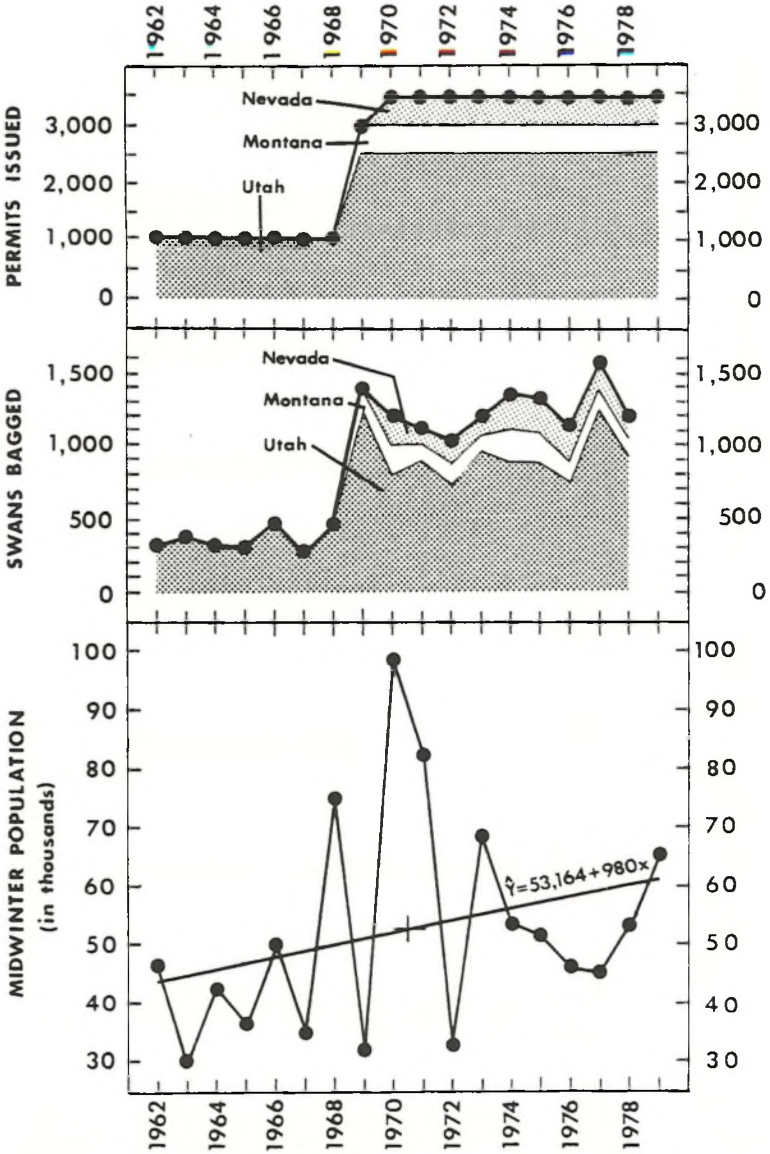

Fig 1. Numbers of hunting permits issued, *C. c. columbianus* bagged, and counted during Midwinter Waterfowl Surveys in the Pacific Flyway. Winter counts were in January and are shown under the preceding hunt season, eg the survey of January 1980 is shown under 1979.

Table 1. Harvest of *C. c. columbianus* by permitted hunters in Utah (statewide), Nevada (Churchill County) and Montana (Teton County), 1962–78.

	Utah[1]			Nevada[2]			Montana[3]		
Hunting season	Permits issued	Estimated harvest of swans	% grey swans in harvest	Permits issued	Estimated harvest of swans	% grey swans in harvest	Permits issued	Estimated harvest of swans	% grey swans in harvest
1962–63	1000	320	38						
1963–64	1000	392	48						
1964–65	1000	335	37						
1965–66	995	336	45						
1966–67	1000	491	42						
1967–68	1000	246	54						
1968–69	1000	520	58						
1969–70	2500	1290	62	500	87	63			
1970–71	2500	812	52	500	208	49	500	179	41
1971–72	2495	916	33	500	102	37	500	91	33
1972–73	2500	754	38	500	124	34	500	150	31
1973–74	2500	981	50	500	109	47	500	101	45
1974–75	2500	928	42	500	190	39	500	259	48
1975–76	2500	929	46	500	188	38	500	247	34
1976–77	2500	764	41	500	206	34	500	139	43
1977–78	2488	1277	54	500	84	46	500	214	35
1978–79	2500	916	45	500	90	47	500	146	–

[1] Regenthal and Provan (1979)
[2] Barngrover (1979)
[3] D Childress, Montana Department of Fish and Game, pers comm

swans with less than optimum shotshell loads.

Forty-seven percent of 14 975 swans harvested in the three states during 18 seasons were grey-plumaged (young) birds (Table 1). Since grey-plumaged swans in wintering areas generally comprise about 15% to 20% of the population, they are being harvested at a greater rate than white-plumaged (subadult and adult) swans. Younger birds are less wary and, therefore, more vulnerable to gunning than are older birds. Some hunters believe the younger birds are better eating. Other hunters seek older birds for display as trophies.

During the 15 seasons (1947 to 1961) immediately prior to regulated swan hunting, the midwinter population of Pacific Flyway *C. c. columbianus* averaged 32 080 birds, with an average annual increase of 1762. During 18 seasons (1962 to 1979) of hunting, the population averaged 53 164, with an average annual increase of 980. Fig 1 shows the number of permits issued and swans bagged and the size of the swan population in winter since hunting has been allowed.

Hunting of swans in Alaska is prohibited. The state requested but was denied a fall season on *C. c. columbianus* in areas where mixing with either *C. c. buccinator* or *C. c. cygnus* would be unlikely. An illegal subsistence harvest of swans is known to occur in Alaska. Klein (1966) reported that residents of the Yukon-Kuskokwim delta took 5600 swans annually. That particular population of swans winters in the Pacific Flyway. Some persons speculate that the harvest has been increasing in proportion to the size of the rapidly increasing human population and because improved modes of transportation facilitate access to hunting areas. Some native leaders report that residents of the delta are purposefully reducing their harvests of swans and of certain geese that have undergone recent declines in numbers. Satisfactory data on this illegal harvest are neither available nor readily obtainable.

Recent efforts by the United States to modify various bi-lateral migratory bird treaties are directed toward allowing a regulated and legal subsistence harvest of waterfowl by residents of rural Alaska. Conceivably, a subsistence season could allow for limited harvest of swans in spring and summer. However, such seasons and sizes of allowable harvests have not been considered or proposed.

The Atlantic Flyway Technical Committee has recommended to its governing Atlantic Flyway Council that a season on *C. c. columbianus* and *C. olor* be initiated. They recommend that early emphasis be given to seasons in Delaware, Maryland, Virginia and North Carolina where crop depredation is increasing. The Committee cites as reasons for this hunt: (1) an increasing number of swans that in no way seem in jeopardy (Bartonek *et al* 1981), (2) the increased hunting opportunities, (3) a desire to substitute hunting mortality for natural mortality, and (4) the need to alleviate crop depredations. The Council has not as yet submitted to the USFWS any specific proposals. It appears likely that there would be strong objections from some quarters to a swan hunting season in the eastern United States.

Depredation

Once it was only the hapless hunter who fell into an 'eat out', a crater caused by foraging swans, and complained about the eating habits of swans. Now, with the recent changes in feeding behaviour of these birds, it is likely to be a farmer who complains about damage to winter wheat, rye or barley caused by swans when they puddle or compact soil. Field feeding by swans was an oddity in the mid-1960s (Nagel 1965), but during the past three to four years *C. c. columbianus* has been observed feeding in dry, disced corn fields on the Sacramento River Delta in early fall and in barley fields in January and February in the Sacramento Valley of California (J R LeDonne pers comm).

The initiation of field feeding by *C. c. columbianus* wintering along the Atlantic Coast can be traced to the winter of 1969/70, when a six-week cold wave forced swans into nearby fields for food. The following fall, some swans moved into the fields, thereby instilling a tradition for field feeding in a segment of the population (Munro 1981).

Depredation complaints come mainly from local areas along the Atlantic Coast, particularly North Carolina. The magnitude and costs of these depredations have not been estimated. Farmers are not hesitant to harass from their fields and occasionally kill those swans causing problems.

Swans regularly eat out submerged aquatic vegetation at the Mattamuskeet National Wildlife Refuge, North Carolina, early in the season. They are thereby forced to move elsewhere for the remainder of their winter sojourn. However, this phenomenon has not produced any irreversible change in the vegetation of the refuge; it most likely influences use of the refuge by other waterfowl.

Swan introduction and restoration efforts

From the 1930s up through the 1960s *C. c. buccinator* taken from the Red Rock Lakes National Wildlife Refuge in Montana were used with varying success to establish breeding flocks at other national wildlife refuges in an effort to bolster the small population. They were established at the National Elk Refuge in Wyoming, Turnbull Refuge in Washington, Malheur Refuge in Oregon, Ruby Lake Refuge in Nevada, and Lacreek Refuge in South Dakota. The USFWS no longer gives priority to establishing breeding flocks of either swans or geese on its refuges, but encourages the development of flocks should they become established through normal pioneering. Goose restoration efforts are now handled mainly by state wildlife agencies.

Further, the USFWS no longer supports supplemental winter feeding on refuges where introductions were attempted. Winter feeding at Red Rock Lakes National Wildlife Refuge where swans occur naturally is the only exception, and even that supplemental feeding programme may be terminated. Before the USFWS will support the release of artificially-reared or transplanted *C. c. buccinator* outside their present range, a plan of the proposed introduction must be brought before the appropriate flyway council and the public for review and discussion. Establishing new flocks of *C. c. buccinator* could pose unacceptable problems in those states where *C. c. columbianus* or *Anser caerulescens* seasons might need to be closed to provide protection for the introduced swans.

Aviculture

C. c. buccinator, both healthy and crippled birds, have been provided to zoos. However, few have been available for sale or exchange among aviculturists and for breeding experiments. This situation occurs at a time when the natural population at Red Rock Lakes National Wildlife Refuge appears to have saturated its environment to the point where productivity is depressed. Since 1978 the USFWS has made limited numbers available to aviculturists for propagation and display purposes but not for release programmes. Six permits are issued annually for the taking of either one clutch of eggs or one male and one female cygnet from either on, or in the vicinity of, Red Rock Lakes Refuge. Conditions of the permit are: (1) the federal government retains ownership of the wild swans or those swans produced from eggs taken in the wild, but the progeny of the wild birds are property of the permittee, (2) the captive swans are to be segregated from free-flying waterfowl to prevent transmittal of contagious pathogens, (3) permission from landowners must be obtained prior to collecting, and (4) the permittee must prevent the swans from being released into the wild.

Generally the USFWS, with co-operation from the Alaska Department of Fish and Game, has been reluctant to make Alaskan *C. c. buccinator* available to aviculturists until such time as differences between the Pacific and Midcontinent populations can be evaluated. If differences are significant, then interbreeding would be undesirable and could be minimized by prohibiting the use of the Alaskan swan by propagators. The USFWS-funded study by Vyse and Barrett (1981) on genetic comparisons in *C. c. buccinator* provides part of the evaluation required. Alaskan *C. c. buccinator* have been given to the Moscow Zoo for display purposes, and others undoubtedly would be available for *bona fide* studies of comparative differences between the two populations.

Cygnets and eggs of *C. c. columbianus* generally are available to aviculturists but the logistical costs make their collection expensive. While state and federal permits are usually available, difficulty often arises in obtaining the required permission from native groups in Alaska to trespass and collect on their lands. Some native groups contend that so long as they may not legally egg or hunt during the spring and summer, aviculturists and scientists should not be allowed to do so by means of special permits.

C. olor is excluded from official lists of migratory birds and thus is unprotected by federal laws. A growing concern is the increasing number and flock size of *C. olor* which became feral after release or escape (Bartonek *et al* 1981). The pugnacious *C. olor* is dominant over *C. c. columbianus* and *C. c. buccinator* and potentially threatens the well-being of some Midcontinent population *C. c. buccinator* in its limited and perhaps overcrowded wintering habitat. We prefer having the native *C. c. buccinator* in those areas where *C. olor* is now found. Substitution of species is a possible solution, provided previously stated conditions regarding the establishment of new flocks is first met. It may require pinioning or neutering of ornamental birds, except those of licensed breeders, if a problem develops.

Acknowledgements

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Summary

In this paper we highlight certain practices, issues and problems of general interest in management of the three swan species occurring naturally in the United States, *Cygnus columbianus columbianus, C. cygnus buccinator* and *C. cygnus cygnus,* and the feral *C. olor.* Descriptions of range, migration and habitat requirements of these swans are for our purpose adequately described by both Bellrose (1978) and Palmer (1976) with supplemental information on population size and status in Bartonek *et al* (1981).

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HUNTING AND MANAGEMENT OF *CYGNUS ATRATUS* IN NEW ZEALAND

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Introduction

Lacking the virginal whiteness, the character of regency and the emotive protection afforded its northern relatives, *Cygnus atratus* throughout its native range of Australia and its introduced range of New Zealand has been subjected to extensive exploitation. Protection is now extended to it on the Australian continent and hunting occurs only irregularly in Tasmania. But in New Zealand *C. atratus* is firmly established as a minor game-bird and, although its exploitation is now limited in both area and numbers and the annual harvest probably lower now than at any time this century, it is unlikely that in the near future it will enjoy total protection.

There are approximately 80 000 waterfowl hunters in New Zealand who collectively harvest about 1.2 million birds during the month-long waterfowl season (Caithness 1978, 1979). *C. atratus* comprises about 0.4% of this kill – an almost negligible proportion which may suggest that little 'management' is required. However, swan hunting is restricted mostly to a handful of large lakes, all of which are major breeding areas for swans. Young swans tend to remain in their natal area throughout most of their first year of life (Williams 1977, unpubl) and intensive hunting on any of the major breeding areas could remove the bulk of each year's production – the long-term consequences of which are obvious. Swans are a 'sensitive' game species requiring close annual monitoring and frequent adjustment of hunting restrictions.

Hunting

Hunting of *C. atratus* extends back over 100 years. Within ten years of its introduction into New Zealand (1864) it was declared a legal game-bird, being initially hunted at Lake Ellesmere near the site of liberation and, by 1900, in every district of the country.

Some details about the intensity of hunting since 1960 are available from two populations – Lake Ellesmere and Waikato lakes. Estimates of kills elsewhere in the country vary but, overall, it seems that during the 1960s the average annual harvest was 10 000 to 12 000, perhaps 8% to 10% of the national swan population.

Part of this kill was made by means of swan drives. These were organized shoots in which swans were herded by boat (sometimes even light aircraft) towards and over

Fig 1. Place names and districts mentioned in the text.

a line of hunters. Drives were held on Tauranga Harbour, Invercargill Estuary and Lake Ellesmere and were sometimes very successful. (Sites mentioned in the text are shown in Fig 1).

The rationale for these drives at Lake Ellesmere was as a further means of population control. At Tauranga Harbour and Invercargill Estuary, the vastness of the tidal mudflats afforded swans a safe refuge from shore-line hunters and it was only by concerted effort that some could be obtained by the sportsman.

During the 1960s and up to 1974 swans were legal game throughout the country, being hunted over a five-week period (three months at Lake Ellesmere) and mostly without limit. Where daily limits were imposed they were usually so high (8—15) that they allowed, in effect, hunting without limit. Band returns for three populations indicated very different rates of population turnover and levels of exploitation.

(i) *Waikato Lakes:* Banding commenced here in 1962, but no bird older than nine years had been shot by 1974, and from cohorts banded 1962 to 1969 only 30 (3.9%) of 768 recoveries had been made of birds in their fifth year of life or older. By 1973 an average of 21.3% (SD 3.9%) of each year's banded sample from 1962 to 1969 cohorts had been reported shot and average of 17.2% (SD 4.5%) of each banded cohort 1962 to 1972 had been reported shot two years after banding. Over the period 1967 to 1973 the age structure of the kill was, on average, 66.7% swans in their first year of life, 15.0% in their second year, 10.7%, 4.7%, 1.9% and 1.0% swans in their third, fourth, fifth and sixth year of life respectively. These statistics are derived from a period during which the daily bag limit varied from no limit to ten, eight and finally five, yet the percentage of each year's banded sample returned after two years showed no correlation with bag limit.

In 1974 the daily limit was reduced to two and has remained so every year since, except that in 1978 four were allowed. Over this period an average of 8.4% (SD 1.9%) of each year's banded sample (ie 1974 to 1978 cohorts) were reported shot two years after banding and the age structure of the kill was, on average, 44.4% swans of the year and 15.5%, 9.6%, 13.9%, 7.0% and 9.6% swans of successive age classes. Thus the main change was a lowering of the harvest, especially on birds of the year, and more swans are now surviving to older ages.

(ii) *Lake Ellesmere:* Banding of cygnets commenced here in 1956. Hunting continued up to 1974 but has not occurred since then, a consequence of the long-term effect of cyclonic storm in 1968 (Williams 1979), discussed later in this paper.

Swans at Lake Ellesmere live longer than in the Waikato. Bands from 20-year-old swans have been returned and, of the 2704 recoveries made of birds banded from 1956 to 1963, 15.3% were of swans 7 to 12 years old. Of all the cohorts which by

1968 had been exposed to six years' hunting, an average of 18.7% (SD 5.7%) of the initial number banded had been reported shot, and an average of 11.3% (SD 4.5%) of the 1956 to 1967 banded samples were reported shot two years after banding. Of the swans shot in their first to sixth years of life during the period 1961 to 1968, 35.8% were in their first year, 24.6% in the second, and 15.6%, 10.8%, 6.0% and 7.2% in their third to sixth year respectively.

Following the 1968 storm, almost no cygnets fledged in 1968, 1969, 1970 and 1972 and only 450 in 1973. Only in 1971 when 3200 fledged was there any production of consequence. However, hunting continued throughout this period and band returns showed that adults were heavily shot. Of the 583 bands returned from 1969 to 1974, 19.3% were first-year swans (all from 1971), 7.9% in their second year, 11.7%, 5.3%, 4.3% swans in their third, fourth and fifth years, and 51.5% birds in their sixth year or older (Williams 1979).

When, in 1974, hunting at Lake Ellesmere finally ceased, it was also prohibited over most of the southern half of South Island, the area over which birds from Lake Ellesmere dispersed. This prohibition remains in force.

(iii) *Other populations:* Swans at Lake Wairarapa are hunted heavily and monitoring of the harvest commenced in 1975 when cygnets were first banded there. After five years' hunting, 23% of the 1975 banded sample have been reported shot; four cohorts have now been exposed to two years' hunting and an average of 15.3% (SD 1.9%) of each have been reported shot in that time. This population has been hunted with daily bag limits of two, two, four, three and five in the years 1975 to 1979 respectively. The percentage of bands returned in the year-of-banding, an index of hunting pressure, was 9.4%, 9.4%, 13.4%, 16.0%, 16.7% respectively in these years, indicating that daily bag limits there are not a particularly sensitive regulator of harvest.

Moulting adults banded annually at Farewell Spit since 1976 have dispersed widely throughout New Zealand (Williams 1981) and many have been shot at Lake Wairarapa. As a 'population', these birds have not been hunted heavily. The year-of-banding recoveries for the years 1976 to 1979 have been 1.5%, 5.1%, 2.6% and 1.7% respectively of the numbers initially banded and 3.8%, 8.9% and 8.4% of the 1976 to 1978 cohorts respectively were reported shot two years after banding. The low year-of-banding recovery rate occurs because most swans do not disperse from the protected area of the moulting site until late during the hunting season. The increased second-year recoveries may result from many banded swans not returning again to the moulting site and therefore being available to hunters throughout the full hunting season.

At present, swans of the Manawatu, Lake Ellesmere and Otago/Southland regional populations may not be hunted. The annual harvest of swans in New Zealand has been reduced from the 10 000 to 12 000 of the 1960s to between 4000 and 5000.

The present harvest represents approximately 6% to 8% of the national swan population but 10% to 12% of the hunted populations.

Management

Regulating the annual harvest

Hunting of swans is restricted to the six-week-long waterfowl hunting season during May and June each year. The impact of this hunting is regulated by (a) season length – swans may be hunted throughout the entire season or for only part of it; (b) a daily limit on the number of swans that may be shot – nowhere in the past five years has this limit exceeded five and it is more usually one or two.

The information on which the administrators base their decisions on season length and daily limits is derived from three sources: aerial surveys, band returns and hunter opinion. Two nationwide censuses of swans are conducted annually: in November, coinciding with the peak of cygnet emergence and nesting to indicate what proportion of the population may be breeding; and again at the end of January, to estimate the season's production and size of the adult population. Band returns, especially the numbers of bands returned from cygnets shot in the year of banding, are used as an index of hunting pressure. They also reveal how the total harvest is distributed amongst birds of various ages. Hunter opinion is sampled in two ways: a diary scheme, to which about 5% of New Zealand's hunters contribute, requests hunters to indicate their impressions of waterfowl abundance simply as 'more', 'some' or 'less' than the previous year, and hunter's associations (Acclimatisation Societies) are requested to suggest limits and season lengths which they think would be appropriate for the game waterfowl species in their districts.

Season lengths and limits vary in different regions of New Zealand. Data from the locations of recoveries of banded birds and from dispersal studies involving conspicuously collar-marked swans have identified the principal areas of dispersal of each major breeding population (Williams 1981). Hunting restrictions relevant to a particular population are now applied uniformly throughout that population's 'area of dispersal', a change from past practices of applying them unevenly over a variety of administrative districts.

Habitat destruction

In New Zealand, where agriculture is, and is likely to remain, the basis of the national economy, the demand for increased agricultural production and more pastoral land is often the sole rationale for major wetland drainage schemes. Attempts to justify wetland retention on hydrological, recreational, aesthetic and other bases are seldom appreciated by land developers nor understood by planning authorities, especially when government subsidies for 'marginal' land development are so freely available. Peatlands, which formerly covered 1600 km^2 (approximately 1% of the New Zealand land area) and contained much excellent swan and waterfowl habitat, have suffered more than any other wetland type. Montane bogs, small and large, have remained largely unmodified but lowland peatswamps have not been so fortunate. In the Waikato and Northland districts of the North Island, where approximately 45% of the country's lowland peatswamps occurred, over 500 km^2 have been converted to pastoral land, a highly dubious long-term proposition.

Protection of low-lying farmland from flooding has also been advanced as the *raison d'etre* for extensive wetland modification. Rivers have been channelled, extensive stopbanks created and drainage patterns altered to prevent lowland flooding. As a result, there remain in New Zealand almost none of the ephemeral wetlands typically associated with lakes, rivers and lagoons. These highly productive areas (for swans and other waterfowl) have been irretrievably lost and converted to pasture.

Loss of these ephemeral or seasonal wetlands is bad enough, but now the trophic levels of many lowland lakes are rapidly altering. As they become permanently eutrophic or even polytrophic, the previously extensive beds of aquatic macrophytes are replaced by dense, year-round phytoplankton blooms and the carrying capacity of the lakes for swans and other grazing waterfowl is drastically reduced. In the past decade, three major lakes, Ellesmere, Rotorua and Waikare, have all suffered severe eutrophication problems. All three receive sewage from nearby municipalities, the sewage undergoing only primary maceration but no nutrient stripping. All three have predominantly agricultural catchments, the source of high nitrate and phosphate inputs. *C. atratus* adapted quickly to these changed limnological conditions by becoming increasingly dependent on lakeside pastures for food, posing new management problems in the process.

There is now a widespread appreciation amongst controlling authorities of the desirability of limiting especially nitrate and phosphate inputs to major lowland lakes and so preventing the year-round presence of phytoplankton blooms and concomitant problems. There is now much greater public awareness of the value of estuarine areas as important feeding and nursery areas for birds, fish and invertebrates and increased public objection to their use as areas for reclamation and the establishment of industrial complexes. Public requirements of lakes and estuaries are sympathetic with those of swans. The greatest threat to swan habitat remains the indiscriminate conversion of wetlands to agricultural land. Concessions by developers to the requirements of waterfowl are occasionally made by leaving one or two small areas permanently flooded but, to date, no wetland drainage scheme has been substantially modified or stopped by arguments on behalf of wildlife.

Pasture depredation

This problem, an old one to northern hemisphere wildlife managers, is novel for

New Zealand farmers. It is mainly seasonal, occurring mostly in winter and early spring when seasonally high lake levels make aquatic plants unavailable. Of the Waikato lakes, for example, the principal breeding and feeding area is Lake Whangape whose level fluctuates considerably according to the level of the adjacent Waikato River. In winter this lake may rise 2 m or more above its summer level and its dense beds of *Egeria densa* are unavailable to swans. In the past, swans left this lake in winter to concentrate on nearby Lake Waikare, whose level is controlled, fluctuating by less than 1 m throughout the year. Its beds of *Egeria densa* were the main winter food for about 10 000 swans until permanent phytoplankton blooms arose, destroying the macrophytes and preventing their re-establishment. With few other winter feeding areas available, these swans now graze lakeside pastures and many swans, it seems, are now exploiting this food source throughout the year.

At Lake Wairarapa changes in lake level also promote pasture grazing by swans. This lake has extensive marginal flats which, when inundated, allow swans to feed over them. But for flood control purposes the lake level is kept low during winter and spring, the marginal flats are dry and barren, and swans are again forced to feed on lakeside pastures. Low river flows and high evaporation rates during summer ensure that the lake margins remain dry for much of the season, thus establishing pasture depredation by swans as a year-round phenomenon at Lake Wairarapa.

Complaints from farmers are responded to by using scaring tactics (these include gas-powered automatic bangers, irregular shooting, fixed mechanical devices and gas-filled balloons) or fencing the lake margin with electrified wire. None of these scaring methods has proved satisfactory other than for very short periods and the most successful deterrent to date has involved farmers stocking very heavily the pastures on which swans were concentrated. The 'control' measures continue to ignore the fact that swans are grazing pasture because food is not available in the lake. Their scaring off one pasture merely shifts the problem to another. The obvious solution of providing swans with grazing, a basic technique in the management of geese in Britain and Europe (Owen 1973), is a suggestion unappreciated by the farming community. When 'control' measures fail to achieve a long-term reduction of the problem, strong demands are made for a permanent and substantial lowering of the swan population.

Lake Ellesmere population

Perhaps the most interesting management problem New Zealand has with *C. atratus* is a consequence of a natural catastrophe. A cyclonic storm ravaged Lake Ellesmere in April 1968, destroying the beds of aquatic macrophytes and killing thousands of swans (Williams 1979). In the decade since that storm, the aquatic macrophytes have failed to re-establish, inhibited by the continuous removal of the lake's finer bottom sediments by wave action and the dense phytoplankton blooms which occur throughout the year. In the decade since that storm, the number of swans at the lake has steadily declined and is now barely 25% of that present prior to 1968. Extensive breeding failure, poor cygnet survival, increased adult mortality and/or permanent emigration — all natural responses to the impoverished food supply — and intensive hunting have all contributed to this population decline.

In each year since the storm only a small percentage of the adult birds present appear to have attempted to breed. Immediately after the storm the population probably exceeded 25 000 but only 1200 nests were established; in 1969 only four nests were located. Only in 1976 and 1977, when approximately 2200 and 1600 nests respectively were established, have 50% or more of the estimated number of birds older than four years (the likely age of first breeding) present attempted to nest.

No cygnets fledged in four of the five years immediately after the storm and in only one year (1971) since 1968 have more than 1500 cygnets survived to independence. However, many of these independent youngsters have been extremely light (less than 4.0 kg when fully feathered); some were incapable of flight and heavy post-fledging mortality undoubtedly occurs.

Since the storm, there is some evidence to suggest that fewer of the swans which dispersed from the lake as juveniles returned there upon reaching sexual maturity than was previously the case (Williams 1977). In addition, the mortality rate of adults at the lake may also have increased.

For six years after the storm, intensive hunting and control of pasture-feeding swans resulted in several thousand adult swans being shot. Prior to the storm, the hunters' kill comprised approximately 15% birds over four years of age; during 1969 to 1974 they comprised 56% of the kill.

The consequence of these events is that many age classes have few or no representatives in the population. At present there are few five- to ten-year-old swans alive, normally the largest breeding component of the population. The last major input into the breeding population were progeny from 1967, the cohort which suffered most during the storm and which experienced considerable shooting pressure in subsequent years. The number of swans hatched since the storm and now of breeding age comprises less than 10% of the total adult population.

A construction of the present size and age structure of the Ellesmere population (assumptions made in this construction are explained fully in Williams 1979) and a projection forward by four years (Fig 2) suggests that the breeding component of the population will decline further, perhaps by about 50%.

How does one 'manage' a population like this? Obviously hunting cannot be considered, although there is strong pressure to allow it. Swans continue their conflict with lakeside farmers and 'destructive' control measures are sought. The full

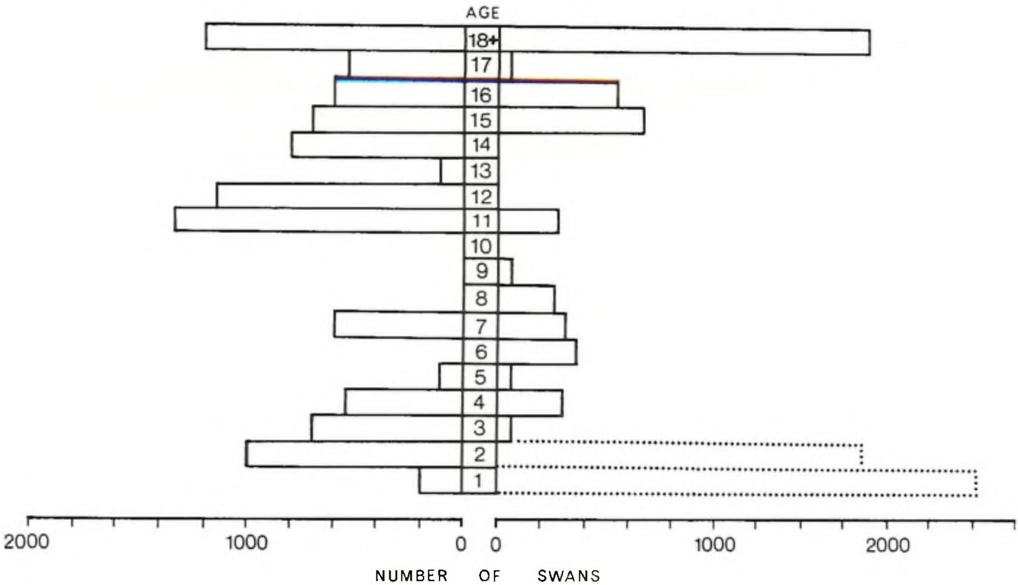

Fig 2. The theoretical size and age structure of the Lake Ellesmere swan population in January 1978 (left) and its likely structure four years later in January 1982 (right).

Cygnets fledged in 1978/79 and 1979/80 seasons are depicted as three- and four-year-olds in 1982, the size of the 1982 one- and two-year-old cohorts assumes a production of one cygnet per pair of swans five years of age or older.

reproductive potential of the population is obviously not being realized and it is important to understand why. Is it simply the quality and quantity of food in the lake that are the determining factors? Lake Ellesmere is a polytrophic lake and as such is deteriorating as a swan habitat. There is little the wildlife manager can do within the bounds of economic reality to reverse this trend and, by so doing, enhance cygnet and adult survival. Apart from providing lakeside grazing, the wildlife manager may have to allow the population to re-adjust naturally to the reduced carrying capacity of the lake; laissez-faire is also a benign form of the manager's art.

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Summary

Approximately 6% to 8% of New Zealand's *C. atratus* are shot annually, the harvest now being less than half that a decade ago. Newly-fledged cygnets and breeding adults comprise most of the kill; pre-breeders frequenting the estuarine areas effectively avoid being hunted. Hunting intensity varies through New Zealand: 17% of each year's banded cohort from the Waikato Lakes were reported shot two years after banding compared with 11% at Lake Ellesmere and 15% at Lake Wairarapa.

Season length and daily harvest limits regulate each year's hunt. Hunting regulations are based on: aerial surveys (conducted before and after each breeding season); the harvest of the previous year as determined from band returns; and opinions of the hunters (expressed individually in hunting diaries or collectively by recommendations from hunters' associations). The regulations relevant to a particular breeding population are applied throughout the 'area of dispersal' of that population.

The preservation of quality habitat is becoming increasingly difficult as eutrophic conditions arise in more of the important lowland lakes and as wetlands are drained. Swans are adapting to the changed limnological conditions by becoming increasingly dependent on lakeside pastures for food. This conflict with agriculture brings with it strong demands for a substantial lowering of New Zealand's swan population.

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Mortality and Disease

POST-MORTEM EXAMINATION OF *CYGNUS CYGNUS CYGNUS* IN JAPAN

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Since 1973, about 70 dead *Cygnus cygnus cygnus* in Hokkaido have been sent to the Hokkaido Institute of Public Health in close co-operation with the Swan Society of Japan, Hokkaido Branch. Dead swans were examined from a hygienic point of view to investigate the cause of their death and also as the indicator of environmental pollution in Hokkaido. Results of chemical analysis of the total mercury in brains and feathers, heavy metal contents in feathers and organic hydrochloride and residues of other chemicals in organs show a lower level in two figures than in examinations of Hokkaido crows, reported in 1974. Nematodes in heart and stomach, trematodes in orbits, intestine and caecum, mites in nasal cavities were found in parasitological examination. Residual pellets of lead shot in muscles were found by x-ray and autopsy. As they were in small numbers per swan, they may not have had a direct effect on the swans. They will, however, be an indirect cause of death by impeding actions and causing clinical infirmity under severe winter conditions.

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MORTALITY FACTORS OF WILD SWANS IN BRITISH COLUMBIA, CANADA

R W McKELVEY and A C MacNEILL

Introduction

Necropsies were performed on 52 *Cygnus columbianus columbianus* and 114 *Cygnus cygnus buccinator* from British Columbia, Canada. The birds were collected between June 1965 and October 1979 in coastal and interior areas. Although a feral *Cygnus olor* population is present on southern Vancouver Island (McKelvey 1979), none has yet been submitted for necropsy.

A few specific cases of diseased swans have been noted for British Columbia (Cowan 1946; Moynihan and Stovell 1955; Munro 1962; MacNeill 1970 and 1975). The information provided in this report shows only the disease conditions observed and does not necessarily indicate the prime cause of death.

Methods

Swan specimens for necropsy were provided by personnel of the Canadian Wildlife Service and the British Columbia Fish and Wildlife Branch.

Routine necropsy procedures were followed; where appropriate, parasitological, bacteriological, toxicological and other diagnostic techniques were used. Most specimens were received frozen, often showing advanced tissue autolysis, precluding histological examination. Tissue samples were retained from all suspected cases of lead poisoning and from all birds collected since the winter of 1978/79. Analysis for toxic chemicals is in progress.

To provide baseline information on the extent of parasitism in apparently healthy birds, 52 droppings of *C. c. buccinator* were collected from Comox Harbour, British Columbia, during the winters of 1977/78 and 1978/79. Parasite ova and larvae were separated by floatation.

Results and discussion

Necropsy conditions

Although 166 swans were necropsied, not all specimens were analysed for all conditions reported. When the cause of death was externally obvious, a complete necropsy was not performed.

Internal parasitism was the most common condition observed. Of 155 specimens examined, 121 (78%) were parasitized, a higher percentage than reported in other free-flying Anatidae (MacNeill and Barnard 1978). Parasites included nematodes, cestodes, trematodes and *Coccida* sp, found alone or in combination with one another.

Nematodes, including acanthocephalids, occurred in 115 swans (74%). *Amidostomum* sp was the most common, occurring in 98 (63%). Intestinal nematodes rarely appeared in sufficient numbers to have a detrimental effect. However, nematodes found in the heart, trachea, proventriculus and gizzard were often felt to have been deleterious, particularly in juvenile swans. Myocardial pathology was usually associated with heartworm *Sarconema* sp infection, the incidence of which appears to be increasing, from 2.9% for the period 1965 to 1976 to 7.8% for the longer period 1965 to 1979. It was found more frequently in *C. c. buccinator* (12) than in *C. c. columbianus* (1).

Cestodes were found in 31 swans (20%), usually with other parasites. The most commonly observed cestode was *Hymenolepsis* sp. Cestodes *per se* did not appear to be directly associated with death. Swans appear to be less frequently parasitized by cestodes than ducks and geese. MacNeill and Barnard (1978) found cestodiasis to be twice as frequent in all free-flying Anatidae.

Trematodes were observed in 11 swans (7%), always with other parasites. The most common fluke was *Echinostomum revolutum* (Frohlich 1802), a species reported widely distributed in British Columbia (Cowan 1946).

Internal parasitism did not usually appear to have affected the general health of most birds analysed. However, gizzard worm *Amidostomum* sp infection, with typical gizzard erosion, was often associated with oesophageal impaction; it was then thought to be directly responsible for the death of the bird.

External parasitism was noted on six occasions. Lice in five *C. c. buccinator* were identified as *Trinoton anserinum* (Fabricius 1805). A *C. c. columbianus* found comatose in Powell Lake, British Columbia, had a heavy attachment of leeches *Theromyzon rude* (Rathke 1862), affecting the conjunctival surfaces. That swan also suffered a pathogenic infection of *Amidostomum anseris* (Zeder 1800).

Trauma was noted in 66 (40%) of 166 birds, gunshot trauma being the most common condition (24). Most swan shootings appear to be malicious rather than through confusion with *Anser caerulescens caerulescens,* because most returns are from areas where there are no wintering *A. c. caerulescens.* Shooting of swans does not seem to be a widespread problem nor does it appear to be adversely affecting populations.

Non-gunshot trauma was usually the result of birds flying into power or fence lines. As the human population expands near swan wintering areas, this type of destruction may increase. One remedy, apart from removing power lines, is to make them more noticeable. Those at Port Alberni, British Columbia, have been almost eliminated as a source of danger, following the attachment of fish net floats to the wires. The swans now seem able to judge the exact position of the lines, even in foggy conditions, and to fly over them without colliding.

Debilitation was evident in 55 specimens (33%) and was usually associated with nematodiasis, aspergillosis and, to a less extent, lead poisoning.

Gizzards from 155 swans were examined and in nine instances lead pellets were observed. In 57 swans, gross pathology suggestive of lead poisoning was followed by chemical analysis of their livers for the presence of significant levels of lead. Significant levels were found in 14 instances (24%).

Cases of lead poisoning in swans from British Columbia have been reported earlier

(Munro 1962). Some areas (Table 1), such as Nanaimo, appear to contribute lead poisoned swans regularly. There is evidence that waterfowl feeding on unnatural

Table 1. Recovery location of swans found to have significant levels of lead in liver tissues

Location and species	Number recovered
Cygnus cygnus buccinator	
Nanaimo	7
Kelsey Bay	1
Fraser Lake (Vanderhoof area)	1
Stuart River (Vanderhoof area)	2
Duncan	1
Cygnus columbianus columbianus	
Boundary Bay (Vancouver area)	1
Duncan	1

foods such as waste corn and soybean meal are highly susceptible to lead poisoning (Irwin 1977). Waterfowl have also been reported to appear malnourished even though feeding on plentiful cereal grains (N Perret pers comm). Many of the swans found to have significant levels of lead are from areas where feeding occurs on cereal grains, available as waste or as handouts. The number of swans possibly succumbing to lead poisoning in British Columbia does not seem to pose a threat to the population and the problem appears to be of a local nature.

Impaction, digestive tract blockage, was most commonly seen in the oesophageal area and was often associated with gizzard erosion of parasitic origin. Gizzard erosion associated with lead pellet ingestion did not result in a significant occurrence of impaction. Impaction due to food overload, as frequently seen in *Branta canadensis* grazing lush green pasture in spring (MacNeill and Barnard 1978), was not observed in any swans.

Other necropsy conditions observed were myocarditis (7.8%), air sacculitis (6.6%), pericarditis (6.6%), nephritis (6.0%), anaemia (5.4%), aspergillosis (5.4%), enteritis (3.0%), exposure to weather (3.0%), bacteremia (3.0%), hepatitis (1.8%), amyloidisis of the liver (1.2%), bumblefoot (1.2%), ruptured aorta (1.2%), wild horseradish poisoning (1.2%), asphyxia (0.6%), avian tuberculosis (0.6%), peritonitis (0.6%), pneumonia (0.6%), sarcospordia (0.6%) and tracheitis (0.6%).

Virus isolation procedures were performed on 50 swans, using 10-day-old chicken embryos. No chick embryo lethal agents were detected.

Faecal samples

The analysis of swan faeces for the ova and larvae of internal parasites seems to

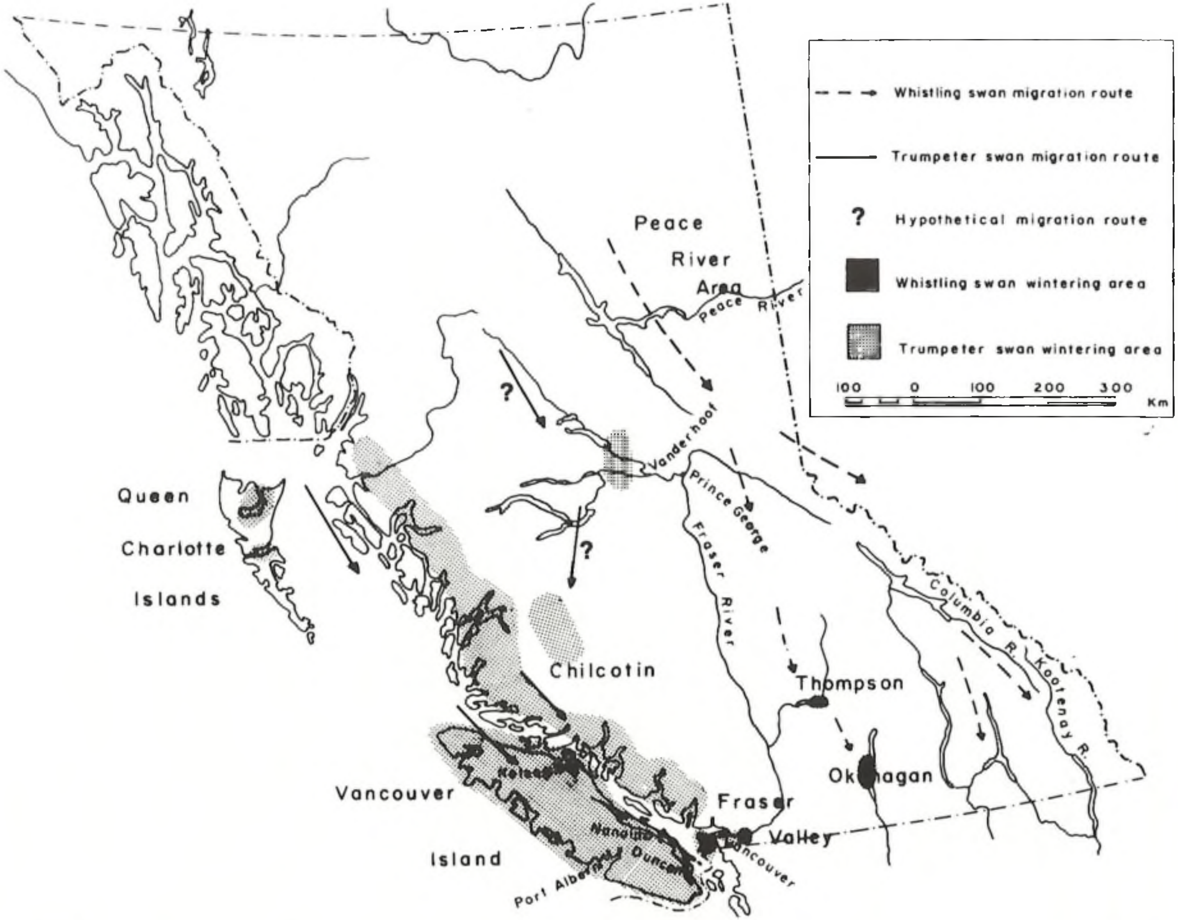

Fig 1. Locations of swans recovered for necropsy and areas of known swan concentrations.
Data from this study, Canadian Wildlife Service files (Delta) and personal observations.

indicate that normal wild swans may not carry many parasites. Of the 52 droppings analysed, 10 contained ova or larvae or both. No attempt was made to identify the species of parasites present.

Distribution of returns

Fig 1 shows the geographic region from which the swans were collected. The distribution of the return of dead swans complements the known population distribution and concentrating areas of both species. Although no systematic searching has ever been possible because of inaccessibility of much of the winter range, the collection of dead birds does not seem to have been too badly biased by proximity to concentrations of human population.

C. c. columbianus is generally less abundant in British Columbia than *C. c. buccinator.* The former migrates through eastern British Columbia and the Peace River district, though few compared with those passing through Alberta. Fewer than 250 winter in the Thompson—Okanagan area and fewer than 150 along the southern coast.

C. c. buccinator winters mainly along the coast of British Columbia, with smaller groups found in north-central areas and in the Fraser Valley (McKelvey in press and 1979). The largest numbers of necropsied swans have come Vancouver Island, an area thought to support about 1000 swans. Lesser numbers have come from interior and north coastal areas, where small populations occur.

The disease conditions reported in this study are thought to be typical, though only a very small part of what is presumed to be the normal winter kill is ever found. The productivity of *C. c. buccinator* wintering on Vancouver Island averages about 25% (McKelvey 1979) but the annual population increment in Alaska is only about 3%.

Some causes of death are obviously related to the presence of men, such as lead poisoning, shooting and collisions with structures. The complete analysis of tissues on hand for pesticide and other toxic chemical residues will eventually give a more complete picture of man's influence. Until then, it seems permissible to conclude that man is not having too great an effect on swans in British Columbia.

Acknowledgements

Special thanks and appreciation are given to Mrs Linda Ronald for excellence in technical assistance and record keeping. Appreciation is also extended to W A Webster of the Animal Disease Research Institute (Eastern), Agriculture Canada, Ottawa, Ontario, for confirmatory identification of many of the parasites found, to the many contributors of specimens used in this study and to N Verbeek for critical review of the manuscript.

Summary

114 *Cygnus cygnus buccinator* and 52 *Cygnus c. columbianus* were necropsied. The sample reported on is representative. The most frequent parasites were gizzard worms. Only when associated with oesophageal impaction did parasitism seem to be responsible for death. Faecal samples collected from apparently healthy wild *C. c. buccinator* indicate that the normal internal parasite load is relatively low. Trauma was caused mainly by gunshot and collision with power lines. Debilitation was associated with nematodiasis, aspergillosis and, to a lesser extent, suspected lead poisoning, which does not appear to be a major problem.

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DISEASE PROBLEMS IN NORTH AMERICAN SWANS

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Infectious, parasitic and toxic disease processes kill many free-living swans in the United States annually. The two most serious diseases affecting *Cygnus* *columbianus columbianus* are lead poisoning and avian cholera. Far less is known about disease problems of *Cygnus cygnus buccinator.* However, heavy parasite burdens in cygnets have been associated with poor cygnet survival in the Yellowstone-Centennial Valley region of northwest Wyoming and southwest Montana. This is the only important breeding area in the contiguous United States.

Ingestion of lead pellets deposited in marshes as a result of waterfowl hunting is the most important source of lead poisoning. Other cases result from the ingestion of lead sinkers used in sport fishing and from pollution due to lead mining. Lead poisoning is especially serious at the Lake Mattamuskeet National Wildlife Refuge in North Carolina. An estimated 7200 *C. c. columbianus* have died from ingestion of lead pellets at that location between winter 1972/73 and winter 1977/78.

Avian cholera has killed numerous *C. c. columbianus* in California. Estimated losses have been as high as 6% of the swans wintering in that state during some years.

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HEARTWORM *SARCONEMA EURYCERCA,* A CIRCUMPOLAR INFECTION IN SWANS

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The heartworm *Sarconema eurycerca* (Wehr 1939), first described from *Cygnus columbianus columbianus,* has now been found to occur on a circumpolar scale in all five swans and three species of geese in the Northern Hemisphere. The biting louse *Trinoton anserinum* has been determined to be the intermediate host in the life cycle of *S. eurycerca.* Results of a study on the microfilarial periodicity of this heartworm in the peripheral circulatory system of *C. c. columbianus* show these larvae to be nocturnal and to concentrate in the blood between 0100 and 0400 hours. This suggests that the feeding behaviour of the louse is periodic.

Prevalence of heartworm has been determined in *C. c. columbianus, Cygnus columbianus bewickii,* and British and American populations of *Cygnus olor.* Prevalence ranges between 3.6% and 30% for all swans sampled. Prevalence is highest in *C. c. columbianus* and British *C. olor,* averaging 20% and 17% respectively. During a four-year neck-band and resighting study of 720 *C. c. columbianus* captured on their wintering grounds in North Carolina and their breeding grounds in Alaska, the ratio of non-parasitized to parasitized swans resighted did not change significantly for either adult or juvenile swans up to four years after capture. This suggests that swans found positive for heartworm by blood examination did not have a significantly higher mortality than birds which were determined to be negative for the parasite.

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Contributions by Non-Professional Researchers

THE WILD SWANS AT LAKE TOFUTSU-KO, HOKKAIDO, JAPAN

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Introduction

Lake Tofutsu-ko is one of many large lakes formed from the sea that dot the sea coast of Okhotsk, Hokkaido. It has an area of 900 ha, National Road 244 and National Railroad Line Semmo run over the land between the lake and the coast. The land surrounding the lake, approximately 2051 ha, has since 1963 been designated a wildlife protection area.

The main species of wild swans at Lake Tofutsu-ko is *Cygnus cygnus cygnus. Cygnus columbianus bewickii* is rare.

Fishermen crossing the lake determine when and where the swans will do their feeding.

Occurrence of swans

Wild swans returning from the north annually arrive early in October and number ten birds. From 25 October to 10 November, 1000 to 3000 swans may arrive in a single day. From this point on, the number of swans returning fluctuates until the middle of December, when ice begins to form on the lake and the swans move south. Tagged swans leaving Lake Tofutsu-ko usually stay at Kominato City, in the Aomori District, north Honshu.

In recent years between 40 and 100 swans have remained in the outskirts of Lake Tofutsu-ko, in its nearby marshes and streams. These wild swans have also been seen in several winters when there was no opening in the lake's ice.

Lake Tofutsu-ko thaws at different times every year. As the ice melts, so the number of swans rises. The peak of swans arriving is around 20 April, when numbers reach 4000.

Most wild swans return north (probably Siberia) by the end of April. Most leave Lake Tofutsu-ko early in the morning and in groups of between 400 and 1500. Sometimes there are up to 2000. A family or single birds may remain when all swans usually have left Lake Tofutsu-ko. By the middle of May all swans have gone.

Conservation implications

In recent years there have been many wild swans fed directly by humans. In order to feed the swans we must take into account the extent of ice cover and the number of swans. Many tourists bring food, for instance bread, which is not appropriate for the wild swans.

As we think about the natural protection of native and wild birds and animals, we realise that we must work diligently to preserve the natural balance between man, the wild swans and the environment.

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THE TRUMPETER SWAN SOCIETY

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Introduction

Cygnus cygnus buccinator is native only to North America. When European settlers arrived, this magnificent bird apparently ranged over much of what is now the United States and Canada. But today, except for isolated regions of the Rocky Mountains, Alaska and Canada, human development of the continent has caused a decline in the number of *C. c. buccinator* to a remnant of the bird's former population. The Trumpeter Swan Society has assumed the responsibility of working with those agencies charged with managing *C. c. buccinator,* such as the US Fish and Wildlife Service, to help assure that *C. c. buccinator* survives and flourishes in the face of further encroachment on wild places.

Its genesis

The Trumpeter Swan Society was founded in the fall of 1968 in Carver Park Reserve about 40 km west of Minneapolis, Minnesota. Fred E King was the Society's first president and acknowledged founding father. A banker by trade and a lover and conserver of natural resources by avocation, it was through his efforts as chairman of the Hennepin County Park Reserve District Board of Commissioners that a *C. c. buccinator* restoration programme was started in Minnesota.

Its purpose

Today, the Trumpeter Swan Society is composed of people from many walks of life. They all share a common interest in maintaining existing wild *C. c. buccinator* populations and in restoring the bird to as much of its original range as possible. To help meet these challenges, this small, international scientific and educational organization of 200 members embraces the following objectives:

- To promote research into the ecology and management of *C. c. buccinator;*
- To advance the science and art of *C. c. buccinator* management, both in captivity and in the wild;
- To be a focal point for assembling known *C. c. buccinator* data;
- To provide a framework for the exchange of knowledge about *C. c. buccinator;* and
- To provide a common meeting ground for all who are interested in *C. c. buccinator.*

Its organization – present

A membership-elected Board of Directors meets twice a year to govern the Society's business. A president, vice-president, secretary-treasurer and four directors comprise the Board. Currently, the secretary-treasurer is the chief administrative officer. He acts without pay, as do all officers.

In responding to enquiries about *C. c. buccinator,* the Society provides an educational function, stimulating aesthetic interests and enlightening many, especially the younger generation. A bibliography of *C. c. buccinator,* as yet incomplete, has been compiled. A biannual newsletter keeps Society members apprised about activities.

In fulfilling its objective 'to provide a common meeting ground for all who are interested in *C. c. buccinator*', the Trumpeter Swan Society holds a biennial conference. At these meetings, biologists and laymen gather and discuss their common interest. The Sixth Conference was held in Anchorage, Alaska, in September 1978. The Seventh Conference will be held in Victoria, British Columbia, in February 1981.

The Propagation Techniques Committee prepared 'A Guideline to Propagation of Captive Trumpeter Swans' based upon the collective experiences of many members, but primarily those of the biologists at the Hennepin County Park Reserve District near Minneapolis, Minnesota. This committee also keeps a record of the status of captive *C. c. buccinator* in North America.

The Restoration Committee has investigated and identified potential breeding and wintering areas in Canada and the United States within *C. c. buccinator's* original range. Currently, a concerted effort is being made to begin a restoration programme for *C. c. buccinator* in the Mississippi Flyway.

The Research Needs Committee reviewed current knowledge of *C. c. buccinator* and determined research priorities. Basic research is needed first because so little is known about *C. c. buccinator* biology. Applied research is aimed mainly at future restoration attempts. Having fulfilled its original charge, this committee was dissolved in September 1979.

The Research Advisory Committee was established to identify newly occurring research opportunities, to review research proposals, and advise the North American Wildlife Foundation on *C. c. buccinator.*

Its organization – future

The Society's Board of Directors believes that the Trumpeter Swan Society must move ahead with its proposed restoration programme if the species is to remain a viable member of the birds of the world. The success of current restoration proposals will influence considerably what might be done in the future.

In September 1979, the Board of Directors agreed to: 1) realize 'political clout' through larger membership; 2) establish a salaried executive secretary position; 3) maintain an active role in management of and research on *C. c. buccinator* in North America, in order to ensure that there is no further decline in existing populations, and, over the next ten years, to bring about reasonable increases in established populations; and 4) establish an active *C. c. buccinator* restoration programme in eastern North America, including at least three newly established *C. c. buccinator* flocks in ten years, and *C. c. buccinator* wintering in the lower Mississippi Flyway.

A membership committee and a concerted public relations effort will be required, including a good brochure. This will be a major change for a group that has prided itself on its small, informal organization. A salaried executive secretary position may be needed to accommodate the increased general administrative duties. A small dues increase is set for 1 July 1980.

Research opportunities

1) *C. c. buccinator* taxonomy is a prime research opportunity that has both fundamental and practical implications. There may be two distinct races: the larger Alaskan and the interior birds. There seems to be no intermixing of the groups. Taxonomy must be clarified before, for example, Alaskan birds could be used as a potential source of eggs and cygnets for transplant to the interior of the continent (see Vyse and Barrett 1981).

2) There are small flocks of *C. c. buccinator* whose annual movements and distribution must be identified to prevent accidental adverse human impact on their breeding or wintering areas. This may require colour- and collar-marking and

radio-tracking.

3) In addition to basic feeding ecology, we must know the impact of birds on their food resources. Ruth Shea studied the breeding ecology of *C. c. buccinator* in Yellowstone National Park and adjacent environs (1979). Her observations on cygnet mortality prompted additional field study in 1979. Another University of Montana graduate student has proposed to study winter habitat requirements.

4) Studies of reproductive energetics, nutrition and food selection with captive birds are needed.

5) Imaginative research is needed to develop restoration methods in areas where *C. c. buccinator* must acquire site-specific migratory habits.

6) Population dynamics of the relatively stable wild *C. c. buccinator* populations, at what appears to be carrying capacity, are of particular interest, as are analyses of habitat carrying capacity.

7) A carefully conceived individual marking programme would allow the study of family member interactions, including parent—offspring and sibling relationships, keeping disturbance to a minimum and precluding changes in behaviour. Spacing, long-term relationships of known individuals, the mating system and many other topics should also be studied, relating temporal adjustments in behaviour and social organization to the seasonal changes of their habitat.

Acknowledgements

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Summary

The paper reviews the origin, aims and organization of the Trumpeter Swan Society, and lists seven fields where further research relating to *Cygnus cygnus buccinator* is required.

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CYGNUS CYGNUS BUCCINATOR IN SKAGIT VALLEY, WASHINGTON, USA

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Introduction

Cygnus cygnus buccinator appeals to professional and nonprofessional ornithologists alike. Increased public awareness of these swans in Washington State has resulted from an increase in the swans. In recent years the Skagit Valley has become the most important wintering area in the State, boasting the largest wintering concentration of Alaskan *C. c. buccinator* south of the Canadian border.

Their winter ecology in the Skagit Valley is becoming better understood through the efforts of private citizens. Previously, annual population counts and a listing of general habitat usage were the only information available through the State Department of Game.

Study area

The Skagit Valley is a fertile agricultural area in northwestern Washington State. The study area was located to the east and north of the city of Mount Vernon, encompassing the Nookachamps watershed and the area north of the Skagit River to Cook Road between Burlington and Sedro Wooley (Fig 1).

History

C. c. buccinator was once abundant and widespread in Washington State. However, by 1940 (Jewett *et al* 1953), its status had changed drastically to: 'formerly migrant and winter resident both east and west of the mountains; no record in recent years'. Most of this decline was caused by habitat loss through land development and commercial hunting for skins (Banko 1960).

In 1957 six *C. c. buccinator* were recorded at Barney Lake near Mount Vernon (Washington Department of Game 1979). There were no further records until 1963, when 20 were identified, again at Barney Lake. In 1972 a yearly census was started. Fig 2 presents the population of the Skagit Valley from 1957 to 1980.

Results

Seasonal fluctuations

Nine *C. c. buccinator* were observed on 28 October 1978. From then on counts were made weekly for November, and every three or four weeks for the rest of

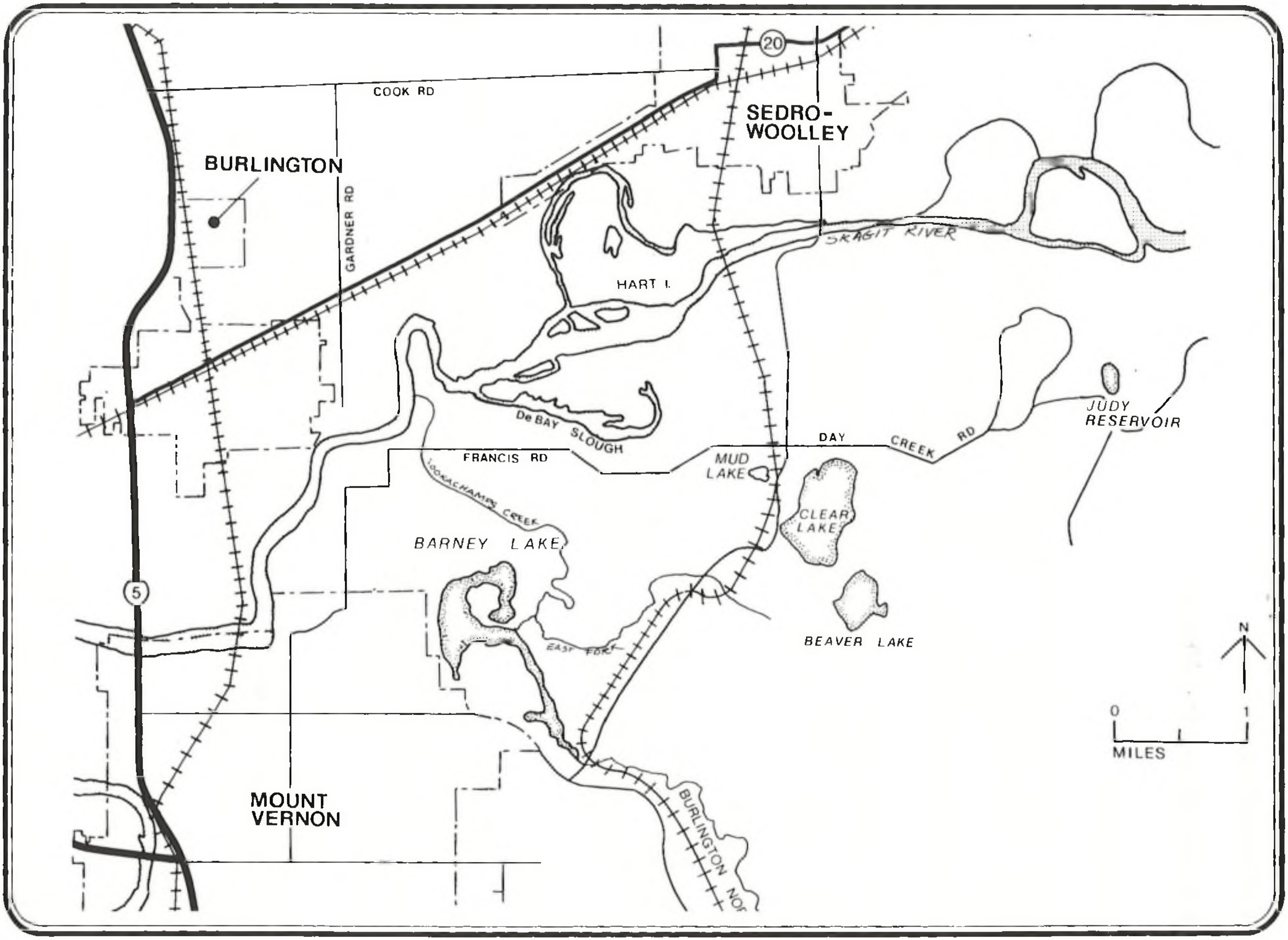
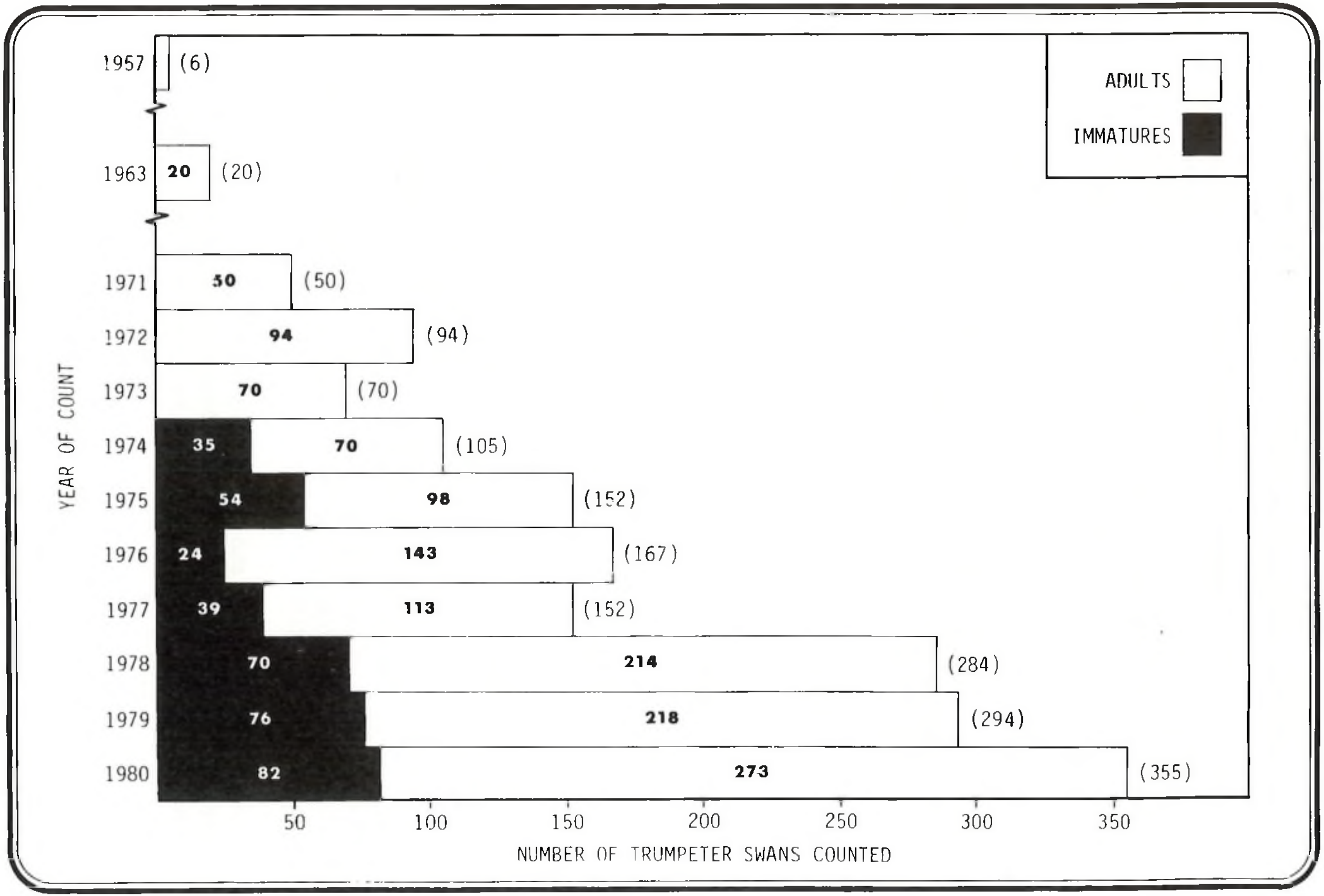


Fig 1. Skagit Valley area used by *Cygnus cygnus buccinator*.



SOURCE: WASHINGTON DEPARTMENT OF GAME; RUSS CANNIFF

Fig 2. Maximum counts of adult and immature *Cygnus cygnus buccinator* near Barney Lake, Skagit County, Washington, 1957–1980.

winter 1978/79. A gradual decline in swans began in late January, and by mid-March more than half of the swans were gone (Fig 3).

Four neck-banded swans arrived with the first sizeable group of *C. c. buccinator* on 18 November. A second influx occurred on 23 November. Most notable of the marked birds was 09VY with her unbanded mate and three cygnets. She was banded at the Kenai National Moose Range in Alaska in 1972 and had been seen previously at Barney Lake in 1973 and 1978. The population peaked in late December at 294.

Swan arrival in 1979/80 began with one juvenile at Barney Lake, again on 28 October. Counts were conducted weekly throughout the season. The population increased rapidly to an initial peak of 114 birds on 11 November. A steady, gradual increase followed until another influx on 25 December, including the arrival of the first neck-banded swan, 34VT. A sharp influx in mid-January occurred with the arrival of 46 swans, including 00VT, formerly 09VY, on 12 January. Following a gradual increase, a maximum population of 355 occurred at the end of January (Fig 3). This peak gradually declined until all swans had departed by the end of March.

Collared swans returning to the valley in 1979/80 were noticeably fewer. Only two bands, one return (00VT) and one new (34VT), were observed, compared with 12 the previous season.

A total of 27 family groups was observed, three more than in the previous year, but the adult/juvenile ratio was 22% compared with 26%.

The 1978/79 season had a sharp, steady rise in population during the first two weeks in November, including eight banded arrivals, with 85% of the population present by 23 November. In contrast, the 1979/80 migration had three noticeable pulses, one each around 11 November, 25 December and 12 January. The majority of the population had not arrived until the end of December, five weeks later than the previous year. This difference between southward migrations might be explained by the severity of the weather on the breeding grounds and along the migratory routes; weather conditions for the fall and early winter of 1979/80 were milder than those of 1978/79.

Cygnus columbianus columbianus also occur. They winter primarily in the salt marsh of Skagit and Port Susan Bays southwest of Mount Vernon. A small number, however, associate with the *C. c. buccinator* in the Barney Lake vicinity. It was not until this year that efforts were made to count systematically the *C. c. columbianus* population (Fig 3).

Habitat areas and swan usage

Barney Lake, located 0.5 km east of the city of Mount Vernon, is an old oxbow

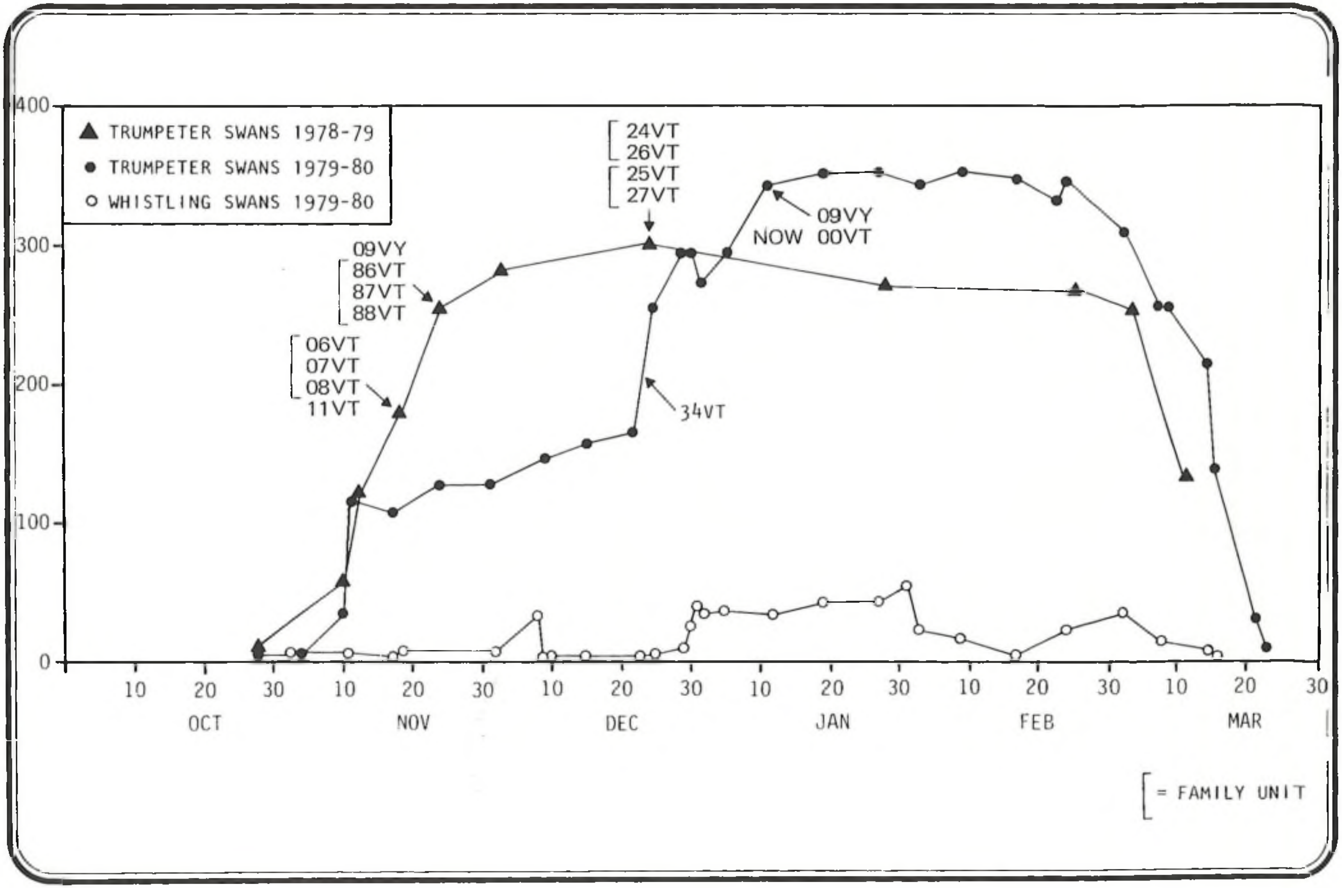


Fig 3. Maximum counts of *Cygnus cygnus buccinator* for the Skagit Valley (and of *Cygnus columbianus columbianus* for Barney Lake).

of Nookachamps Creek and consists of approximately 40 ha of lake/marsh. By September most of the surface area is dry while the subsurface remains wet. Fall and winter rains provide open water, but the level fluctuates throughout the winter. During high water periods, the surface area may double in size, often flooding peripheral pasture land. The lake is primarily used for feeding and night roosting, although late in the season swans may rest and preen here.

Judy Reservoir, approximately 5 km northeast, was built in the early 1940s as a municipal water supply and has a surface area of 64 ha. The reservoir receives the heaviest use by swans from late October through December. Although food resources appear to be minimal, the swans use the east bank for resting, bathing and preening. As dusk approaches they move to roosting areas at Barney Lake and DeBay Slough. The latter, an oxbow of the Skagit River, lies north of Barney Lake. It provides additional roosting area and the shore's dairy pasture is used for grazing.

East of Barney Lake lie the Barney flats, a basin containing wet pastureland. This area receives its heaviest use during January and February. Grass is available for grazing, and the flats are used as another primary resting and preening area.

Clear Lake, with a surface area of approximately 80 ha, is located between Judy Reservoir and Barney Lake, and the swans frequently use its south end as a refuge to escape disturbance or harassment in other areas.

Beaver and Mud Lakes, located near Clear Lake, seem to be used only when the preferred habitats become unfavourable due to human disturbance.

The Francis Road area north of Barney Lake is primarily dairy pasture or grass fields and is used primarily for feeding. In 1979/80, due in part to human disturbance and in part to heavy flooding, use of this area dropped to almost zero by the end of the season.

The most northern part of the Skagit Valley, the Gardener Road area, has dairy pasture and grass fields, with some ploughed grain fields. Most of the pasture is wet with sporadic standing water. This area does not appear to be heavily used by feeding swans in the early part of the season unless there is a hard prolonged freeze.

In general, pastureland in the Skagit Valley appears to play a major role in the winter ecology of *C. c. buccinator.* The swans are attracted to dairy pastures by the abundant vegetation and the standing water in fields.

Pasture areas provided primarily orchard grass *Dactylis glomerata* and ryegrass *Lolium* sp. A variety of water habitats in the area include lakes, flooded fields, reservoirs, and flowing streams and rivers. Prominent vegetation and the most abundant food plants in the central body of Barney Lake are: water plantain

Alisma plantago-aquatica, inflated sedge *Carex vesicaria,* common spikerush *Eleocharis palustris,* ovoid spikerush *E. ovata,* water horsetail rush *Equisetum fluviatile,* spatterdock *Nuphar polysepalum,* reed canary grass *Phalaris arundinacea,* smartweed *Polygonum hydropiper,* waterpepper *P. hydropiperoides,* arrowhead *Sagittaria cuneata,* softstem bulrush *Scirpus validus* and common cat-tail *Typha latifolia.*

Future perspectives

Despite the presence of swans on Barney Lake since 1957, public concern has been growing only since the winter of 1977/78, when people were encouraged to look for neck-banded *C. c. buccinator* by Dr W J L Sladen and to discover the wildlife resources at Barney Lake and in the Skagit Valley.

Involvement with neck-banded resighting became more intense in 1978/79, partly due to the large number of banded swans in the area. Popularity of Barney Lake grew as word spread that *C. c. buccinator* had indeed become a regular winter visitor to the Skagit Valley.

Most of the land in the Skagit Valley is privately owned, including all of Barney Lake. There is little public access to the swan habitats. Trespassing by bird-watchers, photographers and other observers to get 'a closer look' has become a growing problem.

The now frequent disturbance at Barney Lake has been approaching unacceptable limits for landowners and swans alike. Currently, some of the lake landowners and other concerned citizens are working in co-operation with the Washington Department of Game (WDG) to provide an observation blind and controlled public access.

Recently, Mount Vernon expanded its city limits to within 0.5 km of Barney Lake to incorporate a new housing development. Other similar land developments are planned for areas to the south and northwest.

Currently, an effort is under way by concerned citizens of the State, Pilchuck Audubon Society, Friends of the Swan (a local citizen's group), WDG and The Nature Conservancy to ensure that agricultural areas remain available for wildlife use.

Many species of ducks as well as swans use Barney Lake; lead shot use in waterfowl hunting has given rise to an increased mortality for swans from lead poisoning. As a result, in March 1979 Friends of the Swan and other concerned groups encouraged WDG to designate Barney Lake and the surrounding area as a 'steel shot ammunition — only' hunting area for the 1979/80 and future waterfowl seasons. After several months of work with WDG, and a petition drive, Barney Lake and a considerable portion of surrounding land were so designated.

Citizen participation and co-operation with state and federal agencies is a continuing process. The neck-band resighting project involves many people in an ongoing effort. Friends of the Swan provides local information and active support. Pilchuck Audubon Society and other Audubon chapters conduct count surveys and are assisting The Nature Conservancy in its long-range plan to preserve the integrity of Barney Lake and other swan habitats.

Acknowledgements

We are grateful to Dr William Sladen for his comments, suggestions, technical and editorial advice, and to Larry Brewer and Michael Davison of the Washington Department of Game, Michael Kyte, Meredith Pfahl and Elizabeth Parrott Anderson for comments and biological insights. We thank Fugro Northwest, Inc, for their assistance with graphics; and John Munn and others for assistance in the neck-band resighting effort and the many people who have given their time for the swan cause.

Summary

Cygnus cygnus buccinator was first recorded in the Skagit Valley in 1957, but numbers grew in the 1970s and a maximum of 355 wintering birds was recorded in 1980. Details of neck-banded individuals, of the habitat used and its vegetation are given. The resulting increase in public interest has led to designation of Barney Lake as a steel shot only hunting area, and to long-term plans to conserve habitat for wildlife use.

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NON-PROFESSIONAL CONTRIBUTIONS TO SWAN RESEARCH

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Introduction

As non-professional ornithologists the authors have taken an interest in the population of *Cygnus columbianus columbianus* which winters and migrates through the Upper Eastern Shore of the State of Maryland, USA. These swans arrive early to mid-November and continue to migrate through the area to more southerly wintering grounds in the coastal marshes of North Carolina. Some, however, stay for the whole winter in the Upper Eastern Shore counties. The birds spend a considerable amount of their winter feeding in grain fields, chiefly corn and winter wheat, in large flocks sometimes numbering as high as 7000 individuals. Plastic neck-collars and tarsus-bands placed on these birds are readable by the observer with a 60 x spotting scope, at a distance of over 300 m (collars) and of up to 70 m (tarsus-bands).

It is our hobby to pursue these birds, with such a scope, to read the collars and tarsus-bands and report the data observed thereon. The authors spend 10 to 15 hours a week (and drive many hundreds of miles) from 1 November to 1 April each winter, pursuing the swans. Even though this hobby is time-consuming, it is interesting and much like the sport of hunting, to locate and read these collars and report them. The birds are in the area when other outside activities are at a minimum and it is a most enjoyable form of recreation to pursue them.

It is obvious that the use of volunteers by professionals engaged in research, where intense field observation is required, can save the research programme many thousands of dollars which would be required if salary at standard wage rates were paid.

Methods

The birds themselves are highly mobile, normally spending the night (and some of the day) resting on sheltered coves in tidewater areas, usually well isolated from man and his habitations. When the urge comes to feed, they fly in skeins from their resting area to nearby fields. By using available spare time and living in the area, a non-professional can acquire sufficient skill to locate the fields holding the birds on a given day and manoeuvre his or her automobile (or spotting scope on tripod) close enough to these feeding flocks so that he can read the neck-collars and, with luck, even the tarsus-bands.

In order to save gasoline and time, liaison is developed with local people (chiefly farmers) so that they call and tell when they see swans in various fields. In some cases the use of a 'Citizen Band' radio is helpful in learning this information.

or too expensive, they are likely to be less active. In order to gain proper coverage of the population, it should be observed constantly throughout the season because the birds are constantly moving through the area, especially in the early part of the fall migration from November to December and again from February to early April. This means that constant, steady viewing is required in order to get accurate results. One way to maintain the interest of volunteers is to make sure that they are provided with an easy-to-use recording form which requires little time to fill out and return. This way, the volunteer is not spending large amounts of his time doing paperwork. It also helps to maintain interest if the volunteer is supplied with plenty of information as to the progress of the research programme, including banding and other return information from faraway locations. This enables the volunteer, if he wishes, to keep and maintain his own records and appreciate the value of his work in reaching the overall goals of the project. Care should be taken to meet often with the volunteers, most preferably before the beginning of the season, for a luncheon or dinner meeting, and then again towards the end of the season. It may also be helpful to award prizes for the person who reports the most collars. However, lest the prize rather than accuracy become the most important goal, this device should be used with caution.

Summary

'Swan watching' is a most fascinating form of recreation. Other bird-watchers and groups interested in birds can, if properly trained, equipped and motivated, provide a considerable saving in the cost of swan research done by live sightings through neck-collars and other markings. This work will be extremely enhanced if the suggestions and principles presented in the paper are followed.

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THE SWAN SUPPORTER SCHEME AT SLIMBRIDGE AND A PROPOSAL FOR AN AUDIO-VISUAL PROGRAMME ON SWANS

M E EVANS

History of the Swan Supporter Scheme

The Swan Supporter Scheme, by which a member of the public could take an interest in the *Cygnus columbianus bewickii* flock in general and one individual swan in particular was started in 1966. If, in a subsequent winter, there was no news of 'his' swan, he was given another to replace it. If, later on, the original bird returned, the Swan Supporter was allowed to support both it and the replacement bird.

The original concept was for rather an 'expensive' scheme, costing £5.00 per annum, which in today's terms is equivalent to £18.40. Cost of membership of the scheme has not kept pace with inflation and now costs only £7.50 (increase made in 1975). As the number of Swan Supporters grew, they began to exceed the number of swans available. A two-tier system of support was therefore introduced: 'Exclusive' — a particular swan was issued to one Supporter only; and 'Share' — a particular swan was issued to more than one Supporter. Exclusive Supporters paid a double subscription for their privilege.

This, however, still 'tied up' too many swans, especially because of the replacement policy for non-returning birds. An Exclusive Supporter might, through this system, have three or four of 'his' birds return in a particular winter, none of which could be allocated to anyone else. Therefore, the Exclusive category of Supporter has been discontinued and existing Exclusive Supporters are being phased out.

Present arrangements

Supporters are sent:

- A hand-coloured portrait of their swan plus details of its history on a record card on which subsequent news can be recorded.
- An Arrival and a Departure Report covering the *C. c. bewickii* herd at Slimbridge.
- An individual report when their swan is first seen and another at the end of each season about its activities.
- A portrait of a new swan if their bird is not seen. If in a subsequent season there is news of their original swan they will support both birds at no extra cost.
- All issues of the Wildfowl Trust's magazine during the period of their subscription.

Supporters are allowed:

- During the *C. c. bewickii* season (1 October to 31 March) free admission, with one guest, to the grounds and Tropical House at Slimbridge.
- Free admission, with one guest, to the Welney Refuge.
- Free admission, with one guest, to the Observatories (when open) at Slimbridge and Welney.

– Overnight accommodation in Wigeon House, Welney, at the reduced rates applicable to Members of the Wildfowl Trust.

– To purchase the Wildfowl Trust's annual scientific publication 'Wildfowl' at the Membership discount rate.

Schools, firms, hotels, etc

Any organisation may support one or more swans, though each Supporter's card must be made out in the name of an individual nominated by the organisation. One card is issued for each swan supported and the individual nominated has the privileges of a Supporter.

Recent numbers of Swan Supporters in each January are as follows:

1973 – 281	1977 – 419
1974 – 368	1978 – 441
1975 – 393	2979 – 514
1976 – 403	1980 – 733

This last figure provides a useful gross income of £5500 per annum.

Proposal for an audio-visual programme

It is clear that many private citizens are interested in, and involved with, swans, and now may be an appropriate time to produce an audio-visual programme on these birds.

The World Wildlife Fund Education Project specializes in producing audio-visual programmes on wildlife subjects, particularly on endangered species. To produce a special swan programme pack of 40 slides for even only half of the current 733 Slimbridge Supporters would cost relatively little, about the same price as an unused 36 exposure colour film.

A cassette tape (with swan sounds, music and vocal commentary) could be produced to complete the programme. This would be 'pulsed', so that, on suitable equipment, the programme would play entirely automatically. Origination costs may vary according to the amount of editing and mixing necessary, but each finished tape would not cost more than half the slide pack.

The Swan Supporter Schemes could sell the programmes at whatever price they like – possibly at bargain prices to existing Supporters. It could be distributed further through WWF Education Project, who are prepared to add the programme to their current catalogue.

Summary

For an annual fee, interested members of the public may become Swan Supporters, enabling them to receive information about *Cygnus columbianus bewickii* wintering at reserves of the Wildfowl Trust in the UK and to visit the wintering sites. The paper describes the scheme and develops a proposal for a cheap audio-visual slide programme on swans, intended for wide distribution.

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AROUND THE YEAR WITH A DANISH SWAN AMATEUR

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Introduction

Research on swans in Denmark is organized by the Zoological Museum in Copenhagen and previously also by the Institute of Game Biology. However, most of the work is done by a group of amateurs supported by the Zoological Museum.

From its very beginning, the swan project has been managed by P Andersen-Harild, who has succeeded in gathering around him a group of enthusiastic amateurs. The present paper describes the events of a year, from April 1978 to March 1979, as experienced by the author.

The Kingdom of Elleore

The Kingdom of Elleore is an islet in the Fjord of Roskilde, only 15 000 cock-strides from the Danish border. The strange Elleorian folk live there for one week in August, while Elleore is populated only by birds for the rest of the year. As most of you have probably never before heard of Elleore and its brave inhabitants, I will offer a short description before returning to the swans. The inhabitants live in exile in Denmark most of the year but early in August the kingdom is established with bureaucracy, military (land militia, navy service and corps of drakes) and a court. The people are extremely fond of uniforms and decorations. Philatelists are familiar with their famous stamps, among which bottle message stamps with the gumming on the front are unique in the world. I could go on with this ethnographic lecture for a long time but I have to return to the swans.

The swan colony

Elleore houses a colony of *Cygnus olor* and from mid-April to mid-June this colony is visited once a week; all nests are numbered, the swans identified (25% carry neck-collars) and the eggs numbered and measured. When hatching time begins, the swans become so aggressive defending their nests that they can often be caught by hand. The old swans are ringed, while the cygnets are given wing-tags.

During the hatching period the other 30 islets of the fjord are also visited, the populations are counted, ringed swans are identified and others which can be caught are ringed. This tour is very exciting, as 10 000 other birds breed on these very small islets. The broods leave the island colony shortly after hatching and migrate to shore territories where they stay for the rest of the summer. From the shores of the fjord we locate these territories and swans carrying neck-collars are identified.

Moulting

In July and August 1500 to 2000 non-breeding swans moult in the fjord and are searched for neck-collars. One day is used for catching moulting birds from a speed-boat. We establish a base on one of the small islets and while two men in the boat are catching the swans, three to four others are measuring and ringing them at the base. We normally catch about 70 swans in one day and sometimes the boat brings up to 20 swans at a time to the base. Moulting swans are also caught at other places. At Rødsand we get assistance from local fishermen and here we may catch up to 500 in one day.

The breeding swans moult in August and September and become able to fly again simultaneously with their young. Just before they complete moulting, we spend two days capturing the broods and their parents, exchanging the wing-tags with normal rings.

Autumn and winter

The autumn is the most relaxed period. We use the time to consolidate the EDP files and study the results.

One out of ten Danish winters is an ice-winter. Our activities are strongly influenced by such winters as 1979, during which we made great efforts in many areas. When the first ice appears just before Christmas, the number of public observations increases. To encourage these it is very important to give a fast response. The masses of swans which come to the harbours, where people feed them with bread, attract the attention of the press. We got a lot of good publicity in that way, and we never forgot to mention the address of the ringing station. These efforts led to nearly 10 000 observations during the winter. When all natural feeding places are closed by the ice, the swans become very trusting and can be caught by hand, up to 300 in a day. A good part of these are Swedish and Baltic swans. When the winter becomes extremely cold even *Cygnus cygnus cygnus* can be caught. We managed to ring more than 100 of them, with neck-collars.

The ice-winter increased mortality drastically and we actually collected nearly 3000 dead swans in all stages of decomposition. Most of them are still in cold storage, awaiting veterinary and chemical analysis.

Summary

Swan research in Denmark is organized by the Copenhagen Zoological Museum but largely carried out by amateurs. The paper describes a typical year in the life of a subject of the Kingdom of Elleore, with emphasis on catching of colonial swans and operations in ice-winters.

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THE USE OF ELECTRONIC DATA PROCESSING (EDP) IN DANISH SWAN RECORDING

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Introduction

During the ice-winter of 1962/63 the first large-scale ringing of Danish swans was carried out (1500 individuals). In the winter of 1969/70 a further 5000 swans were ringed. In the early 1970s we started catching the moulting swans by boat, and today, after the ice-winter of 1978/79, the total number ringed has exceeded 23 000. In 1971 the use of neck-collars was adopted as a supplement to the normal rings.

The ringing of such large numbers of such big birds in a densely populated area, and especially the use of neck-collars, led to more than 70 000 reports. This caused serious administrative troubles for the ringing centre at the Zoological Museum in Copenhagen.

Design of the EDP system

In 1974, when the total number of reports had reached 50 000, it was decided to establish an EDP system for maintenance of the data on Danish ringed swans and foreign swans observed in Denmark. The EDP system, designed with a potential of 200 000 reports, performs the following functions: 1) Stores all data obtained by ringing, recapture and resighting of ringed swans, including place, time, sex, age, status (moulting, breeding, etc), biometrical information (weight etc), number of eggs and cygnets, partner and other information; 2) Performs translation from neck-collar into ring number; 3) Handles exchange of rings and neck-collars; 4) Converts mnemonic location codes for places into co-ordinates; 5) Writes a letter to the observer, containing a list of all known information about the actual bird, other than some biometrical data.

In the initial phase, the main task was to reorganize and simplify the administration of data on ringing and observations but the long-term goal was to organize the data in a way suitable for later statistical analysis.

The author accepted the designing and implementing of the system. Risø National Laboratory offered free computer time for the project. The design and coding of the system was performed in close collaboration with P Andersen-Harild.

Operation of the system

The next stage was the major task of keypunching all old data from the files of the Zoological Museum. It was done by the Department of Ringing in collaboration with P Andersen-Harild and was completed within two years. Initially, ringing data on neck-collared swans was entered. After that, all new observations of these swans were handled by the system, relieving the administration at the ringing centre at an early stage. Secondly, ringing data for the rest of the swans were entered and, finally, the old observations were punched. Some minor corrections and improvements were made but very soon the system became stable and has since been used unaltered.

The computer programme accepts data coded on punched cards, creates records, and merges these with previous records on magnetic tape. Other transactions make it possible to update or correct existing records or cancel erroneous records. When all transactions have been handled, the computer writes a letter regarding every swan for despatch to the observers, together with a leaflet giving a short description of the project. A more detailed description of the programme is given in the Appendix.

Before the ice-winter of 1978/79 all information had been entered into the system. During that winter 3000 new swans were ringed, more than 10 000 observations were received and quite a few rings were exchanged. The EDP system did not cause any trouble at all, but the keypunching and distribution of the letters heavily loaded the personnel at the ringing centre. However, we succeeded in dispatching a great number of letters before the start of the very cold period which encouraged a lot of people to make an extra effort in collecting more observations. The last observations were not answered before late summer. Without the EDP system it would have been impossible to handle 13 000 records within one winter.

Advantages of the system

The administrative work consists of two functions. First, a card is punched for each observation (two cards if the swan has been measured), and then the computer-generated letters are dispatched to the observers. The latter is the bottleneck of the system but it is the basis for stimulating interest among observers, without whom we could not collect so many observations. For example, one 14-year-old boy collected nearly 3000 observations during the winter of 1978/79.

The storage of data on magnetic tape facilitates the use of EDP for the scientific analyses, which are actually performed by another amateur, P Foldkjaer, in collaboration with P Andersen-Harild.

To illustrate the advantages of using EDP for statistical analysis, the distribution maps shown in Andersen-Harild's paper at this symposium on 'Migration of *Cygnus olor* ringed in Denmark in winter and during moult' were planned, coded, calculated and drawn by the computer within a period of only 14 days of spare time. The calculations included data from 13 500 records

Acknowledgements

Nearly all of the work described in this paper has been done by amateurs. However, it would not be possible to do this without support from the Department of Ringing at the Zoological Museum in Copenhagen and the Risø National Laboratory. The author wishes to thank these institutions, the many, many people who have given much help, especially in the collection of observations, and the Svend Bergsøe Foundation which provided funds to attend this conference.

Summary

Because many swans had been ringed and neck-collared in Denmark, the large numbers of resightings caused administrative problems. Use of an EDP system overcame these problems and enabled quick replies to be sent to observers, thus stimulating their interest. The functions of the system are described and details of the programme given in the Appendix.

Appendix

Technical description of the Danish EDP programme for swan recording

Introduction

This Appendix outlines the technique used in the Danish EDP programme for swan recording. The programme is written in Burroughs Extended Algol for a Burroughs B6700 computer. However, the description is given in general datalogical terms, with no special reference to the actual computer.

Definitions

Identity: Rings are often replaced when they become worn. Thus the ring number is not a unique identification of a swan. The term 'identity' is used for the first ring carried by a swan, while 'ring number' is used for the actual ring.

Record: The information is stored as records on magnetic tape. A record holds the description of one observation, the minimum information being identity, ring number, date and place. Other data are optional, although more are nearly always present.

Transaction: Transactions are used to enter data into the system and are written on punched cards. The programme handles primary, secondary and cancel transactions.

Operation of tne system

The transactions are sorted on different keys. The keys are fields of data used to define the ordering sequence of transactions or records. In most cases more than one field is used as a key and an order of precedence is given. Before being merged, two files must be sorted, using the same sorting key(s). Merging the files combines them into a new file according to a rule. The ordering will be maintained in the new file.

A primary transaction can enter the most commonly recorded data into the record.

Mandatory data are:

Transaction type.
Kind of swan.
Date.
Place (co-ordinates or mnemonic).
Ring number (or neck-collar, if this is already entered into the system).

Optional data are:

Neck-collar.
Code for coloured plastic rings.
Code for how the registration was made.
Age.
Sex and colour phase (Grey or Polish).
Activity.
Status (moulting, breeding, etc).
Ring number of partner.
Licence of ringer.
Country code.
A text used for the location field of the letters.

The secondary transaction is used to amend or to correct data in an existing record. The mandatory data are the same as those of the primary transaction and must exactly match those of the record to be altered.

Optional data are:

Number of eggs.
Number of cygnets.
Colour of beak.
Size of beak knob.
Weight.
Total length of swan.
Total length of wing.
Length of first primary.
Length of longest primary.
Length of fourth primary.
Length of neck.
Size of foot.
Ring number(s) of parent(s).
Ring number of partner.
Activity.
Status.
Moulting percentage of young swans.
Number of eggs destroyed by man.
Precision of date.
Ring number of new ring.

The cancel transaction is used to cancel existing records. The mandatory data are the same as those of the primary transaction and must exactly match those of the record to be cancelled.

During read-in, the transactions are read from the card-reader, checked for formal errors and written in a temporary file on disc. The mnemonic location codes are looked up and co-ordinates are substituted. The transactions are then sorted with the neck-collar as primary key and date as secondary key.

The records are then read in from magnetic tape and stored on a disc file. Records containing neck-collars are extracted and sorted with neck-collar as primary key and date as secondary key. Only the oldest record is retained for each neck-collar.

The transactions and the neck-collar subset of records are then merged. Those transactions which have been entered with a neck-collar only will get the ring number substituted.

The transactions are then sorted with ring number as primary key, date as secondary key, co-ordinate as tertiary key and transaction type as quartic key. In the quartic key cancelling goes before primary which goes before secondary transactions. The records are then sorted with ring number as primary key, date as secondary key and co-ordinates as tertiary key.

The transactions are now merged into the records. Primary transactions will create new records, unless a record with the same key already exists. Secondary transactions will update the matching record. For each record created or updated, a key-record will be written to a key-file. The key-record will contain the identity of the swan and a note that a letter should be written for this swan.

The exchange of rings calls for especial attention. When a record is created, the programme checks if the previous record has the same ring number. If not, the ring number is copied into the identity; otherwise the identity is copied from the identity of the previous record. When a ring is exchanged the new ring number is given in a secondary transaction. The old ring number is simply overwritten by the new one. To make sure that no swan gets two identities, we write a key-record to the key-file. This record gets the new ring number as identity and an indication stating that all possible records with that identity must be cancelled.

Now the records are sorted again, this time with identity as primary key, date as secondary key and co-ordinate as tertiary key. The key-records are sorted with identity as primary key and request for cancelling or letter-writing as secondary key. Cancelling goes before letter-writing. The key-records and the main records are now merged. Those identities requiring letters will have a letter printed showing all records in readable Danish. The records are written onto a new magnetic tape, which is stored for input to the next run.

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Anatomy, Weights and Measurements

ANATOMICAL SKETCH OF WILD SWANS

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Symposium participants were presented with copies of a 44-page booklet on this subject, richly illustrated by line drawings. The very quality and abundance of these illustrations make it impossible to reproduce the booklet within the confines of the Proceedings.

The booklet, in both English and Japanese, is split into five sections: bone structure, muscles, internal organs, feathers and sexing. The first four sections are illustrated with a general 'concept picture', as well as further enlarged drawings of details, and many measurements are given.

The section on sexing, as well as giving details of the cloacal method, suggests two techniques that can be used in the field based on general appearance and colour of the culmen. The back parts of the head are rounder and larger in the male than the female, and from the larynx down to the neck look rounder in the male — a character that can be seen well when a family is swimming together. On arrival in autumn bill colour in the two sexes does not differ, but just before departure in spring, the colour of the culmen in the male gets slightly orange.

Copies of the booklet can be obtained from the author.

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GENETIC COMPARISON OF *CYGNUS CYGNUS BUCCINATOR* POPULATIONS

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Introduction

The historical range of *Cygnus cygnus buccinator* encompassed a large area of the North American continent, from breeding areas in Alaska to wintering grounds along the Gulf of Mexico (Walker 1968) and east to Hudson's Bay (Alison 1975).

The expansion of civilization disturbed or destroyed *C. c. buccinator* habitat, pushing the species to near extinction. The population was reduced to 69 birds south of Canada by 1932 (Hansen 1973). Most of these were in the valleys of the Rocky Mountains in Idaho-Montana-Wyoming. The enactment of the Migratory Bird Conservation Act in 1929 began a reversal in the population trend by outlawing all hunting and trapping of *C. c. buccinator,* as well as authorizing the acquisition of land for waterfowl refuges (Walker 1968). Red Rock Lakes National Wildlife Refuge in Montana was established in 1935 (Hansen 1973) and is dedicated to the preservation of this swan. Today a stable population of about 300 occupies the Refuge, breeding and wintering there, moving only to open water nearby.

The swans at Red Rock Lakes have served as a source of birds for transplants to other refuges. Nine national wildlife refuges have breeding colonies emanating from the transplant programme (Fjetland 1974). All transplanted birds are essentially non-migratory.

In western Alberta, Canada, another small but stable population breeds. These swans, centred in the vicinity of Grande Prairie, Alberta, winter with birds from Red Rock Lakes (Hansen 1973), but limited neck-banding studies have not indicated an exchange of individuals between these populations (R Shea pers comm).

The existence of a previously unknown breeding population was reported by Monson (1956) in the lower Copper River Basin, Alaska. The discovery of this population of about 3000 swans (Hansen *et al* 1971) boosted the species' population status and resulted in its removal from the endangered species list in 1968 (Fjetland 1974).

Based on extensive analysis of the Red Rock Lakes and Alaskan populations, Hansen (1973) suggested that these two isolated populations may be distinct subspecies. Furthermore, he discouraged manipulation of the separate populations until the relationship was clarified.

We have used electrophoresis to study the protein differences between these populations and the Alberta population to determine if there may be a genetic basis for subspecies classifications.

Electrophoresis allows proteins to be screened for changes in amino acid composition. These changes can be extrapolated to the entire genome for comparative population genetics. In the case of *C. c. buccinator,* three populations can be identified with no known genetic exchange among them.

Blood samples from members of all three populations were collected, from both cygnets and adults. Enzymatic proteins from erythrocytes and plasma, and non-enzymatic plasma proteins have been identified by electrophoresis.

Materials and methods

Adult swans were captured on the water during the summer moult with airboats or motorboats. Cygnets were caught in the fall before flight. Three to five ml of blood were drawn from the tarsal vein with a 22 gauge needle on a heparin treated syringe. The blood was transferred to a 5 ml evacuated tube containing either heparin or sodium citrate and then placed on ice. At the end of the day's collecting, the samples were centrifuged to separate the cells from the plasma. Plasma was frozen immediately and stored at $-60^{o}C$. Erythrocytes were washed once in 0.85% sodium chloride and then frozen in one-two volumes of a glycerol-citrate solution, pH 8.4 (VandeBerg and Johnston 1977). Some lysis of cells and decrease of enzyme activity does occur with repeated freezing and thawing but there is little change with undisturbed storage.

Starch gel electrophoresis was performed after Selander *et al* (1971) using 12.5% (w/v) hydrolyzed potato starch cooked in an appropriate buffer. The buffer systems used for electrophoresis were those previously published (Selander *et al* 1971; Clayton and Tretiak 1972; Nelson *et al* 1977). Samples were thawed and applied to the gel on a wick of no 3 Whatman filter paper. Electrophoresis was stopped when the marker dye (bromphenol blue) had migrated to the anodal end of the gel. This took 3 to 5 hours depending on the buffer system used. The gel was then sliced and the individual slices stained with a histochemical stain specific for a particular enzyme or with the general protein stain amido-black (Allendorf *et al* 1977). Slices were incubated in the stain at room temperature in the dark overnight, then fixed in methanol-water-acetic acid (5:5:1) to be scored and photographed later. Many slices were wrapped in plastic film and stored in the refrigerator.

Results and discussion

Erythrocyte enzymes

Malate dehydrogenase (MDH 1.1.1.37). Both cytoplasmic and mitochondrial forms of the enzyme are detectable. The cytoplasmic enzyme appears as a single band anodal to the origin. All birds were presumed homozygous except for a single individual from the Alaskan population which showed three distinct bands, presumably the phenotype of a heterozygote with a rare allele. This phenotype suggests a dimeric form of the enzyme (Kitto and Wilson 1966). The mitochondrial MDH migrates cathodally and is often pale but disappears altogether when samples are centrifuged a second time at 10 000 x g for 20 minutes. One sample consistently showed two bands for the mitochondrial enzyme which is considered to represent a heterozygote, without an active heterodimer.

Lactate dehydrogenase (LDH 1.1.1.27). The five banded pattern typical of vertebrates produced by the random association of four subunits from two loci

(Markert 1975) can be seen in all samples without variation.

Peptidase (PEP 3.4.11). Three bands of peptidase activity are seen after staining of starch gels of erythrocytes. Each band presumably represents the product of a separate locus (Harris and Hopkinson 1976). No consistent variation was observed in any of these peptidases.

Esterase (EST 3.1.1.1). This enzyme has a five banded pattern which is the same for plasma and erythrocyte samples. Esterases are a broad class of enzymes whose function *in vivo* is unclear (Shaw 1965). The staining intensity of esterase from individuals is highly variable. The sample from a single swan from the Alaskan population showed a consistently faster migrating esterase considered to be due to a rare allele at one locus.

Glucose-6-phosphate dehydrogenase (1.1.1.49). One invariant band of G-6-PD activity was seen in the swan samples. Without variation, the subunit structure of the swan enzyme cannot be determined.

Haemoglobin. Electrophoresis of samples shows a major band and a slower streaked minor haemoglobin. Examination of chicken haemoglobin shows that the major (80%) and minor haemoglobins interact with each other and may have one polypeptide chain in common (Manwell *et al* 1966). Thus three monomorphic loci were scored.

Plasma proteins

The conventions established by Baker *et al* (1966) and Baker and Hanson (1966) for the nomenclature of avian serum proteins was adopted for swan plasma proteins.

Albumin. The dominant plasma protein is albumin which migrates anodally ahead of the other plasma proteins except for a slightly faster migrating prealbumin protein. No variation has been seen in the large heavy band that is albumin but dilution of plasma samples with water (1:1) reveals two bands without unveiling any variation.

Carotinoid-binding protein. This protein is described by Baker *et al* (1966) as a protein which migrates in the region behind albumin. As in *Phasianus colchicus,* an occasional swan has a carotinoid-binding zone considerably cathodal to the normal position. The differences could be due either to the protein or the carotinoid. Samples with two bands may be presumed to be heterozygotes, which suggests that the variation is genetic.

Transferrin. Transferrin is an iron-binding protein with a sialic acid side chain (Canham and Cameron 1972). Two phenotypes are seen in swan plasma, the homozygote shows two bands, apparently differing in the carbohydrate portion of the molecule. Heterozygotes are seen with four bands. The homozygote for the rare allele was never observed.

Esterase (EST 3.1.1.1). Plasma esterases show the same pattern and migration distance as erythrocyte esterases but staining is much darker and appears almost immediately after application of the staining mixture, whereas the erythrocyte esterase is slow to appear. The plasma and erythrocyte enzymes are likely products of the same loci.

Population comparisons

The allele frequencies for 17 presumptive genetic loci can be compared for the three major populations of *C. c. buccinator* (Table 1). All populations share a

Table 1. Allele frequencies of presumptive loci in three populations of *Cygnus cygnus buccinator.*

Number of birds sampled in brackets.

		ALASKA		GRANDE PRAIRIE		RED ROCK	
RBC							
	s-MDH	0.988 0.014	(43)	1.000	(26)	1.000	(122)
	m-MDH	0.981 0.089	(26)	1.000	(26)	1.000	(68)
	LDH-1	1.000	(41)	1.000	(26)	1.000	(115)
	LDH-2	1.000	(41)	1.000	(26)	1.000	(115)
	PEP-1	1.000	(40)	1.000	(26)	1.000	(107)
	PEP-2	1.000	(40)	1.000	(26)	1.000	(107)
	PEP-3	1.000	(40)	1.000	(26)	1.000	(107)
	Est-1	0.777	(43)	1.000	(26)	1.000	(128)
	Est-2	1.000	(43)	1.000	(26)	1.000	(128)
	G-6-PD	1.000	(43)	1.000	(26)	1.000	(94)
	Hb-1	1.000	(43)	1.000	(26)	1.000	(128)
	Hb-2	1.000	(43)	1.000	(26)	1.000	(128)
	Hb-3	1.000	(43)	1.000	(26)	1.000	(128)
PLASMA							
	Car	0.965 0.035	(43)	0.897 0.103	(58)	0.960 0.040	(124)
	Tf	0.942 0.058	(43)	1.948 0.052	(58)	0.949 0.052	(128)
	Alb	1.000	(43)	1.000	(58)	1.000	(128)
	Pre alb	1.000	(41)	1.000	(58)	1.000	(23)

common allele for each locus. Polymorphic loci also share the rare allele in all populations where the polymorphism occurs. In those instances where a locus is fixed for one allele, that same allele is either fixed or predominant in the other two populations. This preliminary screening indicates that there is probably very little genetic difference among the three populations analysed. The apparent size differences between the Alaskan and Red Rock Lakes swans (Hansen 1973) may reflect habitat rather than genetic differences. Alternatively, genetic differences may exist that have not been revealed by the limited number of proteins studied to date. The genetic data are even less complete for comparisons between the Alberta and the Red Rock Lakes populations. If the isolation of these two populations is real, sufficient genetic differences may not have arisen by drift or mutation to date to be identified by these techniques.

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Summary

Seventeen presumptive genetic loci have been examined in *Cygnus cygnus buccinator* to determine if the isolation of the three major populations, Alaska, Grande Prairie, Alberta and Red Rock Lakes, has resulted in genetic changes. No major differences in allele frequencies have been found among these populations.

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WEIGHTS OF *CYGNUS COLUMBIANUS COLUMBIANUS* AS AN INDICATOR OF CHANGING RESOURCES

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Review of data

The weights of 2368 *Cygnus columbianus columbianus,* processed and banded between 1967 and 1978, have been analysed. One hundred and two birds, all adults, were captured moulting on their Alaskan breeding grounds. The rest were adults and juveniles (first winter) trapped on their eastern wintering grounds, mostly at Mattamuskeet and Pungo National Wildlife Refuges, North Carolina (1308) and in Maryland (946). The mean weight for all adults was 6.7 kg (males averaging 7.1 kg, females 6.3 kg). The mean weight for all juveniles (first winter) was 5.8 kg with males averaging 6.0 kg and females 5.5 kg (Table 1).

Table 1. Weights (kg) of 2368 *Cygnus columbianus columbianus*, 1967–1978.

Age	Male			Female			Totals	
	Mean	S.d.	N	Mean	S.d.	N	Mean	N
Adult	7.1	0.81	917	6.3	0.61	929	6.7	1846
First winter	6.0	0.81	235	5.5	0.62	287	5.8	522
						Totals	6.3	2368

Variation in weight

The swans were heaviest on arrival at the wintering grounds in November and lightest before departure in spring for both ages and sexes. The relatively small sample (102) from Alaska showed males to average 0.7 kg heavier and females 0.2 kg heavier during their moult than in winter (Table 2).

Table 2. Mean weights (kg) of 2356 *Cygnus columbianus columbianus* in relation to area, 1967 to 1978.

Area	Adult						First winter						Totals
	Male			Female			Male			Female			
	Mean	S.d.	N	Mean	S.d.	N	Mean	S.d.	N	Mean	S.d.	N	
Maryland (1967 to 1977)	7.2	0.95	323	6.7	0.80	364	5.9	1.11	120	5.5	0.85	139	946
North Carolina (1972 to 1978)	7.1	0.94	545	6.3	0.67	512	6.1	0.86	108	5.6	0.74	143	1308
Alaska (1970 to 1977)	7.8	0.94	49	6.7	1.39	53	Not included as cygnets growing						102

The large sample (2254) of winter weights, when averaged for the long study period, demonstrated that adult males and juvenile males and females were almost the same weight in Maryland in North Carolina, whereas adult females averaged 0.4 kg lighter in North Carolina (Table 2). However, within these periods there were fluctuations in weights which are believed to be due to changes in feeding habits and in weather conditions.

Relation of weight changes to feeding habitats

During the 1971/72 winter, thousands of *C. c. columbianus* in Maryland shifted from their traditional food resource, submerged aquatic vegetation, to feeding in fields of harvested corn (maize). At the same time an increasing number of swans flew farther south from the Chesapeake Bay to increase the numbers wintering in North Carolina. The data show that adult and juvenile male weights varied significantly in relation to their changing food resources, there being an increase of

Table 3. Mean weights (kg) of 656 *Cygnus columbianus columbianus* in winter grounds in relation to food resources, 1970 to 1973.

MD =Maryland; NC = North Carolina; SAV = submerged aquatic vegetation; F = field feeding (mostly harvested maize). Mean weight (sample size).

Winter	Location & food resource	Adults Male		Adults Female		First winter Male		First winter Female		Totals
1970/71	MD–SAV	7.7	(14)	6.5	(15)	6.6	(20)	5.6	(20)	69
1971/72	MD–SAV + F	7.1	(15)	6.6	(20)	5.6	(14)	5.8	(23)	72
	NC–F	7.9	(40)	6.9	(64)	6.7	(19)	6.2	(25)	148
1972/73	MD–F	7.6	(71)	6.5	(59)	6.6	(10)	6.6	(14)	154
	NC–SAV + F	7.1	(99)	6.3	(91)	6.2	(7)	6.0	(16)	213

weight when they were exploiting a new and abundant resource such as corn. The changes, though present, were less marked for adult and juvenile females (Table 3). The swans are successfully adapting to changes in their food resources.

Table 4. Mean weights (kg) of 522 adult *Cygnus columbianus columbianus* in winter grounds in relation to low temperatures, 1975 to 1978.

Winter	Degrees C below average	Male Mean wt	(N)	Female Mean wt	(N)	Totals
1975/76	0.2	7.5	(113)	6.9	(107)	220
1976/77	8.0	6.9	(76)	6.2	(46)	122
1977/78	6.0	7.0	(103)	6.1	(77)	180

The winters of 1976/77 and 1977/78 were unusually cold. Adult males averaged at least 0.5 kg and adult females 0.7 kg lighter during these winters than in a winter (1975/76) when the temperatures were average (Table 4).

Summary

Weights of 2368 *Cygnus columbianus columbianus,* caught mainly on wintering grounds, with 102 from Alaskan moulting grounds, are presented by age and sex classes. The data show that

weights increased following a change from feeding on submerged aquatic vegetation to field feeding.

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WEIGHT CHANGES IN *CYGNUS OLOR*

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Introduction

Since 1968 a considerable number of biometric data on Danish *Cygnus olor* have been collected in connection with the swan investigations of the Zoological Museum in Copenhagen. Most of these data have been transferred to magnetic computer tape but not yet analysed. More than 10 000 data on weight are included. The present paper includes only a few chosen aspects concerning the weight of *C. olor* and the possible reasons for some of the differences in weight which have been found. The significance of the weight in relation to mortality will be shown with some examples.

It can be assumed that the growth period of the young and the moulting period represent periods when quality and quantity of food will have great effect on swan weights. The winter period, with frequent food limitation, is also of great significance for the survival of the swans, and the weight development in ice-winters will be dealt with, too.

The Danish breeding population

The Danish population of *C. olor* has increased considerably. In 1925 there were only 4 to 5 pairs but today at least 4000 pairs breed. There are two main types of breeding habitat: freshwater lakes with solitary breeding pairs and brackish or salt shallows with swans breeding in colonies on isles. The number of colonial swans has been increasing over the last 20 years. In 1978 there were 1500 to 2000 pairs breeding in colonies. The biggest colony is on Klaegbanken in Ringkøbing Fjord, Jutland, and consists of 662 pairs. Apart from this one the majority of colonies are situated in southeastern Denmark (Andersen-Harild and Preuss 1978).

Weight conditions in young of solitary breeding pairs

An area in Copenhagen and northern Sjaelland, where on average about 60 pairs breed, was investigated. The population of this area has been more or less constant since investigations started in 1966. Most of the swans are familiar with humans and it is relatively easy to catch the broods by feeding them. Most of the breeding pairs in this area get part of their food from humans but naturally growing plants are still the most important food source.

The area investigated has a much bigger number of vacant potential breeding places for *C. olor.* For the period 1966 to 1975, 95 localities are known where at least for one year a nest was built and eggs laid. However, on average only 44% of these are used.

Examples from two localities show how the plant food available affects the weight of the young:

— (i) Gentofte Lake, in the northern vicinity of Copenhagen, is a eutrophic lake about 1.0 km long and 0.4 km wide. It is very shallow (0.5 to 2.0 m deep) and along the western side there are a number of reedy islets where each year four to eight pairs of *C. olor* nest. Some of these pairs, normally birds without experience, are usually chased away and the remaining pairs split the lake into territories. Originally the submerged vegetation in the lake consisted of a dense growth of *Ceratophyllum, Myriophyllum* and *Potamogeton pectinatus.* In the late summer of 1975 an excavation for a main sewer was started along the eastern side of the lake. This excavation resulted in large amounts of particles being suspended in the water. The water became turbid and the submerged vegetation almost disappeared. The work lasted for about a year and not until the winter 1976/77 was the area re-established. Since then the transparency of the water has increased slowly and water plants, especially *Potamogeton pectinatus,* are once more common.

How these changes affected the weight of the swans is shown on Fig 1. Until 1974 the lake produced big and healthy swans, with females weighing 7 to 8 kg at an age of three months, and males 8 to 9 kg. When captured on 30 August 1975, two of the three broods showed a normal weight, whereas the third, whose territory was in the part of the lake where excavation had started, weighed considerably less. In 1976 the weight of all young was low, about 5 kg. Since then weights have increased slowly so that they were nearly normal again in 1979.

— (ii) Viemose, the other breeding locality, is a reservoir for surplus rainwater, some 150 x 75 m in size. This locality had an extremely dense submerged vegetation of *Elodea canadensis* which is obviously one of the swans' favourite plants. From 1966 to 1968 some big broods with heavy young were produced, weighing about 10 kg at an age of three and a half to four months. For unknown reasons the vegetation was partly spoiled in 1969 and the weight of the young decreased to

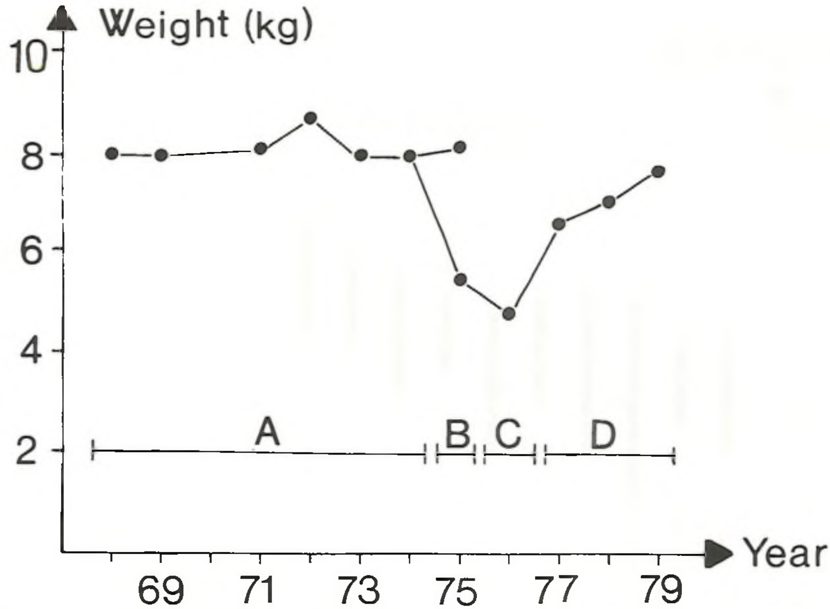

Fig 1. Average weight of *Cygnus olor* cygnets in Gentofte Lake around 1 September, 1968 to 1979.

A: Dense submerged vegetation. B: The submerged vegetation is being spoiled in the southern part of the lake. C: The submerged vegetation of the whole lake is spoiled. D: The submerged vegetation is slowly re-established.

less than half. In 1970 the vegetation of the lake was strongly reduced and the bottom consisted of stinking mud. The cygnets had no chance of going ashore to graze, as the lake is surrounded by a fence. During 1970/71 no swans bred, and in 1972 attempts to breed were unsuccessful. Broods produced in 1973 and 1974 had young weighing 4 to 5 kg by September. In 1974, which was the last year with breeding swans here, a male cygnet weighing only 3.9 kg was caught in the beginning of October.

These two examples illustrate clearly the importance of submerged vegetation for swans. From 1968 to 1975 all weights of birds caught in the period 24 August to 8 September have been examined to see how often the locality in question had been used as a breeding place (Fig 2).

The result is that the less a locality is used, the lower the weight of the young produced there. The picture is distorted to some extent by the fact that at some localities, especially those used least, extra food, eg grain and grass, is given by people living close by, who feel sorry for the poor small young. The picture is further distorted because we tend to avoid catching the lightest broods around 1 September, as their tarsi are often so small that the rings fall off. If these two

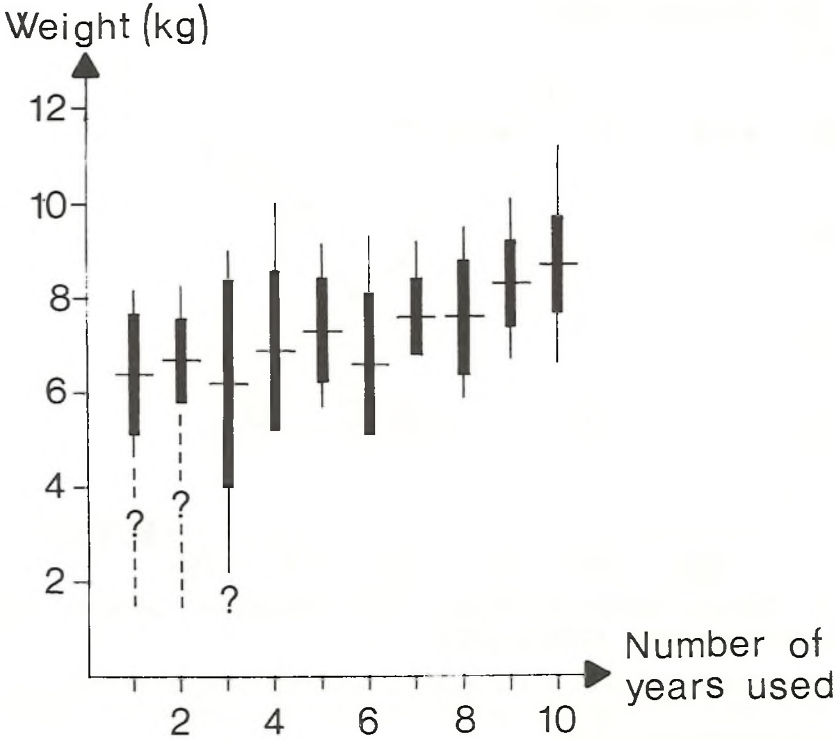

Fig 2. The average weight of young from an area of North Zealand and Copenhagen around 1 September, related to how often the locality has been used as a breeding place.

Average, standard deviation and range of variation are shown. Question marks indicate that there have been broods with low weights which have not been caught.

facts were taken into consideration, the differences would be still more marked.

When botanical conditions, especially submerged vegetation, are investigated, it becomes clear that some of the following conditions are characteristic for bad swan localities:

- acid water with consequent poor vegetation;
- deep lakes with steep shores;
- polluted lakes with poor transparency and consequent absence of submerged plants;
- few opportunities of grazing ashore.

Good swan localities are characterized by some of the following conditions:

- neutral or basic water;

– shallow eutrophic lakes with rich vegetation of *Elodea canadensis, Potamogeton* sp, (eg *P. pectinatus* and *P. gramineus), Myriophyllum, Ceratophyllum, Chara* sp;
– growth of *Phragmites;*
– opportunities of grazing ashore;
– feeding by man.

The size of the lake seems to be of minor consequence. Several ponds situated close to each other can be used by the same swan pair.

Weight conditions in swans breeding in colonies

Young were caught in two areas:

– (i) Roskilde Fjord is a mesohaline, shallow fjord, about 40 km long, and about 30 km west of Copenhagen. There are now several swan colonies in this area, with altogether around 200 breeding pairs. The biggest colony is situated on Langholm, an island about 500 m long, and has 50 to 90 pairs. When the breeding season is over, the broods spread evenly over the whole fjord. The submerged vegetation consists mainly of *Zostera marina* and *Ruppia maritima* as well as *Potamogeton pectinatus* and *Ulva lactuca* in some areas. *Zostera* in summer is overgrown by large amounts of epiphytic algae. Apart from breeding birds, there are in summer 1500 to 2000 non-breeding swans and in winter up to 3500 birds on the fjord. The young fledge from the end of September and are usually caught in the last part of September. Generally they are not as well developed as birds from lakes in Copenhagen and North Sjaelland (see Table 3).

There are rather distinct differences from year to year in the weight of the young (Table 1). These differences are not caused by changes in the breeding time, as this varies only a few days from year to year, with the spring of 1979 an exception.

Table 1. The weight of *Cygnus olor* cygnets in Roskilde Fjord.

Year	Date	Average weight (kg)	Average brood size	Survival up to 1 June in 2nd calendar year (%)	Number of days with ice in Danish waters in the first winter
1971	11–12 September	7.9	4.0	?	39
1972	20–22 September	8.5	3.6	76	4
1973	11–12 September	6.7	3.1	46	3
1974	21 September	8.4	3.3	79	1
1975	17–18 September	8.7	3.7	87	17
1976	17 September	7.5	3.0	29	26
1977	23–25 September	8.1	3.5	22	18
1979	29–30 September	6.7	3.3	?	83

It has not been possible to ascertain important changes in the submerged vegetation in the brackish areas.

— (ii) Bredningen, Guldborgsund, is situated between Lolland and Falster in southern Denmark. The conditions in the fjord are rather like those in Roskilde Fjord but the area is more exposed to wind. There are two big swan colonies with a total of about 100 breeding pairs (Clausen and Lind *in litt).* The area is an important wintering place for *C. olor,* whereas there are only a few moulting swans. Swans have been captured here for four years (Table 2).

Table 2. The weight of *Cygnus olor* cygnets in Guldborgsund.

Year	Date	Average weight (kg)	Average brood size	Survival up to 1 June in 2nd calendar year (%)
1973	23 September	7.8	4.8	94
1975	21 September	8.1	3.4	25
1976	18 September	6.1	2.3	5
1977	18 September	6.5	2.9	19

Causes of differences in weight

The swan broods most often stay in rather shallow water and the small young can often be seen pecking at the water surface. It can be assumed that small invertebrates, eg *Idotea, Gammarus,* are of importance, and possibly mysids and other crustaceans usually found in big numbers in the vegetation.

When the wind is strong it is more difficult for the young to seize these small animals, and at the same time the water level often rises, making the vegetation more difficult to reach. In addition, the wind forces the young to use more energy and their down may get soaked so that they become chilled and eventually die. The development of the survivors will be retarded.

Information about wind and wind speeds in Roskilde Fjord has been obtained from the meteorological station at Risø (M Frederiksen *in litt).* Strong winds in June have a particularly negative impact on the autumn weight of the cygnets. In years where the wind speed exceeded 9 m/sec for 20% to 25% of the time, the cygnets had relatively low weights as compared with calmer years. The first half of June, when the cygnets are 0 to 3 weeks old, appears to be a critical period. Thus in 1973, wind speeds exceeded 9 m/sec for 25% and 12 m/sec for 14% of the time in that period and the average weight of the cygnets in September was only 6.0 kg. In contrast, the weight of the cygnets averaged 7.4 kg in September 1975. June that year was very calm, with wind speeds above 9 m/sec for only 14% of the time.

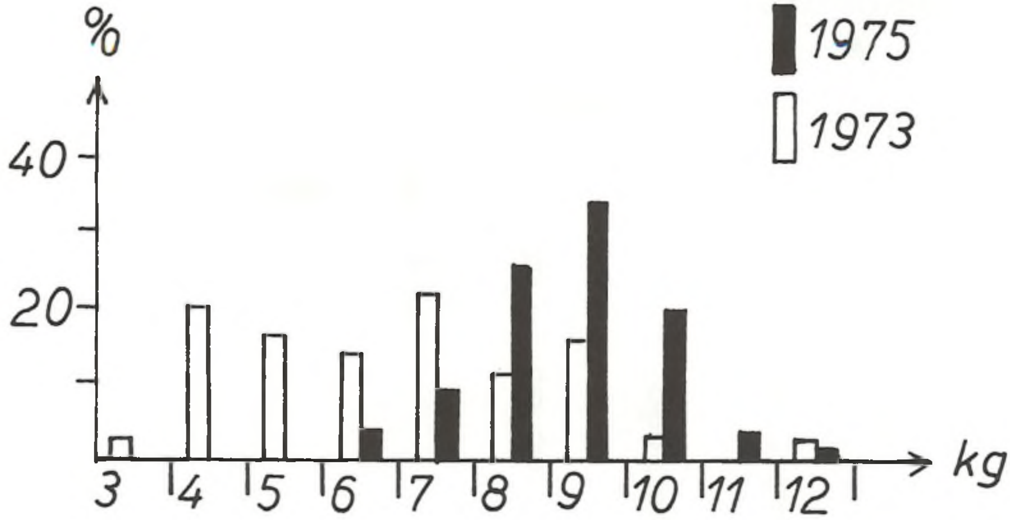

Fig 3. Variation in weight of young *Cygnus olor* in Roskilde Fjord in 1973 and 1975.

Fig 3 shows clearly that, apart from the difference in average weight, the weight variation among the young was largest during the windy year (1973). This is because some of the broods live in more sheltered areas, whereas the 'territory' of others is more exposed to the wind. During calm years, the importance of territory selection for the development of the young will be less.

The average brood size is positively correlated with the average autumn weight of the cygnets (Table 1).

Young from other localities also show significant differences in average weight.

Table 3. Average weight of *Cygnus olor* cygnets caught on different localities.

The weight has been calculated for 1 September, irrespective of differences in day of catching. The data from Tipperne are from 1977, the others from 1973.

Locality	Calculated weight (kg)
Tipperne, west Jutland (brackish water)	5.7
Roskilde Fjord, Sjaelland (brackish water)	6.1
Guldborgsund, Falster (brackish water)	6.6
Takern, Ostergotland, Sweden (fresh water)	6.2
Lakes in northern Sjaelland (fresh water)	7.7

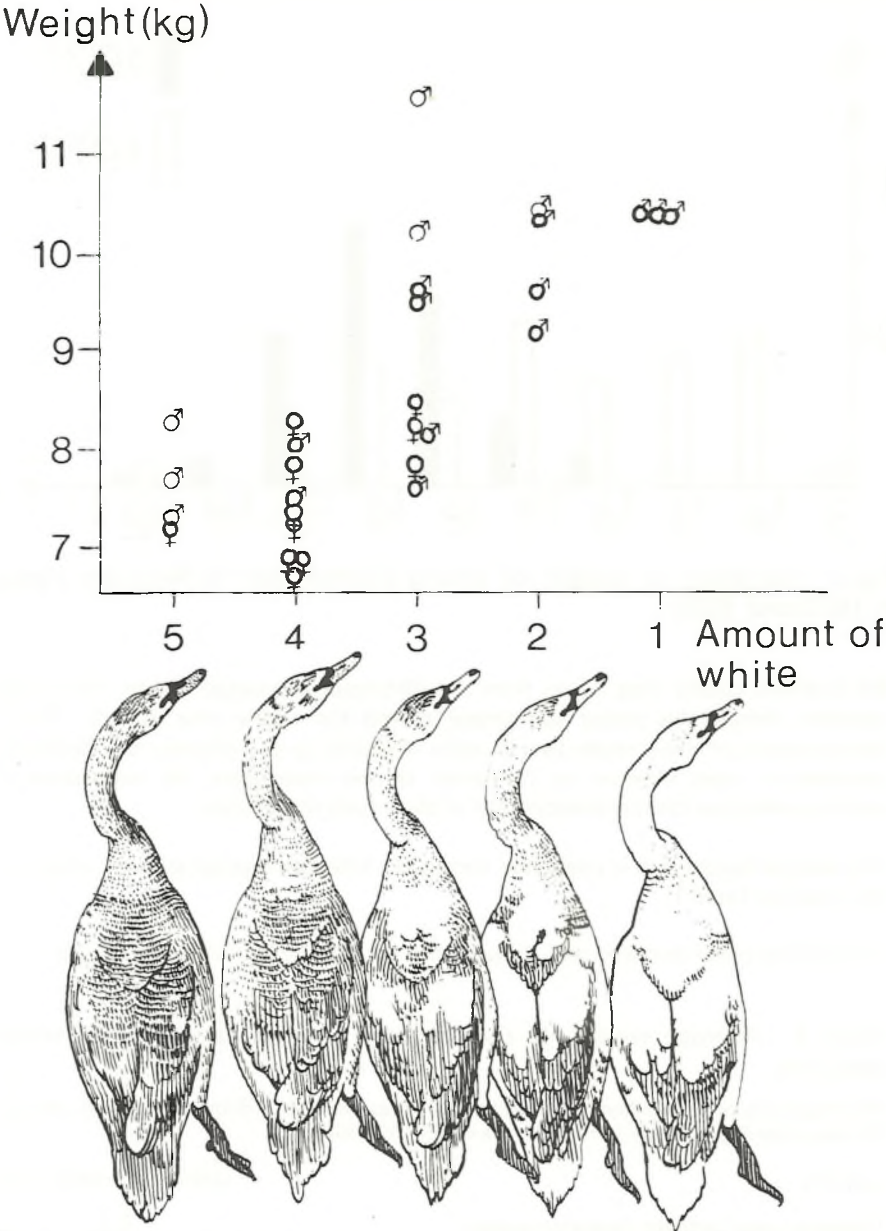

Fig 4. The moult in young in mid-February in relation to their weight around 1 September.

The figures at the bottom show the degree of moult: 1 = intense and early moult; 2 = intense but later moult; 3 = medium moult; 4 = little moult; 5 = none or only a few white feathers.

The moult of young in relation to weight

The moult of young starts during their first winter. The first birds with single white feathers are usually seen in October when the birds are four and a half to five months old. After that the birds gradually grow more and more white feathers but there are very big individual differences. In February and March all states can be seen from completely drab to very variegated young, where neck, upper back and tail coverts are white.

It is evident that during the coldest time of the year the growth of new feathers, which takes a lot of energy, can be carried out only by young which are in a good food situation. Fig 4 shows the relation between the weight of the young in September and their moult by mid-February.

The importance of weight for survival

Tables 1 and 2 and Fig 5 show how large a proportion of the young from Roskilde Fjord and Guldborgsund is known to have survived the first winter. A striking

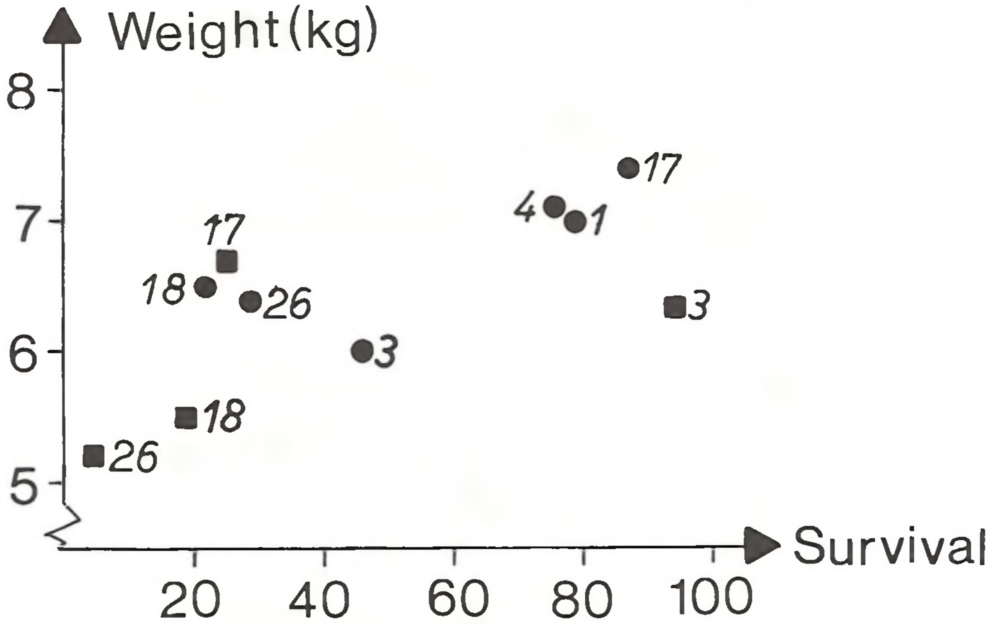

Fig 5. Correlation between the weight of cygnets in September and their survival from the time of ringing to 31 May in their second calendar year.

Circles indicate data from Roskilde Fjord – squares from Guldborgsund. The numbers indicate the number of days with ice in inner Danish waters.

relationship is apparent with the weight of the young, but severity of the winter is also involved. The survival rates are minimum values, as they originate from young ringed with neck-collars, seen after 1 June in their second calendar year. Some young may have lost the neck-collar or may have escaped notice.

Differences in weight in moulting swans

About 35 000 to 40 000 non-breeding *C. olor* stay in Danish waters (including the Swedish coast of Øresund) from June to September (Andersen-Harild 1971). These swans come from the entire Baltic area (Andersen-Harild 1981b) and assemble in certain places to moult their wing feathers. This lasts 6 to 7 weeks. Thereafter the birds leave the moulting places and go to good feeding areas nearby. The moult of body feathers continues through the autumn.

About 9000 birds were caught and a high number were weighed. The investigations have, besides other things, shown that the moult starts in the heaviest individuals.

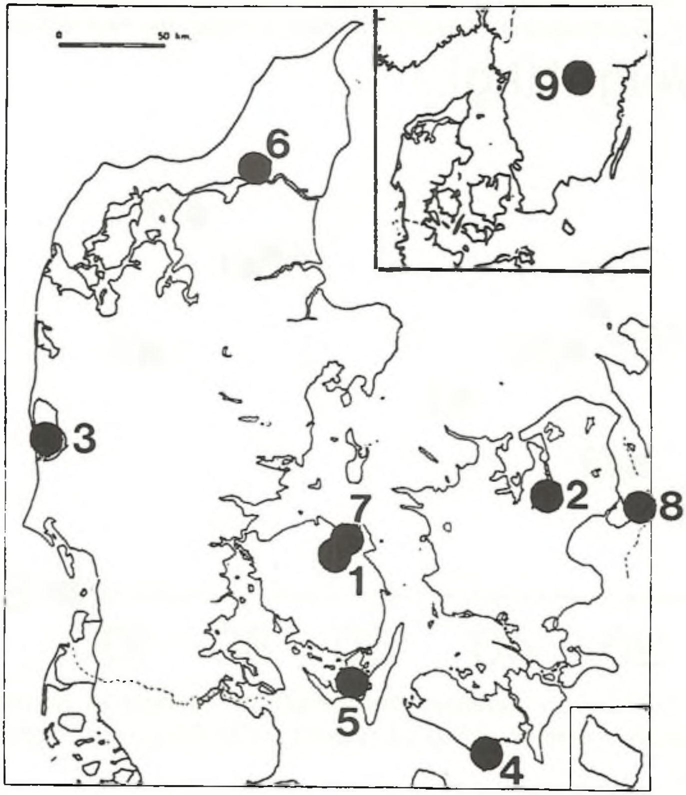

Fig 6. Situation of moulting places.

From year to year there may be a difference in time of onset of the moult but usually not more than one week. During moult the birds can lose up to 20% of their weight.

Description of some moulting places (Fig 6)

— 1 Seden Strand, Funen. The area is a very shallow brackish water area inside Odense Fjord. The renewal of water is poor and the area is influenced by sewage. In the past the fjord was overgrown by *Zostera* but because of sewage pollution this vegetation has gone and is replaced by *Ulva lactuca.* This change started at the end of the 1960s and the number of moulting *C. olor* increased from about 500 in 1968 to 2300 in 1974. *Ulva* is most probably the only summer food for swans in this area.

— 2 Roskilde Fjord has been described on page 363. The main food of the moulting swans is *Zostera* (with epiphytic algae) and *Ulva.* The swan population increased from about 600 in 1968 to 1700 in 1974 and has since then been more or less stable.

— 3 Ringkøbing Fjord, Jutland, is a brackish water area of about 295 km^2. The majority of swans remain on shallows in the southern part of the fjord. These areas, which are less than 1 m deep, are overgrown with *Ruppia* with a dense admixture of *Ulva;* besides there is some *Ranunculus* sp. The growth is very dense. The population of swans increased from 1300 in 1968 to 2500 in 1974.

— 4 Rødsand, south of Lolland, is the biggest moulting place for *C. olor.* The population increased from 4800 in 1968 to 7000 in 1974. The area is shallow with abundant growth of *Zostera, Ruppia* and *Chara.*

— 5 Strynø. The birds in this archipelago feed on the shallow areas off Tasinge or close to Bredholm. The vegetation here is mainly *Zostera.* The population increased from 2800 in 1968 to 4800 in 1974.

— 6 Ulvedybet is a shallow inshore area at Limfjorden in North Jutland. The area is brackish, fringed by extensive growth of *Phragmites.* The submerged vegetation is mainly *Fucus.* The area has a small population of swans — 300 in 1968 increasing to 700 in 1974.

— 7 Odense Yderfjord, Funen, is an area without especial importance for moulting swans, only a few birds staying here. This area is overgrown mainly with *Fucus* sp.

— 8 Saltholm in the Oresund near Copenhagen has long been known as a moulting place for swans. The population in this area decreased from 2300 in 1968 to 1100 in 1974. The majority of the birds stay along the eastern and southern coast of the island, where the bottom is mainly sandy. There is no particularly rich growth of *Zostera* and *Ruppia*, but lots of *Fucus*.

– 9 Lake Takern, Ostergotland, Sweden. This is a big freshwater lake of about 50 km^2, surrounded by reeds. It is shallow and lightly alkaline, with an exceptionally rich vegetation of *Chara tomentosa*, *Myriophyllum* and *Potamogeton crispus*. The population of swans increased from about 1100 in 1968 to about 2700 in 1974.

Thus the ecological conditions differ considerably between the localities used as moulting places, ranging from open seas to estuaries, from inshore brackish water areas to big freshwater lakes. What they all have in common is that they are shallow and that the birds can find shelter from the wind. The vegetation in the areas varies considerably in species composition and density.

However, it seems that there is enough food available. The swans of Roskilde Fjord will, for example, be able to eat only a few percent of the available standing stock of *Zostera*, which is in accordance with the conditions on moulting places along the Swedish west coast (Mathiasson 1973).

Comparison of weights from different localities

When the weights of birds from different localities are compared (Table 4), it is obvious that birds feeding on *Ulva* have the highest weight. As growth of algae,

Table 4. Average weight for male *Cygnus olor* after second calendar year, caught on different moulting places around 1 August.

Moulting place	Average weight (kg)	Main food
Roskilde Fjord	11.6	*Zostera* (with epiphytic algae), *Ulva*
Seden Strand	11.5	*Ulva*
Takern	11.1	*Chara*
Ringkøbing Fjord	10.9	*Ruppia, Ulva*
Rødsand	10.6	*Zostera, Ruppia, Chara*
Strynø	10.5	*Zostera*
Odense Yderfjord	10.4	*Fucus*
Ulvedybet	10.3	*Fucus, Phragmites?*

favoured by sewage, has increased during recent years, there is no doubt that the increased pollution in this case has favoured the species.

Next to *Ulva*, it seems that *Zostera* and the epiphytic algae on it, which may weigh just as much as the *Zostera* itself, *Ruppia* and *Chara* are of high food value for swans, whereas *Fucus* is of less value.

To avoid possible differences in age composition of swan flocks influencing the average weight, only data from localities where the age composition has been roughly equal are included.

The birds from Saltholm originate from eastern Denmark and southern Sweden (Andersen-Harild 1981b). The breeding population of this area is stagnating or slowly decreasing, which has probably led to a lower average age of the moulting population.

The average weight for swans in this area has decreased over the last ten years. In the period 1969 to 1972 the average weight for males after their second calendar year was about 11 kg, but subsequently the weight has decreased to about 10 kg. It is possible that the reason for this decrease is a different age composition of the population but it might also be that the submerged vegetation has changed.

Weight changes in winter

Denmark is a very important wintering area for *C. olor.* In cold winters the population may reach 70 000 birds, whereas in mild winters the Danish population remains at around 45 000 birds (Joensen 1974). The maximum occurs at the end of January and in February.

The mean January temperature in Denmark is close to 0^oC, but from time to time there are winters with lower temperatures, and shallow areas may then be covered with ice for up to three months from December to March (Table 5).

This ice cover causes severe food limitation for feeding swans. Cold weather migration brings birds from other parts of the Baltic to Denmark, but only a few Danish birds leave Denmark for northern Germany and Holland.

Grazing on land, which is commonly seen in *Cygnus cygnus cygnus,* does not occur in *C. olor* in winter. Instead *C. olor* gathers in big numbers in openings in the ice, which are kept free by currents or sewage effluent. At some places the hundreds of hungry swans attract the attention of the public, who feed them bread, grain, etc. However, it must be kept in mind that such places offer space to only about 25% of the population. The rest stay in openings in the ice far from land, where they are not fed.

The value of a high weight at the beginning of the winter can be illustrated by calculating the theoretical loss of weight during starvation (Kendeigh 1970). The necessary metabolized energy (EE) in Kcal per day includes energy for basal metabolism and limited locomotory activity, and this resembles fairly closely the conditions when the swans sleep on the ice at the beginning of a period of hard weather. The formula is:

$$EE_o = 4.337 \times W^{0.53}$$

where EE_o is the energy requirement at a temperature of 0^oC and W is the weight of the bird in g.

Table 5. Data on the winter climate in Denmark 1959/60 to 1978/79.

Winter	Numbers of days with ice in inner Danish waters	Mean temperatures (^{o}C)	
		January	February
1959/60	36	–0.3	–1.0
1960/61	11	0.0	3.3
1961/62	21	2.0	1.3
1962/63	99	–5.3	–4.5
1963/64	27	0.7	0.2
1964/65	21	1.4	–0.4
1965/66	54	–2.2	–1.7
1966/67	6	0.3	2.3
1967/68	24	–0.8	–0.5
1968/69	53	0.4	–2.5
1969/70	95	–2.7	–3.6
1970/71	22	0.5	2.3
1971/72	39	–1.5	0.5
1972/73	4	1.4	2.3
1973/74	3	2.9	3.2
1974/75	1	4.5	1.5
1975/76	17	0.4	0.2
1976/77	26	–0.3	0.0
1977/78	18	1.5	–1.9
1978/79	83	–4.0	–4.0

The mean December weight of male *C. olor* after their second calendar year is about 11.6 kg. For them, therefore, EE^{o} = 619 Kcal per day. The metabolized energy for fat is about 9.5 Kcal per gram and therefore 619/9.5 = 65 gram fat per day should be necessary for a swan under these conditions..

It is estimated that a swan in normal weight conditions has fat reserves of 2.0 to 2.5 kg. Thereafter it will be necessary for the swan to metabolize proteins (muscles) which have a much lower energy content. The fat reserves will last for a maximum of about one month and it is estimated that a swan can starve for one and a half to two months at maximum.

Of course, the actual energy need for a swan will be considerably greater, as locomotory activity is greater and weather conditions (wind, temperature) much more unfavourable. The survival of swans therefore depends very much on their ability to find suitable feeding places. The three coldest recent winters enabled masses of swans to be ringed, and a substantial amount of data on weight and changes in weight was collected.

The winter of 1978/79

The winter started at the end of December 1978 with a period of strong winds from the northeast and a simultaneous drop in temperature to -10^{o} to $15^{o}C$. All shallow areas froze over within a few days, even most of the traditional current openings. In the beginning the swans stayed sleeping on the ice but during the first part of January they assembled in numbers at the gaps in the ice. The temperature stayed below zero and in the middle of February there was another period with strong wind and very low temperatures. At the end of February the weather became milder and from about 1 March temperatures were generally close to zero. The ice disappeared from most areas in the last part of March (see Fig. 7).

Just before the ice period, a small number of swans weighed in the vicinity of Copenhagen had normal weights, namely 11.6 kg average for males and 9.2 kg for females. The first big catch of swans was on 13 and 14 January 1979, at Mariager Fjord in East Jutland. Here the wintering swans originate mostly from Jutland and western Sweden.

Fig 8 shows the weight of the swans. The normal variation with age is quite obvious.

There had been only an insignificant decrease from 'normal' winter weights. Control weighing later in the winter was rather limited, as the birds were so well-fed by the people that they did not come close in order to take food, and so could not be caught. In this area, of an estimated population of 1500 birds only 50 to 100 died, the majority being young.

The condition in the eastern part of Denmark was very much grimmer. Here the population is so big and widespread that adequate artificial feeding of all birds is impossible. Fig 9 shows the change in weights during the winter. It is obvious that the weight of the birds decreased less at places where the birds were fed than at those where there was no feeding.

In many places organized feeding did not start until early February. It was noticed at several of these feeding places that the decrease in weight stopped and some of the birds even increased in weight. At places without feeding, mortality was enormous. In Stavreby, where more than a hundred swans were ringed at the end of January, half of them were found dead by the end of February.

Large-scale mortality of swans occurred from the beginning of February. In January mostly drab second-year birds died; the white birds (in their third calendar year or more) began to die on a larger scale only later. The Zoological Museum and the

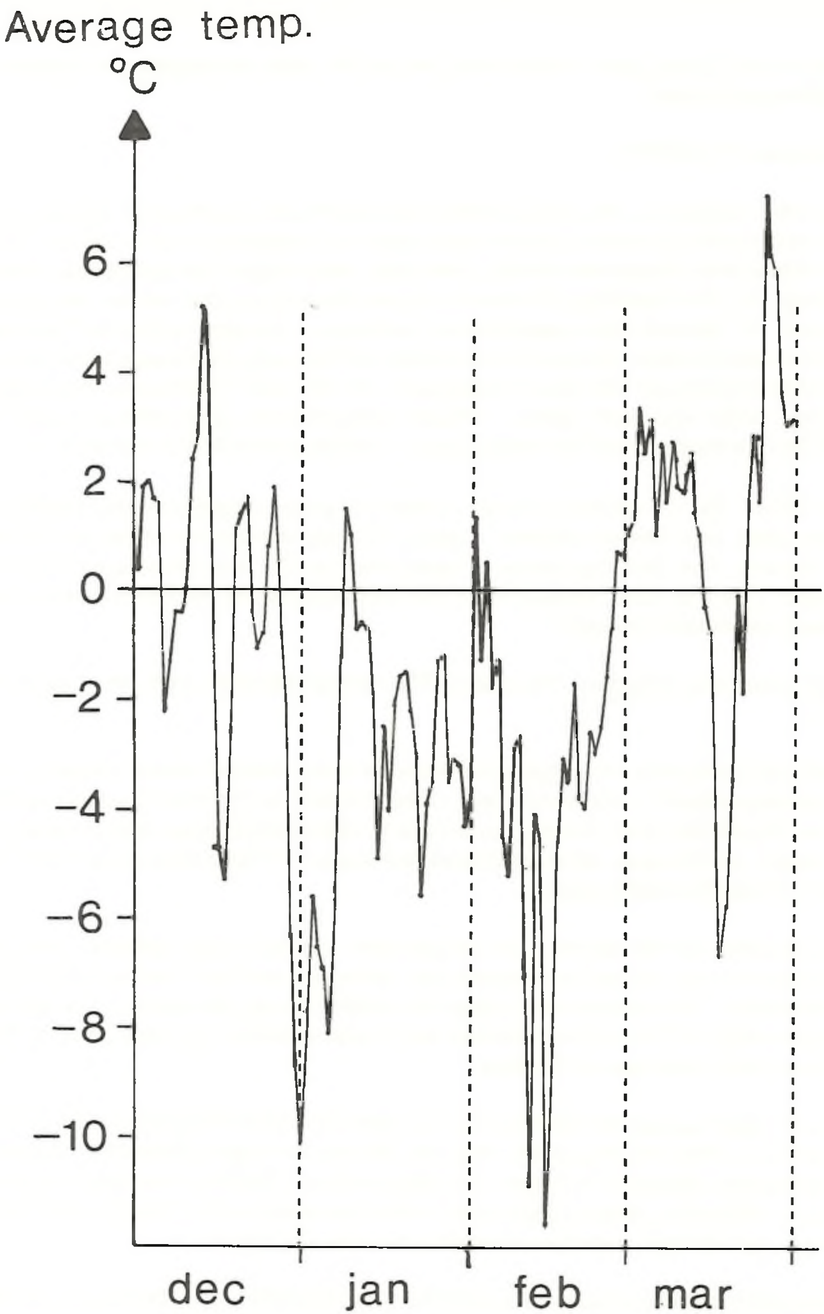

Fig 7. Average temperatures in Roskilde Fjord (Risø) during the winter of 1978/79.

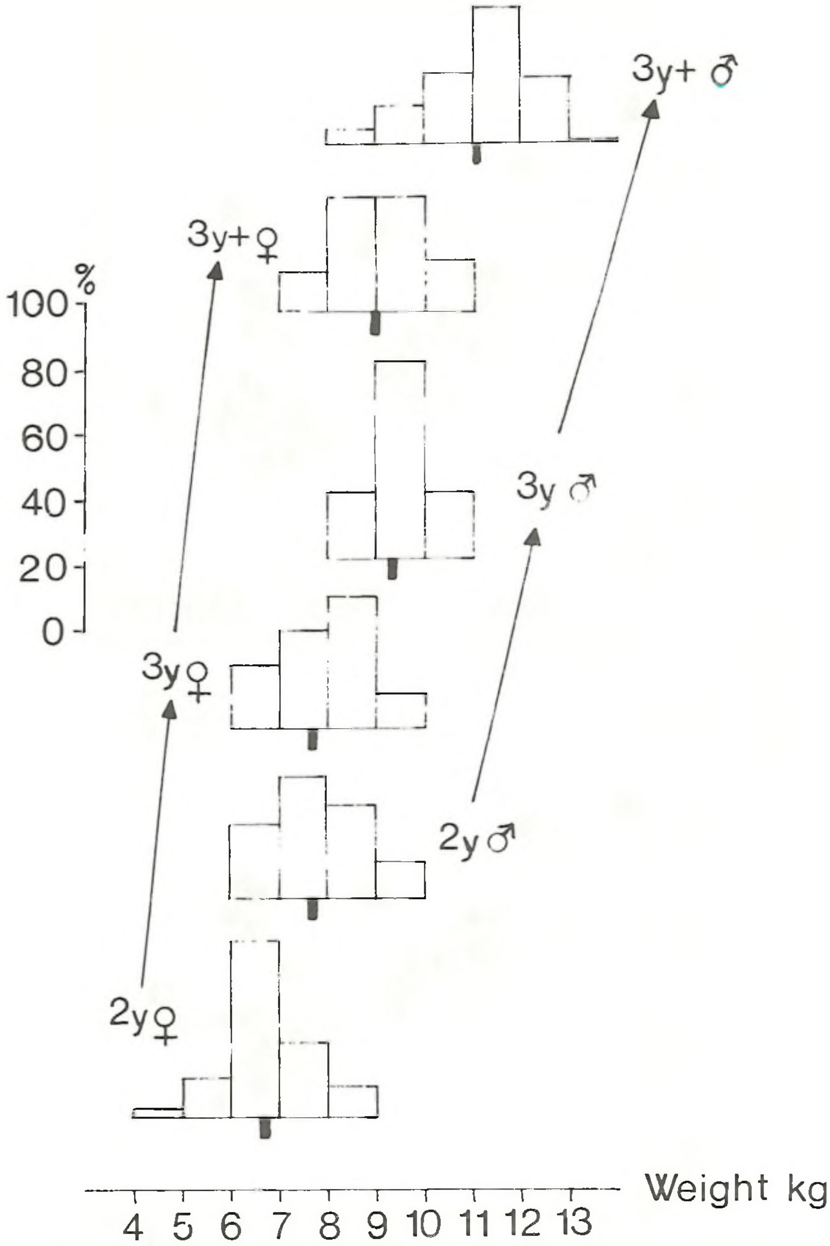

Fig 8. Weights of *Cygnus olor* of different sex and age caught in Mariager Fjord, Jutland, on 13 to 14 January.

2y = swans in their second calendar year etc.

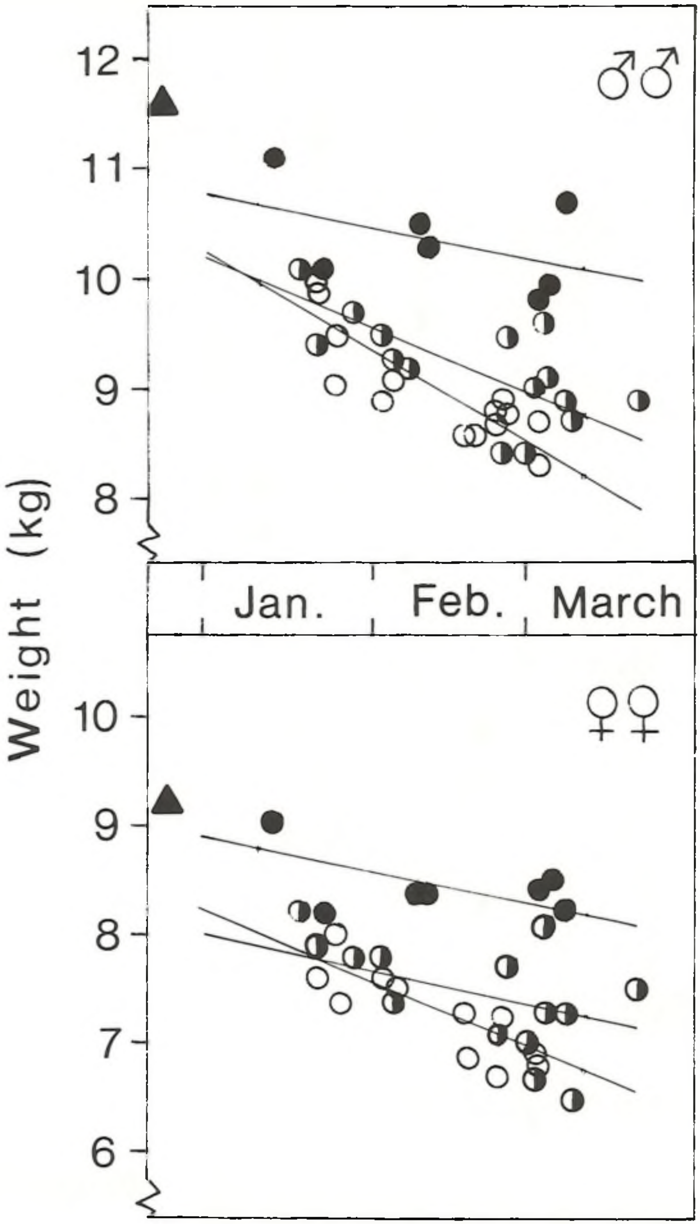

Fig 9. Average weights for males and females of *Cygnus olor* after their third calendar year during the winter of 1978/79.

Shaded circles indicate localities with intensive feeding; half-shaded circles localities with some feeding; unshaded circles localities with no or little feeding. Only localities and days on which at least 50 birds were weighed are included. The triangles indicate the average weights just before the ice period.

Veterinary Serum Laboratory collected about 2700 dead swans.

Survival in relation to weight

The average weight of males dying from starvation was 6.8 kg, of females 5.9 kg (only birds after their second calendar year used). By the end of February and the beginning of March 1970, males surviving the winter weighed 7.5 to 10.3 kg, average 8.1 kg. The corresponding weights for females were 6.5 to 8.5 kg, average 7.4 kg. The weight of birds which were found dead later in the ice-winter was 6.2 to 8.6 kg (average 7.6 kg) for males and 6.0 to 7.2 kg (average 6.6 kg) for females. In severe winters a large number of swans die from starvation if their weight decreases to two-thirds of the normal average weight.

Concluding remarks

The weights of *C. olor* vary greatly, and weight variations may be of decisive importance for survival. Even relatively small decreases in weight will result in increased mortality.

First of all accessibility of food, especially submerged plants, is decisive for the weight. Weather conditions are of great importance for the accessibility of the food but even pollution may play some role.

The stabilization in swan populations in southern Swedish and eastern Danish lakes is probably connected with the fact that, owing to extensive pollution, some lakes no longer have the necessary amount of food to raise 'strong' swans. The observed shift in breeding habitats from lakes to salt and brackish water areas, with establishment of colonies, has involved exposure to rougher physical conditions. Cygnets from coastal sites generally weigh less than those from lakes notwithstanding a generally rich supply of food. This may at some point put a ceiling to further population increases.

The summer weights of moulting swans show modest differences and there are no clear indications of limitations owing to feeding conditions at this time of the year. On the other hand, severe winters result in serious food shortage for the swans, and after such winters the population may decrease by 30%. Hitherto such winters have occurred at long intervals, so that the population has had no difficulties in recovering.

Acknowledgements

Many persons have helped in ringing and weighing operations. Peter Hermansen, Jørgen Grevsen, N O Preuss, Erik Hansen, Hans Lind and Leif Clausen have participated in the field work on numerous occasions and without their co-operation the swan investigations of the Zoological Museum would not have been possible. Morten Frederiksen, Risø National Laboratory, provided meteorological data. N O Preuss has encouraged the study. Jon Fjeldsa read the manuscript and suggested improvements. Ursula Friis made the English translation. My sincere thanks are due to them all. Statens Naturvidenskabelige Forskningsrad is thanked for the grant making it possible for me to present the paper to the Second International Swan Symposium in Sapporo, Japan.

Summary

The paper reviews some aspects on variations in weight noted in 10 000 records of *Cygnus olor* weighed in Denmark and their significance in relation to mortality.

Quality of submerged vegetation affects the weight of cygnets of solitary breeding swans, which require non-acidic water, rich submerged vegetation, *Phragmites* stands, opportunities to graze and artificial feeding. In colonially nesting *C. olor,* exposure to wind severely reduces cygnet weights, so that choice of a sheltered territory is important. Moult in the first winter is also governed by physical condition and hence weight.

For *C. olor* moulting in late summer, the heaviest individuals are the first to moult. Although ecological conditions differ considerably between moulting sites, birds feeding on *Ulva* are heaviest, followed by *Zostera,* then *Ruppia* and *Chara.*

Calculations are made of the energy requirements and fat reserves of *C. olor* in winter. Large numbers die in the occasional ice-winters if their weight decreases to two-thirds of normal weight.

Relatively small decreases in weight result in increased mortality and it is suggested that pollution of lakes, by affecting vegetation, has prevented further increase in some *C. olor* populations.

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WEIGHT AND GROWTH RATES OF MORPHOLOGICAL CHARACTERS OF *CYGNUS OLOR*

S MATHIASSON

Introduction

Study of *Cygnus olor* of the Swedish west coast has emphasized a biometrical background to movements, reproduction and survival, as well as to different behaviour patterns. Especial attention has been paid to: a) growth and maturity; b) sexual dimorphism; c) physical condition, both normal and pathological; d) population characters and e) ecological adaptation.

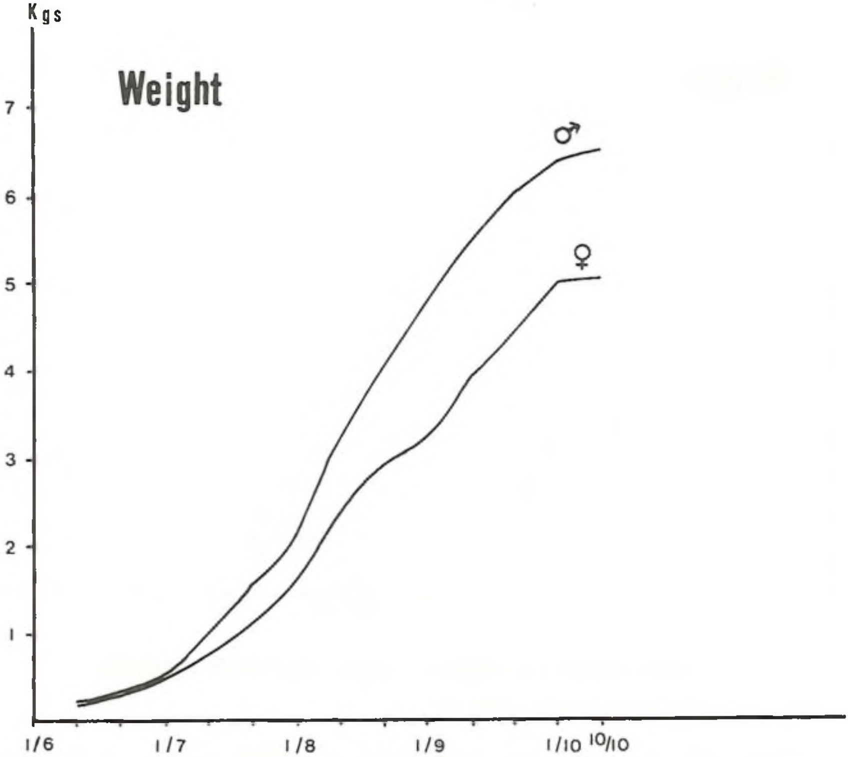

Fig 1. Weight of cygnets as an average of five females and five males measured every second week from hatching to fledging.

Horizontal axis shows date by ten-day periods.

Our working *proformae* therefore include, beside identification codes (ring numbers, neck-collar numbers, colour-rings, etc), columns for: 1) sex; 2) age; 3) weight; 4) size of bill knob; 5) length of fore-arm, neck, tarsus, bill, 5th primary; 6) width of foot web; 7) width and length of bill nail and 8) colour of bill (four grades).

Growth of cygnets

The cygnets of both sexes start their lives at similar body weights, the females from the beginning, however, being slightly lighter than the male cygnets (Fig 1). As time goes on, a clear sex differentiation is observed. At the time of fledging, the middle of October, males are on average 28% heavier than females.

The weight increase from period to period, up to the time when the cygnets are able to fly, is uneven (Fig 2). During their first weeks of life, when they put weight

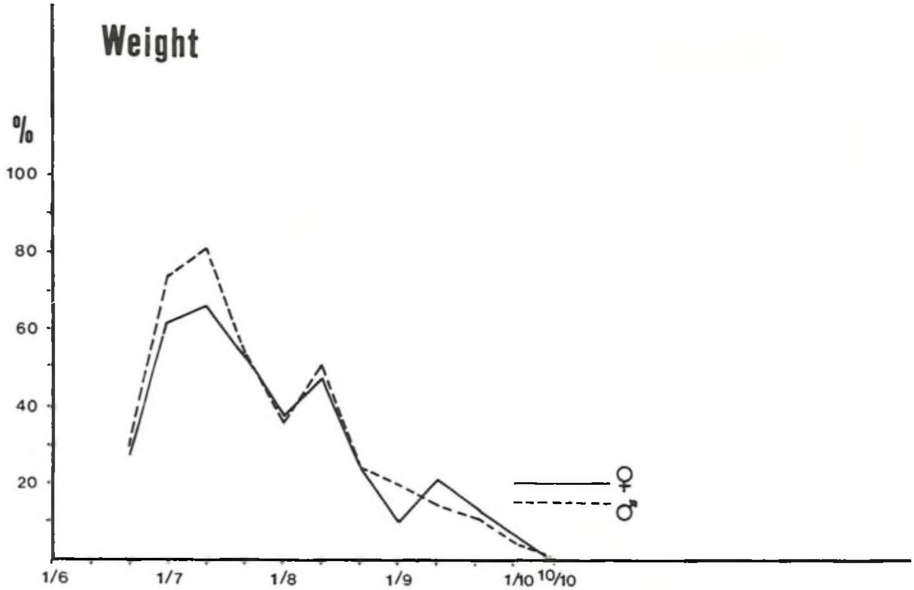

Fig 2. Percentage weight increase in female and male cygnets.

Horizontal axis shows date by ten-day periods.

on proportionally more than later, they increase by 60% to 75%. In the middle of August and in the middle of October increased growth rates are again found.

In this context it is also interesting to consider the growth of other characters. Fig 3 shows that the tarsus length as well as the length of the neck have a similar growth pattern, their growth starting early and plateauing out comparatively soon. The fore-arm (radius and ulna) begins to grow rather late, the 5th primary still

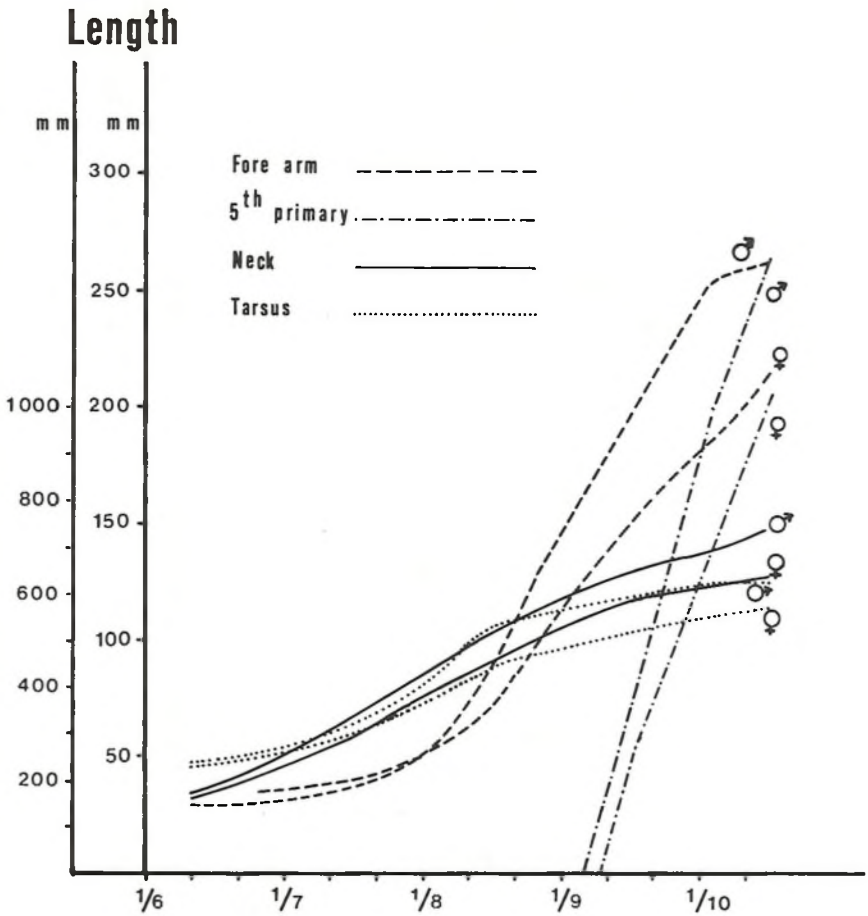

Fig 3. Growth of different anatomical parts of the body of the cygnets.

Horizontal axis shows date by ten-day periods.

later. In other words, the cygnets, being nidifugous, must be able to swim before they can fly. At the time when the cygnets actually are able to fly, their weight is about 70% to 75% of that of adult breeding birds. Consequently, they still put on weight after fledging.

The first weeks with very strong weight increase are connected with losses of

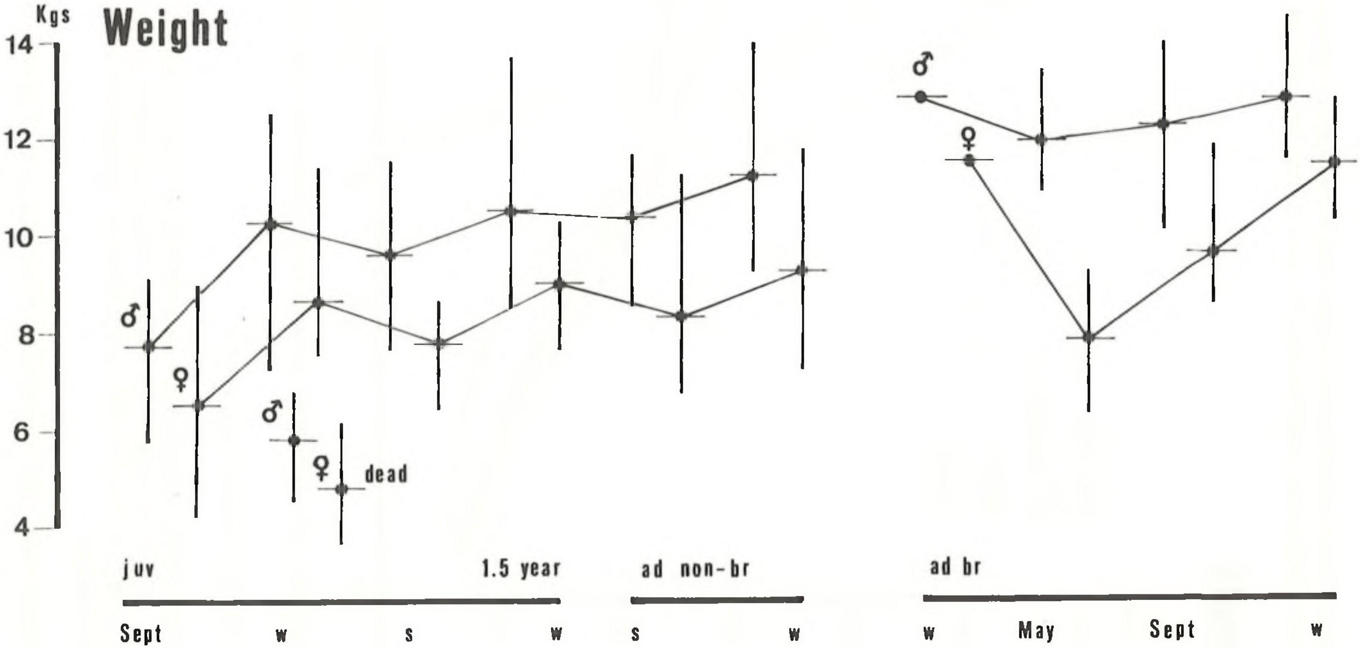

Fig 4. Weight curves of the two sexes showing the weight changes throughout life. Weights of winter-dead swans are also illustrated.

Table 1. Morphological and biometrical characters of *Cygnus olor* of different age classes and categories.

Sex	No	Age	Length of fifth primary (in mm)	Weight (in kg)	Length of neck (in mm)	Length of tarsus (in mm)	Width of foot web (in mm)	Bill nail (in mm)	Bill colour	Length of bill (in mm)	Height of knob (in mm)	Length of fore-arm (in mm)	Time of year/status
Male	41	juvenile	374	7.7	779	130	182	10.9 x 19.7	1	101	5.8	286	January–March
	72	1 year		10.0	814	131	189	11.4 x 20.5	1	101	9.2	294	July–August (moulting)
	20	1½ year	387	8.3	825	132	186	11.2 x 19.6	1–2	99	8.1	291	January–March
	40	2 year		10.2	823	131	189	11.6 x 21.0	1.5–3	100	10.7	292	July–August (moulting)
	47	adult		10.5	825	130	191	11.5 x 20.7	3–4	100	10.9	293	July–August (moulting), knob <13 mm
	90	adult		10.8	831	131	191	11.9 x 21.0	4	101	15.4	297	July–August (moulting), knob >13 mm
Female	46	juvenile	357	6.7	713	119	167	10.4 x 17.8	1	94	6.8	264	January–March
	33	1 year		7.8	739	119	172	10.8 x 19.2	1	94	8.1	270	July–August (moulting)
	29	1½ year	364	7.3	755	120	175	10.9 x 19.2	1–2	95	10.5	269	January–March
	38	2 year		8.2	746	120	175	10.9 x 19.6	1.5–3	94	9.8	270	July–August (moulting)
	44	adult		8.1	751	119	174	11.0 x 19.4	3–4	95	11.0	272	July–August (moulting), non-breeder
	49	adult		8.6	760	119	177	11.0 x 19.6	4	94	10.6	272	July–August (moulting), breeder

NECK - growth related to 1-year length

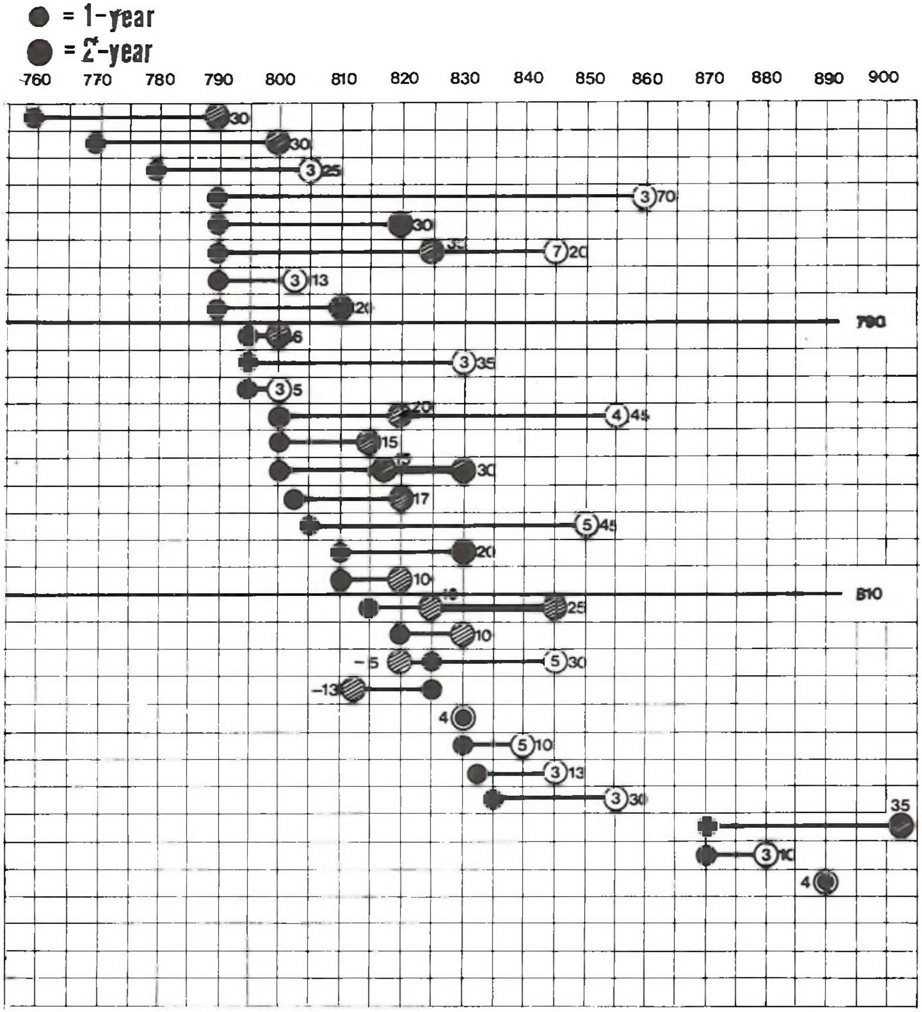

Fig 5. Neck growth between first and second year, in some cases also between the age of one year and higher ages (the number in the circle).

cygnets. In fact, the strongest reduction in numbers of cygnets is recorded here. However, there are normally no differences between the sexes. At the time of fledging (in October) they come out 50:50.

Juvenile and pre-breeding growth

The cygnets continue to grow after fledging (Table 1 and Fig 4), the juvenile sub-adults putting on weight up to the age of 4 to 6 years, when they reach the age of reproductive maturity. Table 1 also shows that in the same period the bill knob is increasing in size and the bill turning orange-red from grey.

From their second summer (one year old) their neck may still increase in length (cf Table 1 and Fig 5), while bill, tarsus, fore-arm and bill nail have stabilized. The length of the primaries is still increasing.

Study of the subsequent neck length of juvenile males (Fig 5), from the time when first caught and measured in their second summer (one year old) to ages of two or more years, shows that those with long necks (more than 810 mm) grow on average 7.7 mm (n = 7), those of middle length (790 to 810 mm) grow 15.8 mm (n = 7) and those with the shortest necks (less than 790 mm) grow 28.3 mm (n = 6). There is thus some adjustment to an appropriate neck length range, which is obviously genetically determined.

Fig 6 illustrates the sizes of fore-arm, tarsus and length of neck among 90 juvenile males caught at their first visit (one year old) to the moulting ground of Kungsbackafjorden. Increasing length of one character is generally associated with increased length of the other two. The normal distribution curve of the dimensions of fore-arm and tarsus as compared with the uneven distribution of the neck lengths (a skew to the small side) reflects the stabilization of the former and the continued growth of the latter.

The bigger males (fore-arm more than 300 mm, 27% of the total number) recur at the moulting ground at the same rate as smaller ones but at higher ages; thus 28% of the bigger ones returned in their second year to the moulting ground, against 56% of the smaller ones. None of the bigger ones were found to shift moulting ground, but six of the smaller (6.7% of the total) did. None of the bigger was reported dead. On the other hand, two of the bigger swans were later on found breeding, but none of the smaller was. These differences, however, need further investigation.

Size and life of adult swans

As shown in Tables 2A and 2B and Fig 4, there is a well-defined difference in weight and in the size of the knob of old breeding swans, as compared with non-breeders in the summer. The knob size is correlated to body weight. An old breeding male has, on an average, a knob which is more than 6 mm higher than a non-breeder of the same age and he is 1.3 kg heavier. The two categories are of similar size according to length of neck and fore-arm. There is also a good correlation between the physical state of the swan and the size and shape of the knob (Table

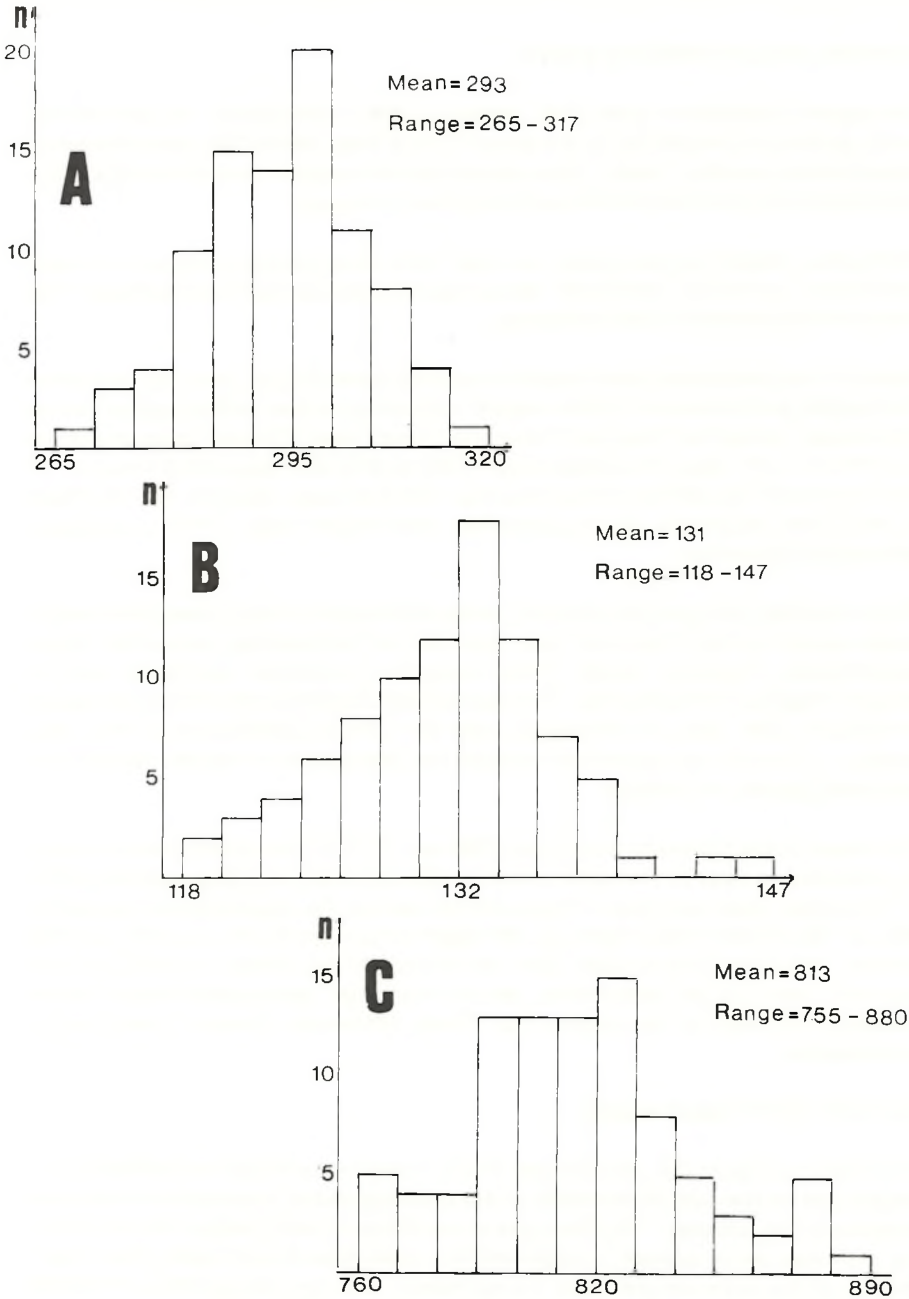

Fig 6. The distribution curves as well as the average and extremes of the dimensions of fore-arms (A), tarsi (B) and neck (C) of 90 one-year-old male *Cygnus olor* caught during moult.

Table 2. Knob dimension in relation to weight, length of neck and length of fore-arm of full-grown swans with bill colour 4, eg more than three years old.

			Knob (in mm)	Weight (in kg)	Length of neck (in mm)	Fore-arm (in mm)
A.	Breeding birds in summer					
	Males	(n = 22–25)	17.4	12.3	827	298.3
	Females	(n = 18–35)	10.7	9.1	758	271.7
B.	Non-breeders in summer					
	Males	(n = 23–24)	11.5	11.0	825	296.1
	Females	(n = 26)	11.0	8.4	754	274.5
C.	Non-breeders with extremely small, shrunk knobs					
	Males	(n = 8)	7.81	9.82	840	289.1
	Females	(n = 17)	7.12	7.77	777	274.1

2C). Adult males with a knob of 7.8, eg less than half the average size of a breeding male, are 2.5 kg (20%) lighter and similar correlations are found among females. These 'small-knobbed, light-weight' adult swans are found in the floating population which circulates between moulting grounds, post- and pre-moulting resting grounds and winter quarters, but does not breed.

If the yearly weight curve of the breeding swans is examined, it transpires that the males display a rather stable curve throughout the year, the females decreasing in weight after egg-laying. The average decrease of the female totals about 30%. When still incubating the females lose about 15% of their body weight (Fig 4). After hatching they must regain the weight losses, which sometimes forces them to move from the nest site to areas with better food supplies. This, however, may result in the death of the offspring because:

a) the transport of the cygnets in this very sensitive period of their lives kills some through food shortage or bad weather;

b) the swans meet competing pairs, causing fights and losses of cygnets. Sometimes the whole clutch or parts of it is kidnapped and adopted by a foreign pair;

c) the swans do not find fully suitable growing grounds for themselves and the cygnets, which reduces the number of the latter.

During winter, breeding as well as non-breeding swans may suffer from food shortage, which influences their future body weight and ability to defend the territory and produce eggs. Fig 7 demonstrates the number of breeding pairs in

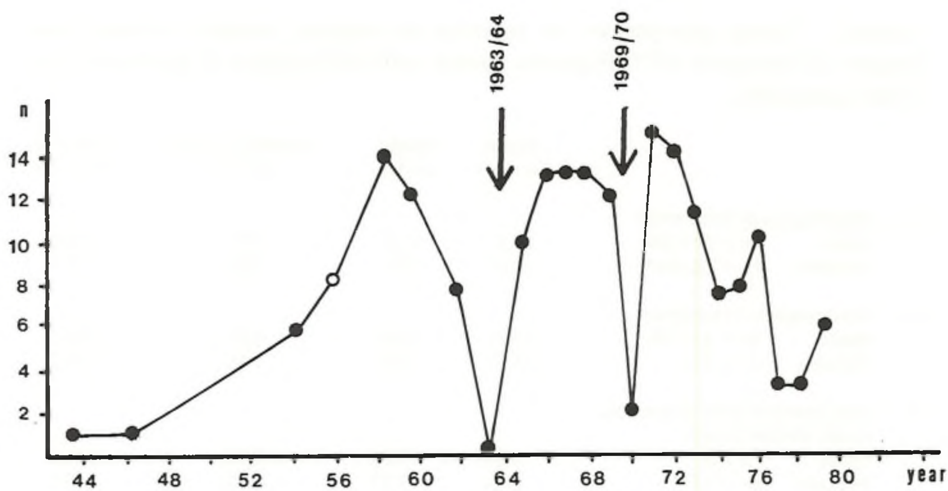

Fig 7. The annual number of breeding pairs of *C. olor* at Lake Kollungerod on the island of Orust on the Swedish west coast. The lowest number of breeding pairs has been found in connection with severe winter conditions.

relation to previous winter condition. It has also been found that the numbers of eggs laid in the clutch show a clear relation to the body weight of the female (Table 3).

Table 3. Number of eggs laid in relation to the body weight of the female in the pre-laying period.

Average and maximum—minimum weight of female before egg-laying	7.5 (7.2–8.1)	10.0 (9.5–10.2)	11.1 (10.6–11.7)	12.7 (12.0–13.2)
Average number of eggs	0	5	6	7.7
Number of females	3	3	4	3

Summary

Studies of *C. olor* have been carried out on the Swedish west coast, mainly in the counties of Halland and Bohuslan. Almost all non-breeders and more than 80% of the breeding pairs occur in shallow coastal bays.

The information is part of an extensive data collection, now being analysed. The examples illustrate the value of some measurable characters for judging the status of certain groups of swans in the process of maturity, which in time is longer for *C. olor* than for most other birds. Examples are also given of the impact of certain physical conditions on reproductive success.

There may be differences in migratory behaviour in relation to the size of juvenile subadults. It is not yet clear whether these differences are related to swans of different geographical origin (different breeding populations) or if they depend on differential growth rates. The necks of short-necked juvenile swans grow more in their second or later years than do those with longer necks. Swans in the study area start breeding comparatively late in life, often not until the ages of 6 to 7 years. Breeding, beside other things, is associated with higher weights than is normal for non-breeders.

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POPULATION GENETICS OF *CYGNUS OLOR*

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Introduction

Genetic variants can be detected from small blood samples by electrophoresis. The proteins in a small blood sample can be separated on starch gels buffered to a specific pH by applying an electric field. The proteins move to different positions and can be located and identified by histological stains. Samples from different individuals may show different patterns on electrophoresis, and some of these differences are genetically determined. In *Cygnus olor* two proteins show such genetic polymorphism — the enzymes esterase and lactate dehydrogenase.

Esterase

Cygnus olor plasma shows three phenotypic patterns for esterase characterized by:

- a) three slow bands, termed *SS;*
- b) six bands, termed *SF;*
- c) three fast bands, termed *FF.*

Blood samples from complete families, both parents and all their cygnets, make it possible to test whether the patterns are inherited. Table 1 shows that the esterase patterns are inherited in a simple Mendelian fashion, behaving as co-dominant alleles at an autosomal locus.

The genotypes occur at similar high frequencies throughout Britain (Fig 1). Since

Table 1. Esterase inheritance data.

Phenotypes of parental mating	Number of cygnets with phenotype			Expected ratios			Chi^2	Probability	
	SS	*SF*	*FF*	*SS*	*SF*	*FF*			
SS x *SS*	90			1	0	0	–	–	
SS x *FF*		42		0	1	0	–	–	
FF x *FF*			4	0	0	1	–	–	
SS x *SF*	56	58		1	1	0	0.035	0.9	$p > 0.8$
SF x *FF*		11	16	0	1	1	0.926	0.5	$p > 0.3$
SF x *SF*	9	20	10	1	2	1	0.077	0.98	$p > 0.9$
Total		316					1.038	0.9	$p > 0.8$

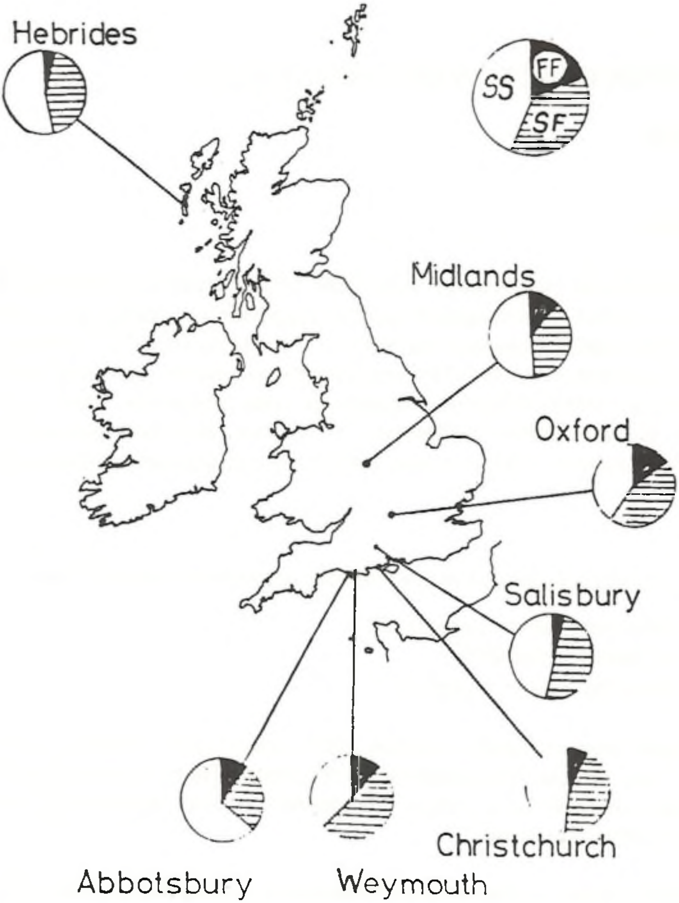

Fig 1. Esterase genotype frequencies in Britain.

genotypic ratios are *SS:SF:FF*, 5:4:1, the question arises of how both the *S* and *F* alleles are maintained in all areas at these high consistent levels.

Most homozygous *S* females lay larger clutches earlier in the season, thus producing more cygnets. Heterozygous females may lay early or late, with large or small clutches. Homozygous *F* females generally lay small clutches late. The whole population does not become homozygous *S*, because the mates of heterozygous males lay larger clutches irrespective of date; there is thus a balance achieved between the genotypes — *S* alleles gain an advantage in *SS* females, while *F* alleles gain an advantage in *SF* males (Figs 2 and 3). It is likely that these differences between genotypes in breeding success may be achieved through habitat preference.

Lactate dehydrogenase

Individuals show two phenotypic patterns for this enzyme, termed *AA* and *Aa*. Complete family data show that these patterns are also inherited as co-dominant alleles at autosomal loci (see Table 2).

Table 2. Abbotsbury breeding data 1978. Number of cygnets per mating type.

Genotypes of parental mating	Genotypes of cygnets *AA*	*Aa*	Expected ratios
AA x *AA*	45	0	1:0:0
AA x *Aa*	22	16	1:1:0

Note: The ratio of cygnet genotypes was not significantly different from the expected ratios.

The *Aa* heterozygote is localized and rare. It generally occurs at less than 1% frequency; however, in the colonies at Abbotsbury and Weymouth it is above 15% frequency and is particularly frequent in the resident breeding segments of these two populations (Fig 4). Yet even at the site where it is most frequent, a natural *Aa* x *Aa* mating has not been observed.

Within the Abbotsbury population, *Aa* individuals are more likely to breed, to fledge cygnets and to have larger broods at fledging (see Table 3 and Bacon 1979).

These factors give *Aa* individuals a relative fitness of about 2.4 compared with *AA* individuals. A selected advantage of this magnitude is required to keep the *a* allele at the observed high frequency in the face of diluting forces from a high frequency of *AA* immigrant breeders at the colony.

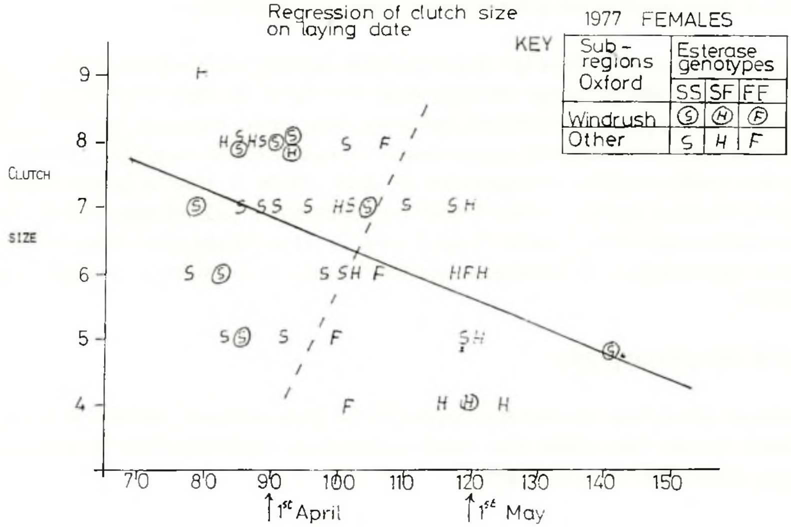

Fig 2. Relative breeding success of females by genotype.

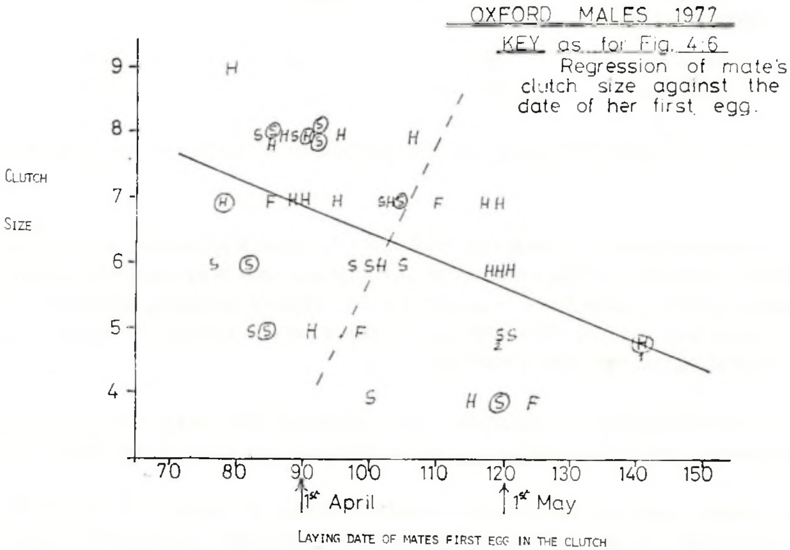

Fig 3. Relative breeding success of males by genotype.

Table 3. Relative fitnesses at Abbotsbury for three attributes by lactate dehydrogenase (LDH) genotype.

Fitness due to factor	LDH genotype *AA*	LDH genotype *Aa*	Relative fitness of *Aa*
Probability of nesting	0.14	0.19	1.35
Probability of fledging	0.52	0.82	1.58
Mean brood size*	5.00	5.56	1.13
Total advantage			2.40

* For broods greater than 0, therefore independent of the probability of fledging.

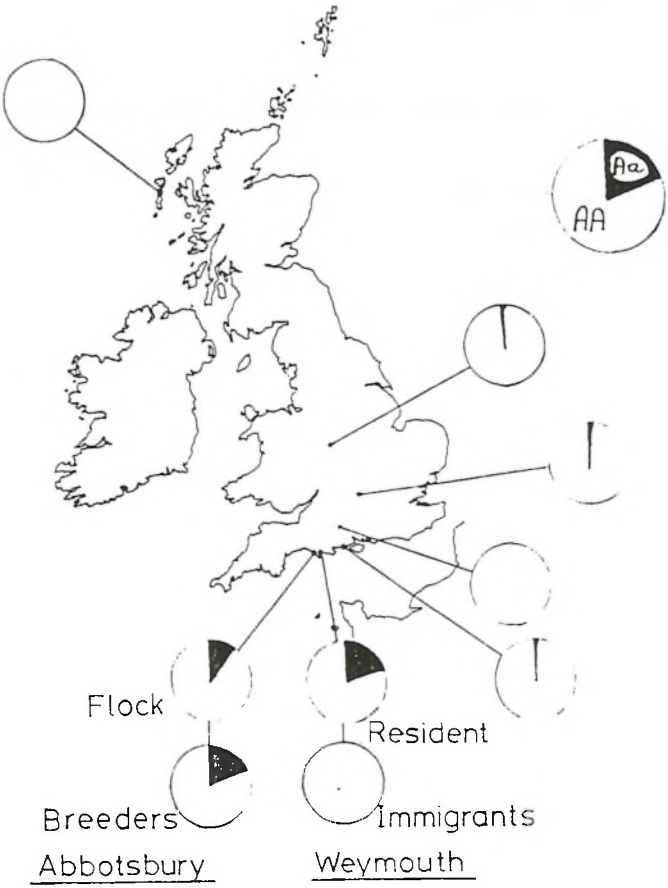

Fig 4. Lactate dehydrogenase genotype frequencies in Britain.

Summary

Electrophoretic methods were used to separate biochemical variants which were used as genetic markers. Protein samples were obtained from small blood samples and separated in horizontal starch gels. Complete family data for two polymorphic enzymes were entirely consistent with their patterns being determined by Mendelian inheritance of two co-dominant alleles at autosomal loci; these loci were not linked. Some 2500 blood samples from *Cygnus olor* were collected, representing eight study sites.

At a lactate dehydrogenase locus the *a* allele was generally rare, with less than 1% *Aa* heterozygotes; however, at two colonial sites the heterozygote frequency was significantly higher.

The esterase polymorphism displayed genotypic frequencies of 5:4:1 at all sites except one colony where they were 6:3:1. *SS* females laid significantly earlier in the season than other genotypes and the mates of *SF* males produced larger than average clutches at all seasons. The data further support the suggestion that the productivity differences between esterase genotypes are influences by habitat factors.

References

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Appendix

Scientific names of birds used in this work

Where possible, the scientific names used in this work conform with the 'List of Recent Holarctic Bird Species: Non-Passerines' by K H Voous printed in *Ibis* 115 (1973) pages 612–638 and the same author's 'List of Recent Holarctic Bird Species: Passerines' published in *Ibis* 119 (1977) pages 223–250 and 376–406. In the list below, names are given in alphabetical order for ease of reference. The English names below also follow Voous as far as possible. For scientific names of swans, see the Editorial Note at the beginning of this volume.

Aix sponsa	Wood Duck
Anas acuta	Pintail
Anas clypeata	Northern Shoveler
Anas crecca	Teal
Anas platyrhynchos	Mallard
Anas rubripes	(North American) Black Duck
Anas sparsa	(African) Black Duck
Anas strepera	Gadwall
Anatidae	Swans, geese and ducks (Family)
Anser albifrons	White-fronted Goose
Anser anser	Greylag Goose
Anser brachyrhynchus	Pink-footed Goose
Anser caerulescens caerulescens	(Lesser) Snow Goose
Anser rossii	Ross's Goose
Aquila chrysaetos	Golden Eagle
Aythya americana	Redhead
Aythya ferina	Pochard
Aythya valisneria	Canvasback
Branta bernicla nigricans	Brent Goose (Black Brant)
Branta canadensis	Canada Goose
Branta canadensis minima	(Cackling) Canada Goose
Bubulcus ibis	Cattle Egret
Bucephala clangula	Common Goldeneye
Columba palumbus	Woodpigeon
Corvus frugilegus	Rook
Eurynorhynchus pygmeus	Spoon-billed Sandpiper
Glareola maldivarum	Eastern Collared Pratincole
Grus vipio	White-naped Crane

Lagopus lagopus	Willow Grouse
Larus spp	Gulls (Family)
Mergus albellus	Smew
Mergus merganser	Goosander
Numenius arquata	Eurasian Curlew
Phalacrocorax carbo sinensis	Great Cormorant (Eurasian continental race)
Phasianus colchicus	Common Pheasant
Platalea minor	Black-faced Spoonbill
Passerina	Buntings (Family)
Sturnus vulgaris	Starling
Tadorna tadorna	Shelduck
Tadornini	Shelducks (Tribe)