

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

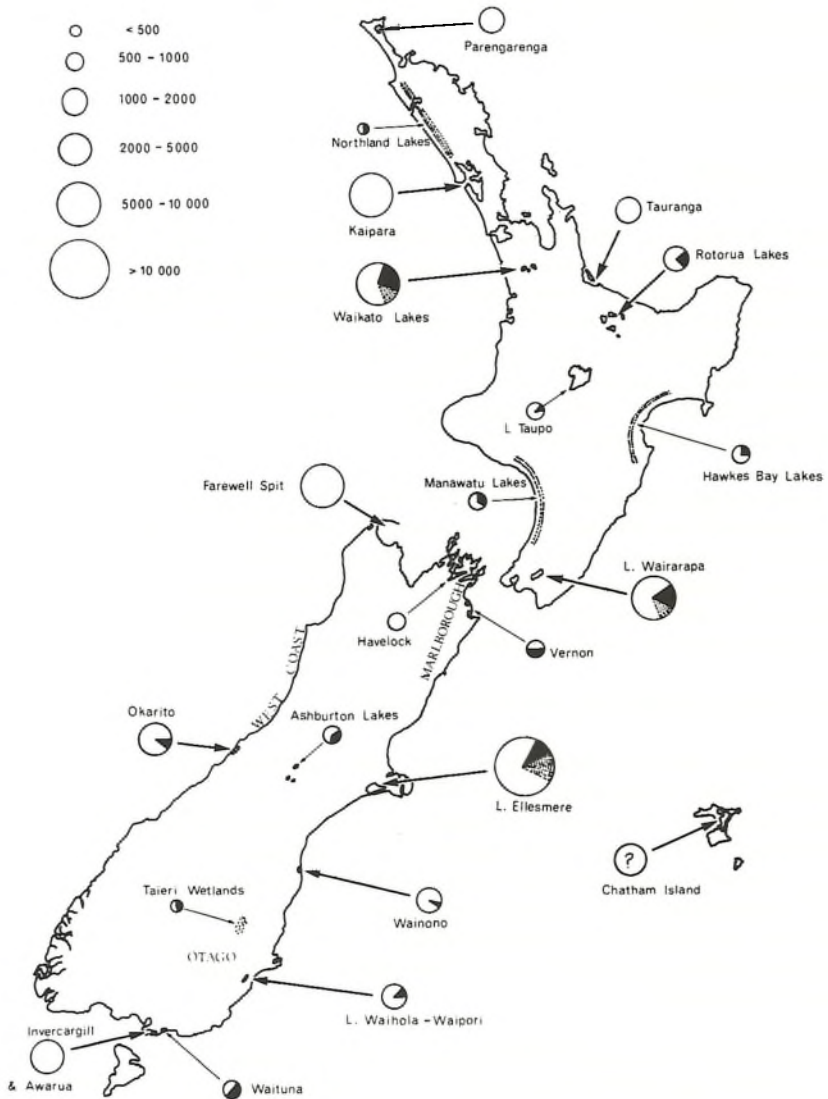


Fig 1. Principal concentrations of *Cygnus atratus* in New Zealand in January 1979, showing the proportion of the population at each locality which bred (black sector), an additional proportion which in the past three years has also bred (stippled sector) and the non-breeding fraction (open).

(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 Waiholo 1971 | 23 | 246 | 19 |

seem to have participated in nesting. Censuses of broods at three areas (Lake Emma 1973, Lake Waiholo 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

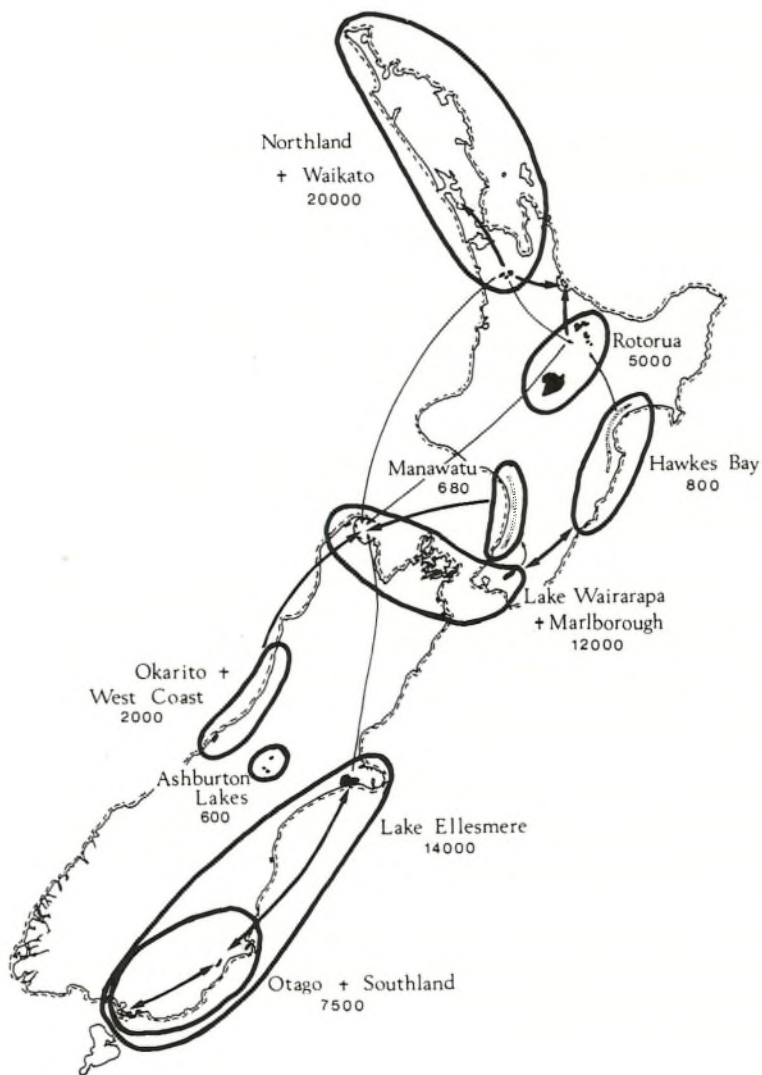


Fig 2. The geographic sub-division and size of New Zealand's mainland *Cygnus atratus* population and the pattern of major (thick arrow) and minor (thin arrow) movements between sub-populations.

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 freshwater 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 freshwater. Possibly some movement south to Lake Wairarapa | Widely scattered on all freshwater wetlands. Concentrations on Lakes Horowhenua and Papatonga toward 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 decline which exposes islands in lake. Elsewhere 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 elsewhere 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 ephemeral waters creche. Vernon Lagoon — both family broods and creches |
| Cygnets 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 extended 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 |
| Principal breeding area | OKARITO/ WEST COAST Okarito Lagoon (estuarine) | LAKE ELLESMERE Lake Ellesmere – fresh/brackish | OTAGO/ SOUTHLAND Waituna Lagoon (estuarine); Lake Waihola/Waipori (freshwater); Taieri River wetland (freshwater) | ASHBURTON LAKES 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 | |
| Cygnnet 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.

Cygnets 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 km² 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).