Nesting of the Black Swan at Lake Ellesmere, New Zealand

K. H. MIERS and MURRAY WILLIAMS

Introduction

Black Swans *Cygnus atratus* were introduced to New Zealand last century. Thompson (1922) reported the first birds were introduced by the Nelson Acclimatisation Society 'in, or just before, 1864'. The Canterbury Acclimatisation Society (now the North Canterbury Acclimatisation Society — N.C.A.S.) released four birds on to the Avon River in Christchurch in 1864 and in the following year, the Christchurch City Council liberated a further 13 pairs in an effort to control watercress in the river (Lamb 1964). Seventy birds were liberated in the Southland and Otago Acclimatisation Society districts prior to 1870, the largest liberation being 42 on to Kaitangata Lake, Otago, in 1867 (Drummond 1906b). The only North Island records prior to 1870 were Sir George Grey's liberation of 'some' on Kawau Island in 1864 and the Auckland Acclimatisation Society's liberation of four in 1867 (Thompson 1922).

Within a few years, considerable numbers were seen hundreds of miles from liberation sites. Drummond (1906a) reported Christchurch birds making 'long and rather notable migrations to the wild country on the West Coast, and to Otago, and even Marlborough' in 1867, and Lamb (1964) recorded 'In September 1867, thirty-three swan eggs were collected from nests found floating on Lake Ellesmere. There the swans were particularly numerous, and large flocks were continually being seen by sportsmen'. Lamb also quoted a letter dated March 1871, which makes mention of 300 or more swans in a mob at the mouth of the Halswell River. The success of establishment may be judged from the comments of Kirk (1895) who remarked that the Black Swan 'sometimes occurs in thousands as in the great lagoon at the entrance to the Opawa River (Marlborough) . . . Its simultaneous appearance in so many localities between 1865 and 1868 proves that it must have been a spontaneous immigrant and that its naturalisation is not due in any large degree to its having been introduced by man'. Although no similar comment can be found in early literature, Kirk's hypothesis of spontaneous immigration is not unreasonable despite the remarkable coincidence involved. The sudden appearance of large numbers of the Australian White-eye *Aythya australis* in 1867 (Oliver 1955) adds further support to this idea. However, growth of the swan population was very rapid. By 1900 the species was common throughout New Zealand and Thompson (1926) remarked that 'it is now so common that it is often difficult to make people believe that it is not a native'.

Today the species is to be seen on all major waterways, occupying a wide variety of habitats, ranging from extensive inland harbours (for example Kaipara, Tauranga) to lakes (with particularly heavy concentrations on Lakes Whangape and Ellesmere) and small coastal lagoons.

On Lake Ellesmere, swans quickly increased in numbers and were shot as game from 1875. The very large numbers in the early 1900s resulted in considerable damage and fouling of surrounding pasture. As a means of control, the N.C.A.S. were, in 1915, granted statutory authority to collect eggs, a practice that has continued to the present day. It is the policy of the Society to limit the number of cygnets hatching around the lake to an average of 20,000 per year. The figure fluctuates according to the success of the previous year's breeding and shooting season. The aim of this study was to assess the management programme and to gather details on the productivity of the Ellesmere swan population and factors likely to affect that productivity.

Study area

Lake Ellesmere (43° 47′ S, 172° 30′ E) lies on the coast to the south of Banks Peninsula (Figure 1). It is 14 miles long, 7½ miles wide at its widest point with an indented margin of approximately 58 miles, and, at a height of 3.5 feet above mean sea level, its area is about 60 square miles. The North Canterbury Catchment Board controls the level and is required to open the lake to the sea when it reaches 3.45 feet above mean sea level in summer and 3.7 feet above mean sea level in winter. Occasionally, as in 1959 when stormy weather prevented drainage to the sea, the lake may rise as high as 7.0 feet above mean sea level.

Ellesmere is shallow, with approximately 80 per cent. of the bed lying just below mean sea level and with only a

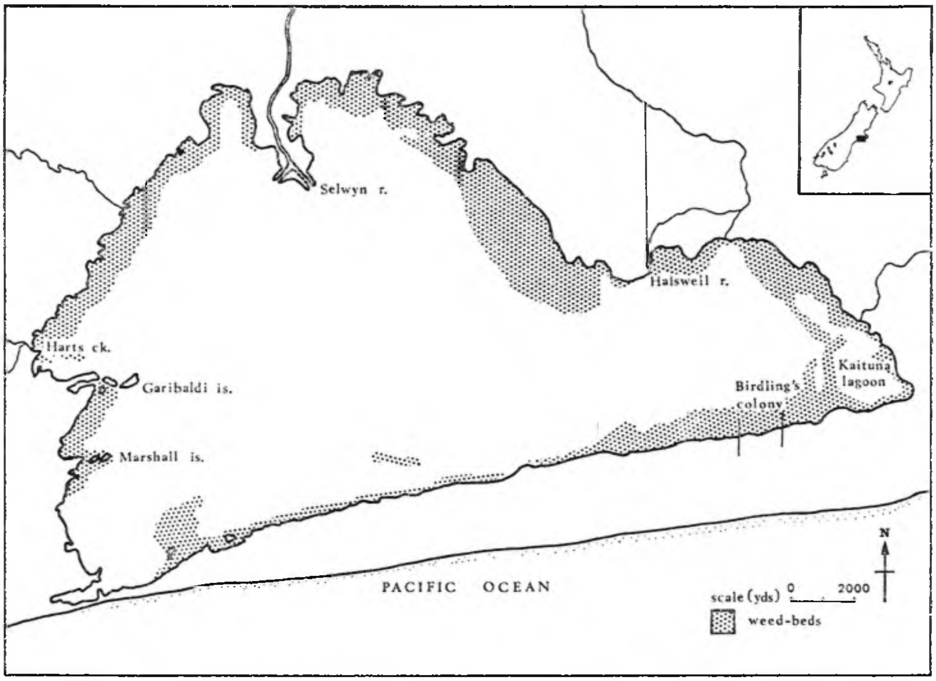


Figure 1. Lake Ellesmere showing main weed-beds and place names mentioned in text.

few channels deeper than 7 feet below mean sea level. When the lake is low the sea may enter through the drainage channel during high tides. This, with water interchange through the gravel banks during tide cycles and waves breaking over the spit at the western end during storms, maintains the lake's salinity. Fresh water enters through several rivers and canals, of which the Selwyn River is the largest and most important.

The main feeding areas for swans are inshore of a line from the Selwyn River mouth to the Marshall Islands. Smaller but important weed beds lie west of the Halswell River outlet and in and adjacent Kaituna Lagoon. Weed beds consist mainly of *Ruppia spiralis* but near freshwater influence, particularly Harts Creek and Selwyn River, *Myriophyllum elatinoides* occurs. The *Ruppia* beds are however the more extensive and the more important food source.

Breeding is concentrated on Birdling's Flat (Figure 2) at the eastern end of the lake although pairs are to be found scattered around most of the lake margin and on Garibaldi and Marshall Islands. Current management practice is aimed at preventing breeding in all areas other than on Birdling's Flat.

Materials and methods

At the commencement of this study on 13th September 1960, there were 5,322 active nests in the Birdling's colony; and of these 1,050 were marked with wooden pegs. Lake Ellesmere was at that time 3.6 feet above mean sea level and the greater part of the colony was at risk of being flooded. Because of this, and the immediate necessity of recording nesting details, the sample was pegged in groups of 100 to 200 nests. Each group was judged representative of a particular area and contained approximately one-fifth of the nests in it. The areas were however selected in order to give a cross-section of ground-type, i.e. high and low ground, marginal or central within the colony. The pegged nests were visited daily till the breeding season end in December.

The 1961 sample of 650 nests was pegged on 11th September when the colony contained 5,160 occupied nests. The method of sampling differed from that used in the previous year in that nests were pegged in groups of ten. Each group was chosen in a random manner by throwing a tennis ball over one's shoulder. The nest closest to where the ball landed was taken as the first of the group. Individual nests within each group were pegged following a systematic procedure. After the first nest was marked, the nearest adjacent nest was pegged; the 'nearest adjacent unpegged nest' rule being followed until the sample was complete. At the date of pegging, many clutches were complete and the sample was restricted to nests containing one or more eggs.

Details of each clutch were recorded daily between 09.30 hrs. and 13.30 hrs., following a set route through the colony, commencing at its western part. In the second year data were usually completed by noon. Afterwards, details of each nest were transferred from record books to coded, edge-punched cards, from which most analyses were made.

Many of the pegged nests were used more than once during the course of the season, with the result that details were gathered from 1,477 nests in 1960 and 821 nests in 1961.

Lake Ellesmere reaches a height of between 3.5 and 4.0 feet above mean sea level about three times a year (Figure 3)

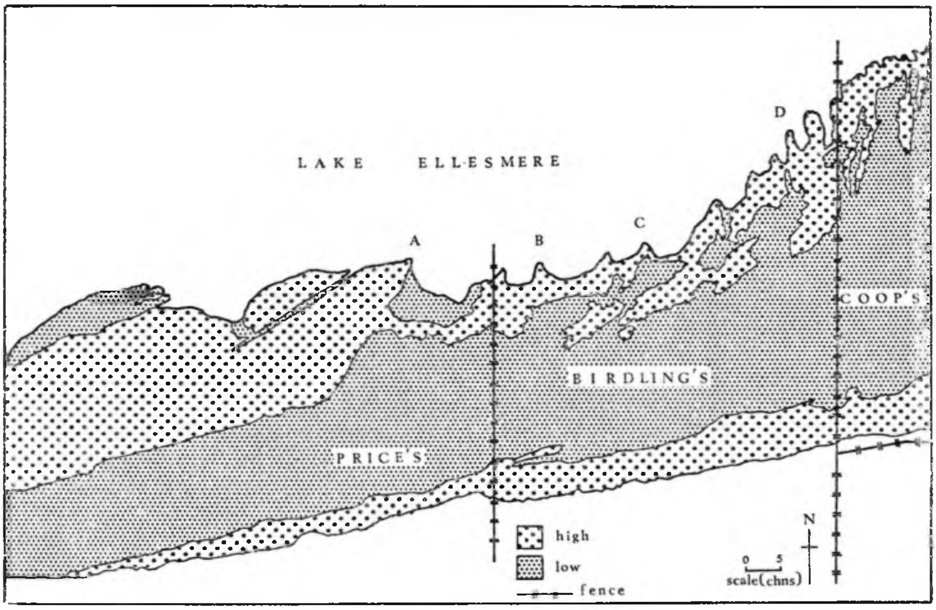


Figure 2. Nesting area showing land contour and sample areas.

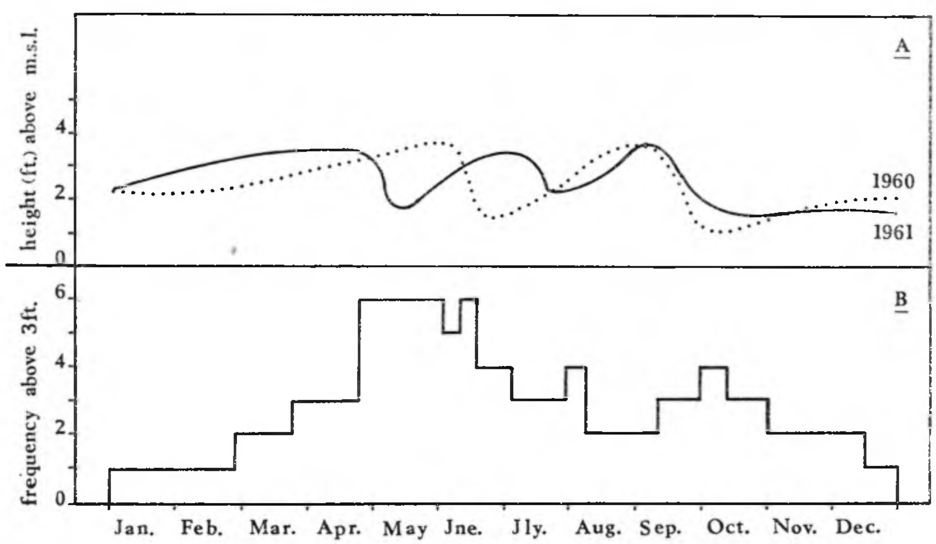


Figure 3. Fluctuations in the level of Lake Ellesmere throughout the year (based on figures supplied by the North Canterbury Catchment Board).

and swans usually breed just after the final winter peak. During July, adult swans begin to gather off the Birdling's breeding ground and by the end of the month, many go ashore to spend most of the day near their future nest.

Breeding season and dispersion

Nests (See Plate II, p. 33)

First nests were established on points of relatively high ground jutting into the lake (Figure 2, points B, C, D) and later around the margin on suitable high ground up to 150 yards from the water. Within a fortnight, most of the area was occupied and there was gradual occupation of high ground to the west on Price's property (Figure 2, point A).

Nests are a miscellany of shape and size depending on availability of material. Those along the lake edge, where there is ample nest material, mostly wind-driven *Ruppia* and other debris, are very large. The bird simply stands in one spot and heaps material up about it, gathering all within reach. Conversely, those further inland where nest material is sparse and consists mainly of *Salicornia australis* are little more than ringed depressions with a characteristic rosette of denuded, bare ground around them, caused by birds plucking every available stem of *Salicornia* within reach. Stealing of nest material occurs, particularly where nests are close together, and abandoned nests are quickly incorporated into adjacent ones. Stealing also occurs just prior to hatching; the cob of a pair with eggs about to hatch will gather considerable extra material and add it to the nest. Abandoned nests (without eggs) or those vacated upon successful hatching may become occupied by new pairs.

Practically every rush *Juncus* sp., tussock *Poa caespitosa* or shrub *Olearia virgata* becomes the focal point of more than one nest. A rush or tussock a foot high can be an effective barrier between nests as close as two feet apart. As the distribution of these plants is discontinuous and patchy, except for rushes at the western end of Price's property, so the distribution of nests tends to involve dense aggregations surrounded by less densely packed nests. This is especially so on Birdling's property.

Nest spacing

Measurements of spacing were made to the nearest foot and from centre to centre of nest bowls. Data refers to the nearest adjacent nest and was collected three days after pegging in both years.

In 1960, when large blocks of nests were pegged, those on the edge of the block may have been closer to an unpegged nest than to a pegged nest. The method of sampling in 1961 ensures that the nearest adjacent nest is pegged.

Nest spacing varies throughout the season. Once hatching commences, considerable destruction of vacated nests, rebuilding by re-nesters and re-occupation of vacated and successful nests occurs. Measuring immediately after peak laying and before hatching ensures that these complicating factors are minimized and correspond to peak occupation of nests.

Mean distances between nests differ markedly in the two years; being 10.0 feet in 1960 and 7.9 feet in 1961. While 93% and 94% of nests in 1960 and 1961 respectively were spaced within 20 feet of another nest, 7% in 1960 and 38.3% in 1961 were spaced at five feet or less. This difference is significant and is probably a reflection of lake level affecting availability of nesting ground. The implications of this are discussed elsewhere.

Figure 4 gives details of lake level fluctuation and the spacing of nests. In 1960 when laying commenced the lake level was at 2.5 ft. and reached 3.0 ft. on about 19th August. On this date and later, much of Birdling's area was under water and unsuitable for nesting. Many swans therefore nested in the adjacent Price's area where there was ample room and less competition. Consequently, spacing was greater (mean distance 10.0 ft.) than in the following year when conditions were in marked contrast. In 1961 the lake was at about 2.5 ft. when laying began. It was, however, receding and reached a low point of about 1.9 ft. on or about 15th August. Throughout the weeks of peak egg laying until approximately 9th September the lake stayed below the 3.0 ft. level. For the greatest part of this time the traditional Birdling's area was available for nesting and the birds made use of the opportunity. Since the lake was rising quite sharply from about 25th August through to 18th September more and more birds tended to pack on to the limited high grounds of the Birdling's lake margin. Consequently, nests were closer than in 1960 (mean distance 7.9 ft.) with greatest number of nests being spaced at or less than 5 ft.

Laying

Laying usually begins in the first week of August but may start as early as mid-

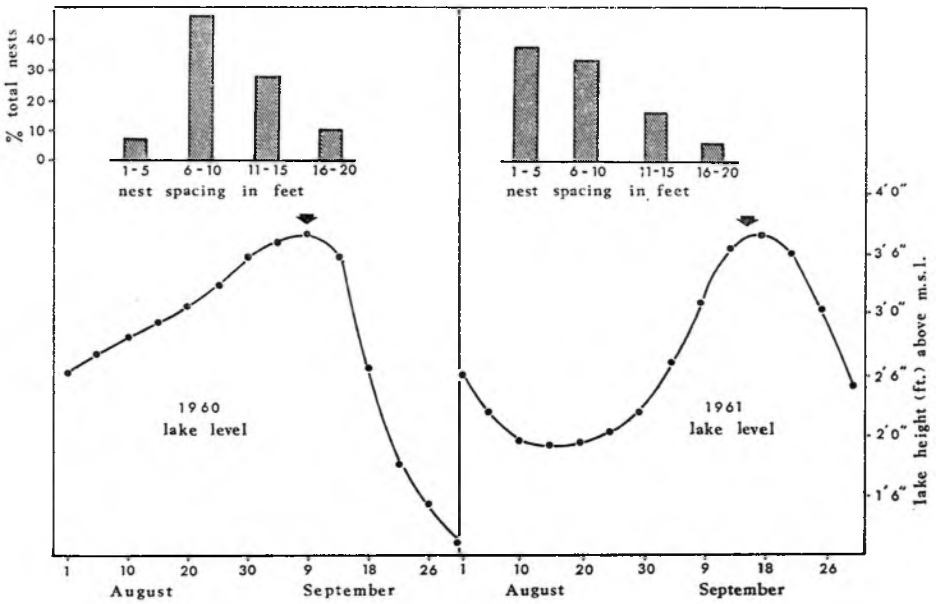


Figure 4. Lake level fluctuation during period of peak nesting. Arrow indicates date on which nest spacing was measured.

Table I. Laying period of clutch in days.

Clutch size	*Days* 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	*Number of clutches*	*Mean days per egg*	*Mean days per clutch*	*S.D. days per clutch ±*
2	2	5	8	2	.	1											18	1.4	2.8	1.1
3			7	11	11	5	2										36	1.5	4.5	1.1
4			1	5	10	47	27	11	5	2	2						110	1.6	6.5	1.1
5				1	2	10	28	83	20	13	4	1					162	1.6	8.0	1.2
6					1	2	13	30	50	19	6	3	1				125	1.5	8.8	1.2
7							3	8	8	9	4	1	.	1	1		35	1.4	9.5	1.8
8							1	1	3	1	2	2	.	.	1		11	1.3	10.3	2.1
9								1	.	.	.	1	.	.	.	1	3	1.3	12.0	—
10										1	.	1					2	1.1	11.0	—
																	502	1.5	7.7	2.1

July (as in 1957) or as late as the last week of August (as in 1959 following heavy winter mortality). In the two years of study, first eggs appeared on or about 4th August and first clutches hatched on 17th September in 1960 and on 18th September in 1961. Laying usually ceases in early December.

Breeding at Lake Ellesmere is markedly seasonal, whereas in more northern parts of New Zealand, such as Lake Whangape, downy cygnets may be seen in most months of the year.

The number of new nests increases rapidly during August, reaches a peak during the first week of September then tapers gradually to the beginning of October when a smaller secondary peak occurs. Thereafter numbers drop rapidly. This secondary peak is made up of late nesting birds supplemented by re-nesters.

Eggs are laid at intervals of about 1.5 days although 33 (6.5%) of 502 clutches for which the laying period is known, were completed at a rate of one egg per day or less. Table I gives details of the laying period for 502 clutches. The mean clutch size for the sample is 5.1, the clutch being completed in 7.7 days. As the mean clutch size for the overall study was 5.4 (see below), a correction gives 8.1 days as the mean laying period of the average clutch. There is a tendency for small and large clutches to be laid at a faster rate than intermediate clutches. However, the difference is not statistically significant.

Breeding rate

Clutch-size

For the purpose of this study, a clutch was considered complete when, after an interval of six days, no additional eggs were laid. The maximum number of eggs appearing in the nest up to that time, making allowance for any losses during laying, was taken as the true clutch-size. The mean clutch-size was 5.4 eggs (S.D. ± 1.7) based on a sample of 1790 clutches known to have been completed. Their distribution is given in Table II.

The mean differs slightly from the figure of 5.9 obtained by Cutten (1966) from a sample of 225 nests of the Ellesmere population in 1963, but agrees closely with Frith's (1967) 5.5 for 407 nests at Canberra. There is however a large difference from the figures of Lavery (1964) who obtained a mean of 4.5 eggs from 187 nests in Queensland and Guiler (1966) who recorded 4.4 from Tasmania.

Table II. Distribution of clutch-size.

Number of eggs	1	2	3	4	5	6	7	8	9	10	11	12
Number of nests	5	39	136	277	501	449	233	97	27	21	4	1
Total: 1790			*Mean:* 5.4				S.D. ± 1.7					

Clutch-size is however dependent on the condition of adult birds following the winter months. In 1959, following a heavy winter die-off due to starvation, swans did not begin breeding until late September, and clutch-size was significantly lower with a mean of 4.3 eggs. Similar results were obtained in 1968.

The range of clutch-size is similar to that of Cutten (1966) but higher than that reported from Australia. Two nests, one of 13 eggs and one of 14 eggs, were located during this study, but both failed to hatch any young. Because of the zeal with which pairs guard their clutches, it is considered unlikely that an interloping female would have the opportunity of dumping eggs in or stealing eggs from other occupied nests. The larger clutches recorded here are thus considered as laid by one bird.

The size of clutches completed during the initial egg-laying peak in late August/ early September was 5.60 (S.D. ± 1.54) while those completed during the secondary peak in early October were smaller with a mean of 5.17 (S.D. ± 1.23). The difference between means is significant (standard error = 0.083) and is caused by smaller clutches being laid by re-nesting and late nesting (usually young) birds (Brakhage 1965, Sowls 1949, 1955).

Egg dimensions

Cutten (1966) recorded the mean egg size for Ellesmere swans as 104.1 × 67.2 mm. with a range of 87.2 — 114.0 × 58.0 — 71.2 mm. These figures are very close to those given by Frith (1967) at a mean of 104.0 × 67.0 mm. and a range of 96 — 115 × 60 — 73 mm. for Canberra birds. However, both these authorities have figures considerably lower than those of Guiler (1966) whose Tasmanian birds had eggs with a mean of 106.9 × 69.8 mm. and a range of 98.0 — 118.2 × 65.2 — 79.2 mm. Unfortunately, standard deviations are omitted from all of these works.

Incubation

Incubation period is here defined as the time (in days) elapsing between the completion of the clutch and the hatching of the last egg. The last egg laid is usually the last to hatch but this is not always so.

Records of 495 clutches (Figure 5) give a mean incubation period of 36.4 days (S.D. ± 1.7 days). There was no significant difference between the two breeding seasons and records from both years are combined. The range of 32-43 days was greater than expected and cannot be statistically correlated to differences in clutch-size although small and large clutches tend to be incubated longer than clutches near mean size (5.3 eggs for this sample).

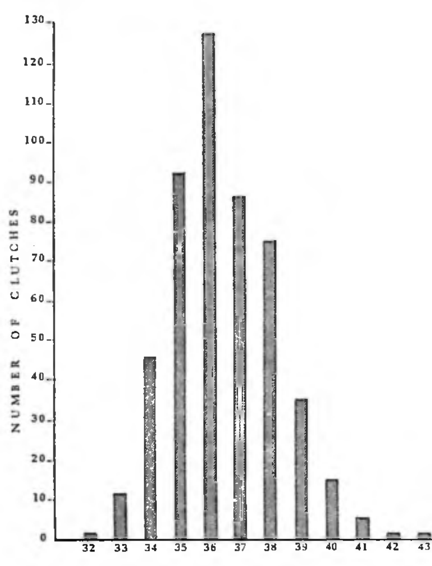


Figure 5. Distribution of incubation periods of 495 clutches.

Soper (1960) reported an unusually long incubation period of 44, perhaps 45, days for a pair of Black Swans at Lake Hayes, Otago. Soper's account indicates unusual behaviour as the cob never sat and both birds often left the eggs unattended for 1-2 hours. This behaviour at Lake Ellesmere would almost certainly have resulted in eggs being predated by Black-backed Gulls *Larus dominicanus*.

Black Swan incubation periods are recorded by several authorities. Delacour (1954) gave 34-37 days, Frith (1967), 39.7 (35-45) days from 44 clutches, while those from captive birds in the northern hemisphere are similar, for example Japan, 33-39 days (Kikkawa and Yamashina 1967), Wildfowl Trust, U.K., 36 days from 12 clutches (J. Kear, pers. com.). Guiler (1966) recorded 42 ± 1 days but remarked that some eggs of the clutch were incubated up to four days longer than the last egg laid. In his summary and abstract, Guiler gave an (undefined) incubation period of 39 ± 2 days.

Frith (1967), like Guiler, considers effective incubation to commence before the laying of the last egg of the clutch. Examination of a small sample of clutches of four or more eggs shows clearly that the incubation period is fairly constant for the first, second and penultimate eggs (Table III). The difference in incubation periods between the last two eggs (0.6 days) is not significant statistically but it does indicate that incubation may commence with the laying of the penultimate egg. Incubation is shared by the sexes, a feature apparently unique amongst swans (Delacour 1954).

Hatching

All eggs hatch within a 24-48 hour period and although the last egg laid is usually the last to hatch, this is not always so. First eggs hatched 17th September 1960 and 18th September 1961. The number of eggs hatching rises very quickly, reaching a peak in early October. Although hatching commenced on roughly the same day in both years, the peak in 1961 was about a week behind that of 1960. The number of eggs hatching drops off very rapidly but rises to the secondary peak in mid-November. This peak was considerably lower in 1961 than 1960 (Figure 6). Hatching was almost completely finished by the end of November and only exceptionally (for example in 1959) does hatching continue into December and January.

Breeding success

Details of overall nesting success are presented in Table IV. Successful nests are defined as those hatching one or more cygnets. Unsuccessful nests are those from which no birds hatched and include those abandoned during incubation or destroyed while laying was still proceeding and before incubation had commenced. Nests occupied but abandoned before eggs were laid are not included.

Including all nests in both years, there was a 67.3% hatch of eggs, giving a mean hatch per nest of 3.62 cygnets. There is, however, a considerable difference in mean hatch per nest figures for the two years. When breeding pairs number approximately 5,500 such a variation accounts for a difference of almost 4,000

Table III. Incubation period for different eggs of a clutch.

	First egg	*Second egg*	*Penultimate egg*	*Last egg*
No. of clutches	46	44	47	47
Total days incubated	1622	1562	1672	1701
Mean incubation period (days)	35.3	35.5	35.6	36.2

Table IV. Overall nesting success.

		1960	*1961*	*Both years*
Total nests		1477	821	2298
Successful	— number	1247	543	1790
	— per cent.	84.4	66.1	78.0
Unsuccessful	— number	230	278	508
	— per cent.	15.6	33.9	22.0
Total eggs		7725	4618	12343
Total hatch	— number	5714	2594	8308
	— per cent.	74.0	56.2	67.3
Mean hatch per nest		3.87	3.16	3.62

cygnets hatching. If 3.62 cygnets per nest is taken as the representative figure, close to 20,000 cygnets are hatched annually from the Birdling's breeding ground.

Reasons for failure of nests were categorised as follows: nests in which eggs were laid but not incubated (clutches may or may not have been complete), nests lost because of flooding, nests predated and finally those abandoned during incubation (mostly infertile or dead embryos). Non-incubated and abandoned nests comprised a remarkably constant percentage of total nests over the two years — being an average of 2.9% and 4.7% respectively. The lower nesting success in 1961, however, was due almost entirely to the effects both direct and indirect of flooding. No nests were flooded in 1960 but 11.3% of total nests were lost for this reason in 1961. Losses due to predation increased from 8.2% to 14.4% of total nests. The Black-backed Gull is the only significant predator and a small breeding colony of

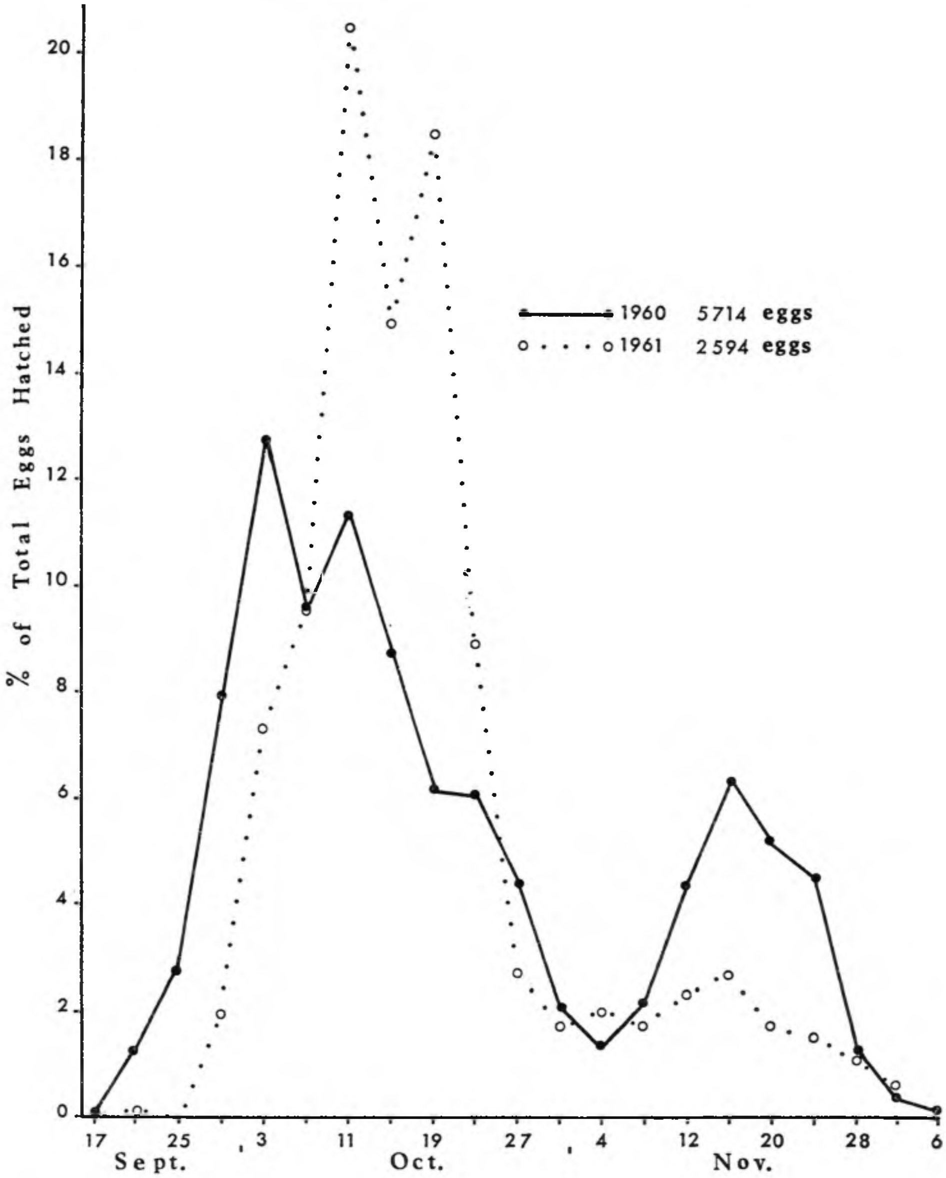


Figure 6. Distribution of hatching with time. Note the difference in the secondary peaks in the two years, illustrating the effect of flood waters on re-nesting.

80 — 100 pairs is located less than two miles north-east of Birdling's Flat. The rising floodwaters and the subsequent large number of nests abandoned allowed many gulls the opportunity to specialise on eggs as a food source.

Figure 2 shows the four areas in which nests were pegged. Predation was greater on the margins of the colony (points A and D) than in the centre (points B and C). In 1960 predation caused the loss of 11.8% of total nests marked in areas A and D as opposed to 4.6% in B and C. The 1961 figures were 18.0% and 10.8%.

Success may also be related to nest density. The proportion of unsuccessful nests was significantly greater amongst those spaced up to five feet apart (26%) than amongst those in the modal group spaced six to ten feet apart (18%). Amongst the more distantly spaced nests, the percentage of unsuccessful nests shows little variation from the mean of 19%. The figure of 22% for nests spaced 31-35 feet apart is not significant as only nine nests are involved.

Clutch-size and nesting success cannot be related because of the obvious complication that many nests are lost before the clutch is complete, and unless incubation has begun, there is no positive way of knowing if all eggs have been laid.

Discussion

Lake level appears to be one of the most important factors in the ecology of the Black Swan at Lake Ellesmere. Not only does the level determine the food availability but it has a significant effect on breeding success both at the nesting and brood stages. This study suggests lake level, not always acting of its own accord but in combination with other agencies such as predators, Man's management practices, etc., determine such factors as the start and duration of the breeding season, nest density, nest and egg destruction, the number of birds likely to re-nest, and therefore the overall success.

Frith (1967) concluded the breeding season of Black Swans in Australia was controlled by fixed annual factors although the species had the capacity to breed at any time should conditions prove suitable. The onset of breeding varies from place to place but in all cases is related to the wet season and the availability of suitable water areas. There is evidence to suggest that water-levels are a factor in the timing of the breeding season in New Zealand. In the Waikato district of the North Island, breeding extends over six to eight months of the year but with a well defined start to the season in June. Water-levels in the lower Waikato River valley are stabilised to an extent by the activities of hydro-dams on the Waikato River. Swamps and lakes reach peak levels in June and high levels are maintained by the dams well into the summer. (R. T. Adams, pers. com.). At Lake Ellesmere, breeding follows closely the lake level's winter peak. The rivers flowing into the lake quickly dry up in summer and the lake level drops rapidly. Here the nesting season is considerably shorter than in the Waikato and water levels may be a factor influencing the length of the season. Water-levels could also be an important factor in fixing the onset of laying in Tasmania three to four weeks earlier than at Lake Ellesmere.

High water-levels can have quite a different effect on the length of a breeding season. Depending on the time at which floodwaters invade the nesting ground, the breeding season may be shortened by the prevention of large-scale re-nesting. Figure 6 shows considerably less re-nesting to have taken place in 1961 and this is considered to be the result of floodwaters invading the colony at a time when most nests were at least two weeks incubated and early nests almost ready to hatch. The ability of a female to lay more eggs the same season is probably lost very soon after the completion of the clutch. Destruction of nests once incubation had commenced meant that these birds would not re-nest. The small re-nesting peak in 1961 therefore comprised those already late nesting birds whose nests were destroyed before egg-laying had ceased. A period of three to four weeks appears to elapse before re-nesting occurs.

The influence of lake level on nest spacing has already been illustrated. The N.C.A.S. management programme of deterring swans from nesting beyond the confines of Birdling's Flat must play a part in determining nest density, the effect being more pronounced in years of high lake level when suitable nesting space is limited. High nesting density can affect nesting success in various ways as illustrated by the results of breeding in 1961; aggressive encounters between birds nesting very close together may cause abandonment of the nest and clutch; nest spacings influence predation levels. The lower nesting success of 1961 is therefore causally related to a high lake level in the middle of the nesting season.

Acknowledgements

It is a pleasure to thank Messrs. H. McAllum, T. A. Caithness, C. D. Roderick, J. O'Brien, P. Morrison, and D. Arthur of the Wildlife Service and Messrs. L. Hoff, V. Henderson and D. Wright of the North Canterbury Acclimatisation Society for their assistance to the senior author in the field; and Mrs. Helen Morrison and Mrs. Lorraine Tietjens for their help in analysing of data. We wish to record our gratitude to Dr. G. M. Dunnett and our Wildlife Research Section colleagues for helpful criticism of the manuscript and constructive comment.

A considerable debt of thanks is due to the North Canterbury Acclimatisation Society whose willing assistance at all times made this study possible.

Summary

A total of 2,298 nests of Black Swans *Cygnus atratus* at Lake Ellesmere, New Zealand, were studied during the 1960 and 1961 breeding seasons. Systematic egg collection begun in 1915 has concentrated nesting at the eastern end of the lake. Occupation of the breeding ground starts in late July following the lake level's winter peak. Higher ground along the lake margin is occupied first. Birds nesting later are forced to utilise lower, more flood-prone land on the margins of the colony. Nests were significantly closer together in 1961, a reflection of lake level affecting the availability of nesting ground at the time of occupation. Egg laying is markedly seasonal, in contrast to more northern parts of New Zealand, in the first week of August, reaching a peak in late-August early-September, followed by a secondary peak (mainly re-nesters) in early October. Mean clutch size of 1,790 nests is 5.4. Mean incubation period of 495 clutches is 36.4 days. Effective incubation may commence with the laying of the penultimate egg. All eggs hatch within a 24—48 hour period, the last egg laid usually being the last to hatch. Successful nests, those hatching one or more cygnets, comprised 78.0% of nests studied in the two years and hatched 67.3% of all eggs laid. Mean number of cygnets hatched per nest was 3.62. Predation, by Black-backed Gulls, and flooding were the main causes of nest loss. Predation was greatest on the margins of the colony. Success is related to nest density. Lake level appears to be one of the most important factors in the ecology of Black Swans at Lake Ellesmere, affecting not only food availability but also length and duration of nesting season, availability of nesting ground, nest spacings, nest destruction, the number of birds likely to re-nest and therefore, the overall nesting success.

References

BRAKHAGE, G. K. 1965. Biology and behavior of tub-nesting canada geese. *J. Wildl. Mgmt.* 29 : 751-71.

CUTTEN, F. E. A. 1966. Clutch size and egg dimensions of the black swan *Cygnus atratus* at Lake Ellesmere, Canterbury, New Zealand. *Emu* 65 : 223-5.

DAVIS, D. E. 1955. Breeding biology of birds. In Wolfson, A (ed.), *Recent studies in avian biology*. Urbana: Univ. of Illinois Press.

DELACOUR, J. 1954. *The Waterfowl of the World*, Vol. I. London: Country Life.

DRUMMOND, J. 1906a. On introduced birds. *Trans. N.Z. Inst.* 39 : 227-52.

DRUMMOND, J. 1906b. Dates on which introduced birds have been liberated, or have appeared in different districts of New Zealand. *Trans. N.Z. Inst.* 39 : 503-8.

FRITH, H. 1967. *Waterfowl in Australia*. Sydney: Angus and Robertson.

GUILER, E. R. 1966. The breeding of the black swan (*Cynus atratus* Latham) in Tasmania with special reference to some management problems. *Papers and Proc. R. Soc. Tasmania* 100 : 31-52.

KIKKAWA, J. and Y. YAMASHINA. 1967. Breeding of introduced black swans in Japan. *Emu* 66 : 377-81.

KIRK, T. 1895. The displacement of species in New Zealand. *Trans. N.Z. Inst.* 28 : 1-27.

LAMB, R. C. 1964. *Birds, beasts and fishes*. Christchurch, New Zealand: The North Canterbury Acclimatisation Society.

LAVERY, H. J. 1964. An investigation of the biology and ecology of waterfowl (Anatidae: Anseriformes) in North Queensland. M.Sc. Thesis, Univ. of Queensland. (quoted in Frith 1967).

OLIVER, W. R. B. 1955. *New Zealand Birds*. Wellington: A. H. and A. W. Reed.

SOPER, M. F. 1960. Long incubation period of black swan. *Notornis* 9 : 61.

SOWLS, L. K. 1949. A preliminary report on renesting in waterfowl. *Trans. N. Amer. Wildlife Conf.* 14 : 260-75.

SOWLS, L. K. 1955. *Prairie Ducks*. Harrisburg, U.S.A.: Stackpole & Co.

THOMPSON, G. M. 1922. *Naturalization of animals and plants in New Zealand*. Cambridge: Univ. Press.

THOMPSON, G. M. 1926. *Wild life in New Zealand, Part II*. Wellington: Govt. Printer.

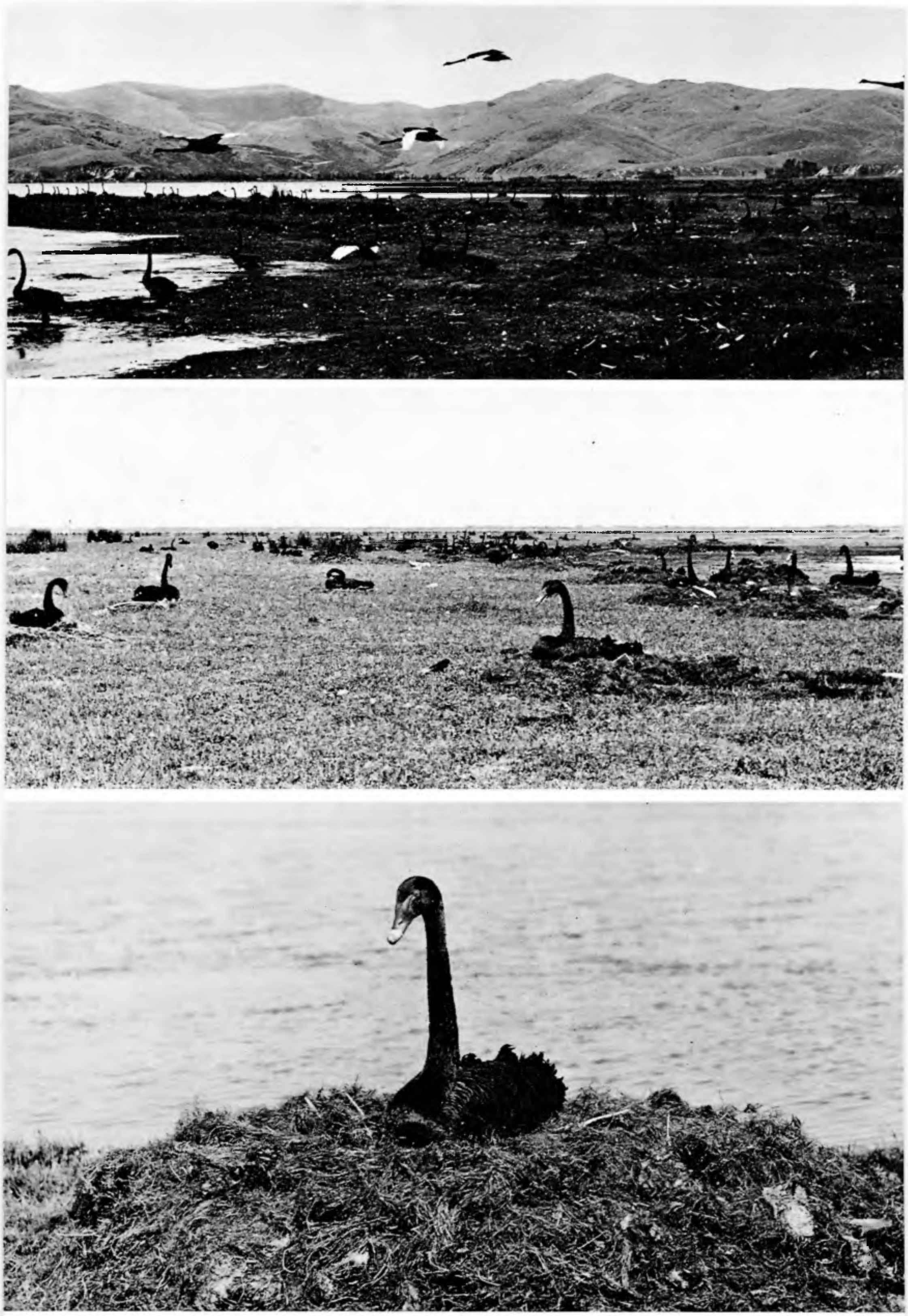
K. H. Miers, Protection Forestry Division, New Zealand Forest Service, Wellington, N.Z.
Murray Williams, Wildlife Service, Department of Internal Affairs, Wellington, N.Z.

J. Hori

Plate I. (a) A multiple nest of Common Shelduck *Tadorna tadorna* in a hollow tree. The female is hiding from the photographer (see p. 5).

(b) Two Shelduck nests close together in the same straw stack.

J. Hori



New Zealand Wildlife Servic

Plate II. Black Swans *Cygnus atratus* at their nesting colony at Lake Ellesmere, New Zealand (see p. 23).