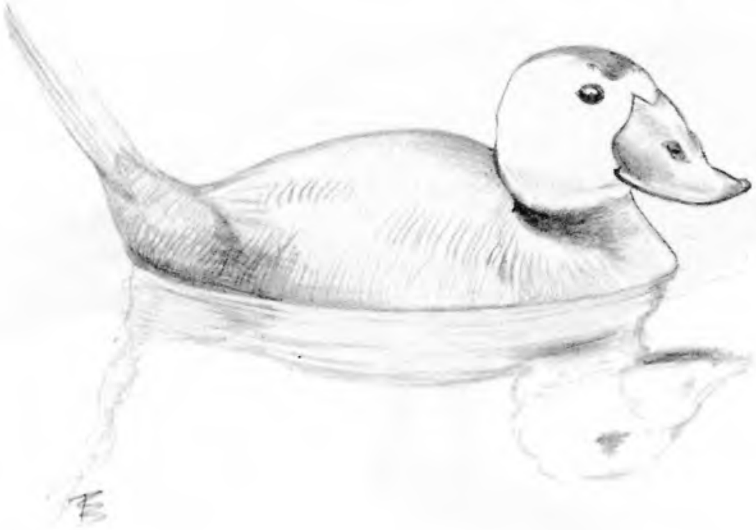

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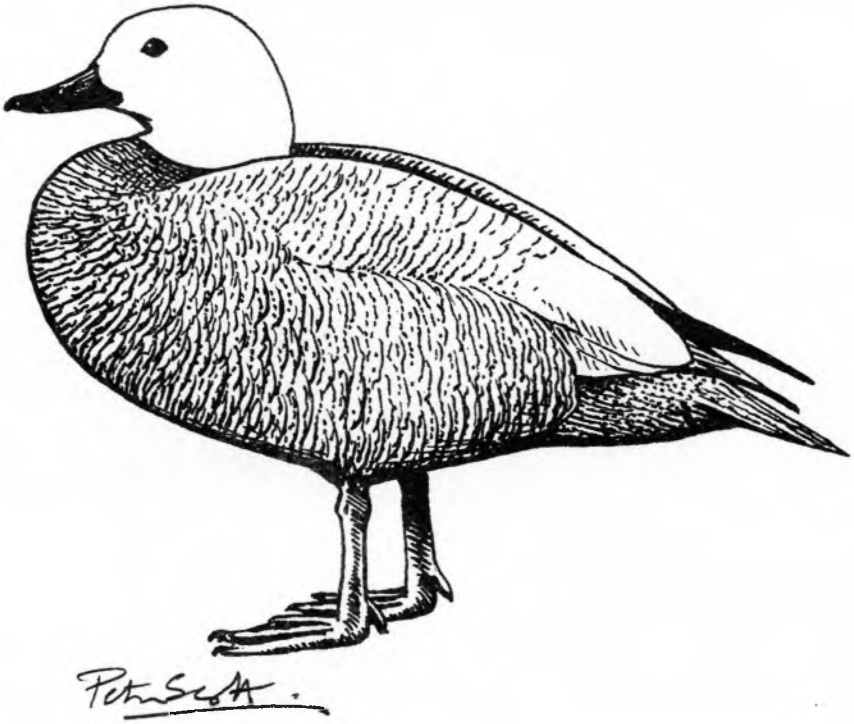

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Contents

On the biology of the Spectacled Eider

A. A. KISTCHINSKI AND V. E. FLINT

The range of the Spectacled Eider *Somateria fischeri* is rather restricted, and its biology is poorly known. Some biological observations have been made in the Siberian tundras between the Yana and Kolyma rivers (Birula, 1907; Mikhel, 1935; Uspenski *et al*., 1962; Vorobyev, 1963) and in Alaska (Nelson, 1887; Conover, 1926; Brandt, 1943; Bailey, 1948; Johnsgard, 1964a). In the summer of 1971, we obtained new ecological information in the delta of the Indigirka (*c*. 71°N, 150°E) where this eider is the most common duck species. Our work proceeded from 3 June to 6 August, and we were able to visit both inner and maritime parts of the delta where life conditions for Spectacled Eider are different.

Breeding habitats and numbers

The Spectacled Eider is the most common duck in the delta of the Indigirka river; the fact having been recorded by Mikhel (1935). It is most numerous in the maritime half of the delta, up to 40–50 km from the sea. Eiders live here in the moist low tundra with numerous shallow ponds bordered by coastal flooded growth of *Arctophila fulva*, with underwater beds of *Hippurus* sp., and with small islets. The so-called 'laydas'—vast depressions (2–5 km in diameter) that are flooded in June, after snow-melting, and overgrown by *A. fulva* and sedges—are especially characteristic as a habitat of Spectacled Eider. Usually, in the middle of a 'layda' there are deeper patches of open water, and among grass-sedge thickets and these patches, small islets and the dry tussocks are scattered. By the end of the summer the water level falls and most of the area of 'laydas' dries; nevertheless, they remain hardly passable. On such lakes Spectacled Eider is the most numerous duck (besides, there live a few Long-tailed Duck, *Clangula hyemalis*).

Spectacled Eider needs large areas of coastal shallows (0–10 cm deep) for summer living, most of which is a temporarily flooded moss-sedge bog. This bog is inhabited by great numbers of hydrophilous larvae of crane-flies *Prionocera* spp. (Tipulidae) and those of various caddisflies which make together the bulk of the summer diet of this eider.

Farther from the sea, in the inner parts of the delta, favourite eider habitats are less extensive, and accordingly, eider numbers

Table 1. Population density and total numbers of the Spectacled Eider in the delta of the Indigirka river

Territory within the delta	Number of census plots	Total area of census plots (km^2)	Pairs (June) or females (July) per 10 km^2		Total area of the territory	Total spring numbers (pairs)
			Limits	Mean		
Maritime parts, south-westwards to the settlements Yar and Tabor	5	66	33–60	47	3,100	14,570
Central parts from Yar and Tabor south-westwards to the settlement Polyarni and mouth of the Keremesit river	3	39	8–12·5	10	1,800	1,800
Innermost parts and the tundras southwards of the Kolymskaya channel	4	41	0–5	2·5	4,300	1,075
Total	12	146			9,200	17,445

are lower. Southwards of the Kolymski channel, near the Keremesit river, Spectacled Eiders were rare; they lived there near shallow lakes 10–200 m in diameter bordered by polygonal bogs flooded by melt-water in June.

In July, a good number of females were also observed in the narrow strip of maritime meadows dominated by *Dupontia psilosantha*, sedges and cotton-grass, rich in brackish potholes devoid of *Arctophila* and dotted with small islets.

We have determined the numbers of Spectacled Eiders on census plots 6–30 km^2 by surveying all the lakes and ponds on them during one or more days. At courtship time, pairs on lakes are easily visible. In July, males are nearly absent in the tundra; non-breeding females and those which have lost their clutches gather in flocks and sit for hours on the favourite resting spots situated on dry lakeside tussocks or islets where they can easily be counted. Incubating females in July could be either identified by their behaviour when feeding on channels and lakes or frightened from the nests. Of course, some females were missed. Nevertheless, we consider our estimates to be reliable enough—especially because in July of 1971 successful females made up quite a small part of the population (see below). When calculating we equated the number of females in July to the number of pairs in June (the spring sex ratio being 1:1).

In order to estimate total numbers, we have divided the delta into three zones with different population densities of Spectacled Eider (Table 1). Calculations have shown that, in spring, the numbers of the eider in the delta and tundras adjacent to it in the south are close to 17,000–18,000 pairs, of which 15,000 are in the maritime half of the delta.

According to local people, the numbers of Spectacled Eider in the delta fluctuate in different years, but the species is always common here. In 1971, the numbers were said to be slightly lower than usual.

Arrival

Eiders arrive at the breeding grounds at the beginning of June. In 1971, they appeared on 8 June; an intensive passage took place on 9–10 June and ended on 13 June. Eiders flew directly from the east, in flocks of seven to thirty birds, very low—usually 2–3 m above the ground. Probably eiders flew great distances without landing—from the resting grounds on marine bays to the breeding lake.

The sex ratio in the arriving flocks was near to 1:1. From 9 to 13 June 1971, seventy-two males and sixty-nine females were counted. Pairs were easily visible in the flocks.

Breeding

Spectacled Eiders arrive in pairs. We were not able to see courtship behaviour at the breeding grounds; only on 19 June were residual displays of this type observed. Males performed a display close to 'Head-forward-lifting', and females—'Chin-lifting' (in terms of Johnsgard, 1964b) (Figure 1).

Eiders were in pairs up to 24 June. On 25, 29 June and 4 July we saw and collected females which had just finished egg-laying. (In 1960, in the mouth of the river Bogdashkina, north of the delta, a nest with two eggs was found on 15 June, and a full clutch with five eggs on 24 June (Uspenski *et al.*, 1962).) At the end of June, pairs were broken, and the males disappeared. In 1960, an eastward passage of males along the sea shore north of the delta was observed at the end of June (Uspenski *et al.*, 1962). However, we saw single drakes from time to time in the flocks of non-breeding females up to 15 July. According to Brandt (1943),

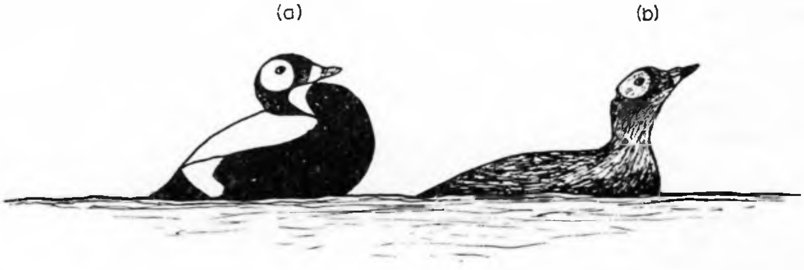

Figure 1. 'Residual' courtship displays in *Somateria fischeri*. (a) Male performing 'Head-forward-rearing'; (b) female performing 'Chin-lifting' (according to Johnsgard, 1964a).

sometimes a male remains near the nest even up to the end of the incubation.

As in other eiders, two types of nesting occur in the Spectacled Eider: (1) scattered in the uniform tundra rich in lakes, and (2) on islets in lakes or 'laydas' with, as a rule, several females close to each other. At courtship time, we saw up to six to fifteen pairs on one lake. No territorial aggressive displays were observed between them. Frequently two or three pairs swam and fed together, and rested alongside each other on tussocks or islets. Johnsgard (1964a) reports a similar lack of interaction in Alaska.

On islets, Spectacled Eiders nested in colonies of gulls and terns—Herring Gull *Larus argentatus*, Glaucous Gull *L. hyperboreus*, Sabine's Gull *Xema sabini*, Ross's Gull *Rhodostethia rosea*, Arctic Tern *Sterna paradisaea*—close to the gull nests. On 9 July, we surveyed such a colony on a large 'layda' with a lot of islets and open water patches. In this colony, nine pairs of Herring Gulls, seven pairs of Glaucous Gulls, two or more pairs of Black-throated Divers *Gavia arctica*, and fourteen Spectacled Eider pairs bred (Figure 2). The eider nests were within 0·5 m (1), 1·0 m (3), 1·5 m (2), 2·0 m (1), 2·5 m (2), 3 m (1), 4 m (1), 5 m (2) and 7 m (1) of the gull's nest. On the same lake, there were about fifty eider females which have not bred or have lost their clutches.

Similar 'mixed colonies' were met with in other places. Near the Keremesit river, six pairs of eiders were found on 15–20 June on the lake where four pairs of Ross' Gulls, a pair of Arctic Terns, and a pair of Herring Gulls had nests. Eiders did not then have clutches but seemed to have settled here for breeding. On 17 July, we found a nest of eider with four eggs on the eve of hatching. It was on an islet, about 15 m from another islet where a pair of Ross' Gulls has bred; within 50–70 m, on other islets, three pairs of Arctic Terns nested. On the same lake, two eider nests (without eggs but which seemed not to have been destroyed, having a large amount of down) were found on an island where two pairs of Sabine Gulls bred; nests of eiders were within 40–50 m from gull's nests, within gull's territories which were violently defended.

Large gulls (*L. argentatus*, *L. hyperboreus*) made nests on the highest and driest tops of islets. They laid eggs in the first half of June, while fresh eggs of Terns and Ross' Gulls appeared on 17–20 June. Eiders' laying began later—judging from examination of collected birds, after 20 June. Undoubtedly, the eiders actively chose the neighbourhood of gulls, and joined their already formed colonies.

Nests of Spectacled Eiders on islets 3–15 m in diameter were made near their edge, among dense growth of *Carex stans*, *Dupontia* and *A. fulva*. Due to manuring by birds, grass is especially luxuriant on such places, and in July its bright green colour was very noticeable. The nest is lined by dry sedges and grasses, as well as by down. The amount of down in nests differs considerably; when laying is repeated, even a nest with one egg or without eggs can contain much down.

Nesting of Spectacled Eiders on lake islets was mentioned by Birula (1907) and Brandt (1943). In the Yukon–Kuskokwim delta, Johnsgard (1964a) has found only one nest on an islet, while eleven were seen along the shores of lakes (average distance 1 m from water), and one in the tundra, 18 m from water. Nests were often situated a considerable distance from one another. During our observations, in the mixed 'eider-gull' colony, the distance between eider nests was often 40–80 m. Sometimes, two or three nests were made on the same islet; then, they were 2–9 m from each other, and once even within 30 cm (Figure 2). These facts certainly indicate a certain degree of incipient colonialism in the Spectacled Eider.

Nesting of ducks in gulls' and terns' colonies is well known. Gulls and terns defend their rookeries, so providing for the protection of duck nests as well. Of the species which inhabit our delta, Sabine's Gull and Arctic Tern are the most aggressive. The least active are Ross' Gulls, but even they successfully drive away large gulls and skuas at distances up to 50 m of the nest. Nesting near to these three small species which do not destroy duck nests but provide effective protection from large gulls, skuas and probably Arctic fox, seems to be most favourable for eiders. Large gulls keep foxes and skuas out of the colony but destroy eider nests themselves. In their colonies and around them we found a lot of destroyed eggs of eiders. In this connection, the following facts are worth mentioning.

In the mixed colony surveyed on 9 July, the only eiders successfully to incubate their clutches had made nests not farther than 7 m (usually at 1–3 m, once at 50 cm) from a gull's nest (Figure 2), i.e. within territories of gulls. On numerous islets situated over 5–10 m from gull nests, we have found dozens of eider nests, and all of them were destroyed. As was said before, about fifty females without nests (non-breeders or unsuccessful) remained in flocks on the same lake. Of fourteen clutches, four were well incubated and had four to seven eggs; other ones were fresh and contained one to four eggs (average 2·1, $n=10$). Apparently, these clutches were repeat ones.

We try to explain these facts in the following way. The pair of gulls do not allow any other gull to penetrate into their defended territory, while in their own behaviour aggressive intentions predominate. Eider clutches noticed by 'host' gulls are certainly destroyed even in the close vicinity of their own nest; we have found up to six destroyed eider nests around some gull nests (Figure 2). However, eiders are threatened here by only one pair of gulls, and some clutches have a chance to survive. At greater distances from the nests (usually over 5 m) gulls do not drive their 'neighbours' away, although foxes and skuas are not tolerated. Therefore, eider nests can be destroyed here by all the gulls of the colony, and their chance is negligible.

Despite heavy losses, nesting in the colonies of large gulls is of advantage for eiders. When surveying islets on numerous lakes without gull colonies, we have found twenty to thirty eider nests altogether. All of them were destroyed—probably, mainly during laying (the amount of down was small).

In normal years, large gulls and skuas feed in the Indigirka tundras mainly on rodents. According to Perfilyev (1967), microtines made more than 30% of their 'average' summer food. Old gull pellets found in the delta consisted, as a rule, of lemmings. In non-lemming years, as in 1971, gulls and skuas are probably especially active in destroying nests. In such years, it is almost hopeless for eiders to attempt to nest on lake islets (where they are open

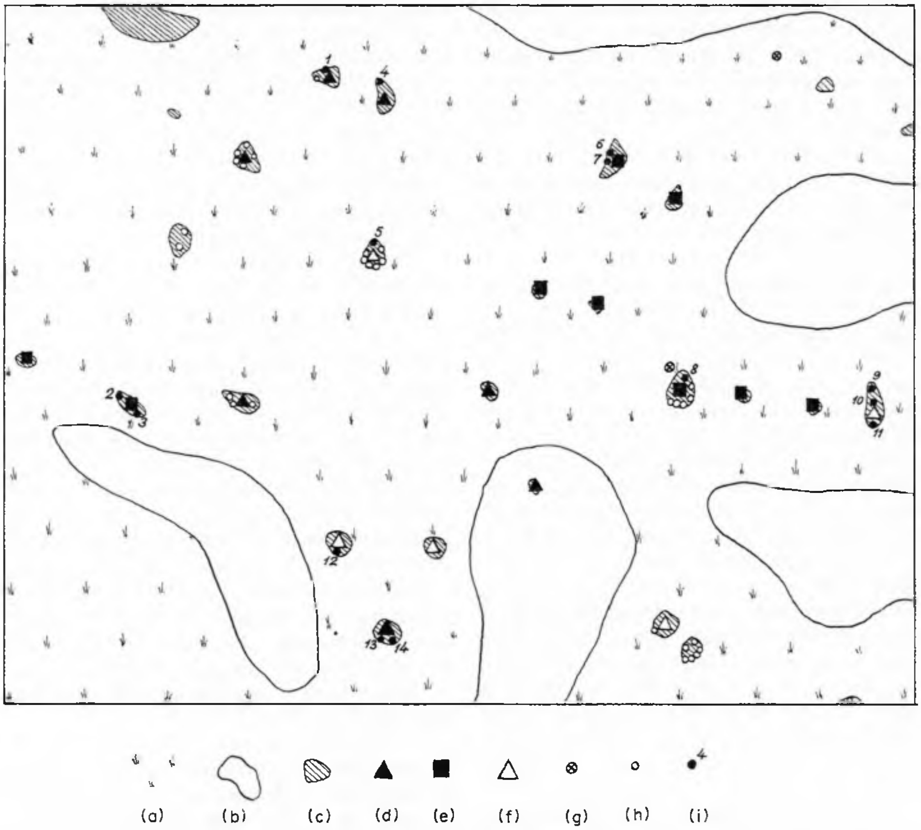

Figure 2. Scheme of the mixed colony of gulls and eiders. Delta of the Indigirka river, 9 July 1971. Scale 1:2,000. (a) Flooded *Carex* and *Arctophila* thickets; (b) pieces of the open water; (c) islets; (d) occupied nest of *Larus hyperboreus*; (e) the same of *L. argentatus*; (f) empty nest of a large gull; (g) nest of *Gavia arctica*; (h) destroyed nest of *S. fischeri*; (i) nest of *S. fischeri* with clutch. Figures point to the number of each occupied nest (see text).

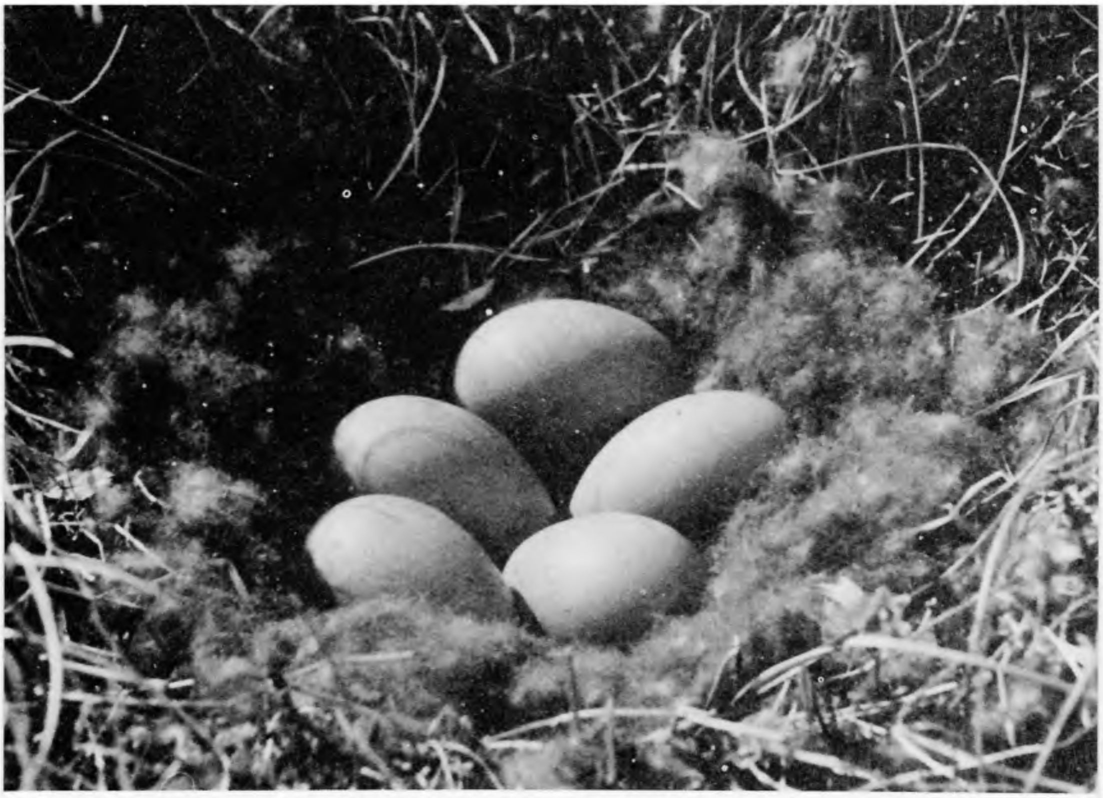

Figure 3. Clutch of *Somateria fischeri*, mouth of the Keremesit river. *A. A. Kistchinski*

to 'purposeful' searching) without protection by aggressive birds (even if the same large gulls).

Thus, many Spectacled Eiders after arrival at tundra, search for 'laydas' and lakes where gull colonies are forming at the time, and try to nest in the colonies. If Herring or Glaucous Gulls are the main breeders, they destroy most clutches; eiders lay repeat clutches, and their fate is the same—except those birds who made nests in the very vicinity of gulls' nests. In this way the specialized nesting pattern may have evolved through selection.

Another type of nest is found scattered in uniform tundra not far from the ponds. Such a nest with the full clutch (five fresh eggs) was found on 25 June on the low wet moss tussock among the polygonal tundra (Figure 3). It was 5–10 m from small ponds which had become almost dry by the end of July. Similar nests were found by Uspenski *et al.* (1962) Vorobyev (1963) and Johnsgard (1964a). We regularly saw females which, judging by their behaviour, kept near nests of this type. In this case, clutches are unprotected from predators, but due to the absence of any 'guiding-points', such a nest can be found only by accident.

The measurements of twenty-three eggs averaged 67·4 × 45·4 mm, the extremes being 62·0–71·0 mm length and 44·2–46·8 mm width. There was no significant difference in the size of eggs from different clutches. Eggs measured in Alaska were 66·0–71·6 mm long and 43·0–47·4 mm wide (Nelson, 1887; Johnsgard, 1964a); twelve eggs averaged 69·0 × 43·7 mm (Johnsgard, 1964a).

Nesting behaviour of the Spectacled Eider resembles that of the Eider *Somateria mollissima* and King Eider *Somateria spectabilis.* The female incubates strongly and hardly leaves the nest. She allows one to approach to within 1–4 m, then she flies, staining the eggs with excreta. Afterwards she swims on the pond 20–30 m away and sometimes begins to 'feed'. While swimming the female performs postures resembling those of King Eider, for instance she tilts her head back and to one side, or rises in the water, so that all the breast is exposed. If the bird is not disturbed, after 10–15 minutes it comes back to the nest and sits on the clutch (Figure 4).

Breeding females feed singly or in groups of two to four. Group-feeding in breeding female King Eiders was also observed in July 1970 (Kistchinski, unpublished).

Females which have not bred or have ceased nesting after the loss of their clutches, remain in July at the breeding grounds. They keep in groups from two to fifty, usually of four to eleven birds (Table 2). They feed

Figure 4. The incubating female of the Spectacled Eider. *A. A. Kistchinski*

together on channels and lakes of the delta, and rest in close clusters on favourite spots — rather high, dry mounds on the lakesides or islets. They can be accompanied by single males which have lingered on the tundra, and, when feeding, by breeding females as well. Thus, on 4 July, we collected simultaneously an incubating and a non-breeding female from a group of three ducks feeding together on a channel. Little by little, these non-breeder groups are joined by new females which have lost their nests and stopped breeding attempts. Such groups were observed up to 30 July.

In 1971, we did not see downy young of the Spectacled Eider. Broods of fledging young have been seen in the Indigirka tundras on 24 July and 5 August (Uspenski *et al.*, 1962), and of poorly flying ones — on 30 and 31 August (Mikhel, 1935).

Table 2. Composition of flocks of non-breeding females of the Spectacled Eider

Size of flocks	2–3	4–7	8–11	13–15	20–50	Total
Number of flocks	8+	33	9	3	3	56+
Total numbers of birds	20+	179	88	42	92	421+

Table 3. The ratio of different colour types in the females of the Spectacled Eider, collected 24 June–26 July

Colour type (see text)	Total number of birds collected	Number breeding
The first type (definitive?)	5	4
Intermediate birds	4	2
The second type (2nd or 3rd year?)	8	2
Total	17	8

Population composition and reproduction

As mentioned above, sex ratio on arrival is near to 1 : 1. Only adult males in full breeding plumage appear in the tundra. Two main types of female plumage occur on the breeding grounds; their ratio (by specimens collected) is shown in Table 3. Birds of the first type have bright 'yellow-rusty' colours of breast and sides, 'rusty' tones on the back and intensive brown-black abdomen with chestnut-coloured bars. The second type has a duller, 'sandy-yellow' breast and sides, and 'rusty-yellowish' (buff) ground colour of the back, rump and scapulars which are also dull compared to the first type. The black streaks marking the upper parts are slightly wider: the blackish (sooty) colour of underparts is less intensive than in the first type, and covers a smaller area.

The differences between the colour types can be obscured because of the various extent of feather wear as well as of moult stage. Some birds have an intermediate plumage (Table 3). The types of birds taken in the field were easily distinguished, but on the same specimens after 6-month storage in the museum, the types were more difficult to discern.

'Spectacles' are well developed in both the types of birds. Coloration of a head as a whole (degree of contrast between 'spectacles' and the rest of the head, intensity of the main colour, width and blackness of streaks) varies strongly between individuals and shows no correlation with the two types outlined.

Age differences in the female plumages of the Spectacled Eider are not too well known (Portenko, 1952). So, we do not know if our types are correlated to the age of the birds. We can only suppose that the first type is definitive while ducks of the second one are 2 or 3 years old, which (contrary to the males of the same age) arrive at the breeding grounds in spring.

Still smaller and lighter females, distinguishable in the field (probably yearlings) were observed and collected as a rarity on the West Alaskan breeding grounds (Conover, 1926; Johnsgard, 1964a). We did not see such birds in the Indigirka tundras.

Some of the females arriving in spring do not breed. Of sixteen ducks taken on 24 June–17 July, eight had undeveloped ovaries and did not attempt to nest. Among them, there were birds of both the colour types, mainly of the second one (Table 3).

Females having just finished egg-laying and collected on 28 June–4 July, weighed 1,750–1,800 g (mean 1,767 g, $n=3$). They had a 3–4 mm layer of fat and were not moulting. Non-breeding ducks, taken on 24 June–11 July, weighed only 1,400–1,550 g (mean 1,485 g, $n=8$). They had almost no fat or were even exhausted; all of them were intensively moulting contour feathers. Participation in the breeding cycle was probably determined by physiological state of females, including their degree of fatness.

As mentioned above, many clutches are lost, and ducks lay repeat ones. Three of five females taken on 9–17 July, had ten or more 'scars' of broken follicles in the ovaries—i.e., they had tried to nest repeatedly, and possibly more than once. The fourth duck had one to two old 'scars' (probably an uncomplete clutch had been destroyed), and the fifth one—seven to eight 'scars' and a belly with down fully stripped; probably only this duck was successful. The birds had almost no fat and weighed 1,400–1,600 g (average 1,440 g, $n=5$).

In order to estimate breeding success we tried to count breeding females (including those who seemed to have nests judging by their behaviour) and, separately, ducks in non-breeding flocks including unsuccessful birds. The ratio obtained was 1 : 6·6 (63 : 415). Two souces of error were probable: (a) scattered-nesting, 'non-colonial' ducks can be rather easily missed during surveys, and (b) incubating females can join non-breeding groups when feeding. However, we are able roughly to assume that in 1971, only 10–15% of the females at the breeding grounds successfully incubated their clutches.

The size of a complete clutch (including data from autopsies of ducks having just finished egg-laying) was four to seven (mean 5·56, $n=9$). The number of eggs in all the clutches including repeat ones was one to seven (mean 3·74, $n=19$). Assuming that in spring there were forty-nine females per 100 adult birds (see sex ratio, p. 6), and five to seven (10–15%) of them were successful, the total number of eggs in clutches in 1971 would be nineteen to twenty-six per 100 adults in spring. Duckling survival rate was unknown, but population gain this summer could hardly exceed 15–25% of the spring population.

Large numbers of non-breeding Spectacled Eiders were also observed in Alaskan tundras (Johnsgard, 1964a).

Voice

As it was already mentioned by Nelson (1887) and Johnsgard (1964a), the Spectacled

Eider is a very silent bird. We never heard any male call. A female's call, which can be only rarely heard, is a hoarse 'krro', resembling a remote Raven's croaking. When swimming in flocks, ducks communicate by a quiet 'cro cro ko ko . . . cro cro ko ko . . .'; similar calls are uttered by a duck replying to the courtship display of a drake.

Food

Data were obtained through the analysis of the oesophagi and stomachs of the birds collected (Table 4) and by visual observations (Table 5). In the first case, we roughly estimated the percent of the total volume of a sample occupied by each sort of food. Finally, average volume per cent of each food was calculated. Contents of the stomach and of the oesophagus of one bird were usually considered as one sample but in some cases they were treated as separate samples (if the foods contained were quite different, i.e. reflected different feeding bouts).

From arrival at breeding grounds to the end of June, eiders fed on temporary ponds and the shallows of lakes—on the places where moss-sedge bog was flooded by 10–30 cm of melt-water. In the stomachs of eiders collected on 5–8 June 1960, there were mainly seeds of *Ranunculus pallasii*, and, in small numbers, insects washed by thawed waters out of the bog or from its surface (larvae of flies Rhagionidae, beetles *Elaphrus* sp., Carabidae sp.), as well as remnants of shells of marine gastropods (Uspenski *et al.*, 1962). After thawing of the bog to the depth of 5–7 cm, usually about 10 June, there appear a large amount of the hydrophilous larvae of crane-flies *Prionocera* spp. (Tipu-

Table 4. Contents of digestive tracts of Spectacled Eiders

	Volume % of the total amount of food		
	24 June (*n*=4)	28 June–17 July (*n*=16)	26 July–10 August (*n*=4)*
Diptera	99·7	17·12	–
Tipulidae, larvae	99·5	3·06	–
Prionocera spp.	99·5	2·81	–
Tipula sp., hydrophilous forms	–	0·25	–
Chironomidae, larvae	–	13·00	–
Empididae, larvae	0·2	0·13	–
Diptera sp., larvae	–	0·31	–
Dolichopodidae, larvae	–	0·06	–
Tipula sp., imagines	–	0·50	–
Scatophaga sp., imagines	–	0·06	–
Trichoptera spp., larvae	0·2	55·94	53·8
Trichoptera spp., imagines	–	0·31	–
Coleoptera, imagines	–	6·63	–
Agabus spp.	–	3·69	–
Carabus spp.	–	0·63	–
Pterostichus costatus	–	0·31	–
Hydroporus sp.	–	0·13	–
Lepyrus sp.	–	1·87	–
Crustacea (Gammaridae)	–	6·75	–
Mollusca (*Sibirenauta elongata* + *Physa arctica*)	–	0·69	–
Oligochaeta (Enchytraeidae)	–	0·06	–
Seeds			
Ranunculus pallasii	0·1	12·50	46·2
Others	–	+	+
Plant Material (remnants of sedges, moss, roots, small twigs etc.)	–	+	+
Shells (marine molluscs)	–	+	–
Gastrolites (gravel)	–	few	few
Total	100·0	100·0	100·0

* Among these, three samples were received from Dr S. M. Uspenski and analysed according to our method.

Table 5. Seasonal changes of feeding habitats in the Spectacled Eider

Type of habitat	Number of feeding eiders observed							
	10–25 June		28 June–7 July		9–17 July		22–30 July	
	Birds	%	Birds	%	Birds	%	Birds	%
Temporary water bodies	4	12·1	–	–	–	–	–	–
Shallows of permanent lakes	29	87·9	38	48·1	128	99·2	66	77·6
Channels of the delta (fresh)	–	–	41	51·9	1	0·8	5	5·9
Estuary of the Kolymskaya channel (slightly brackish)	No data		No data		No data		14	16·5
Total	33	100·0	79	100·0	129	100·0	85	100·0

lidae) which seem to make the bulk of the diet of Spectacled Eiders at courtship time (Table 4). Oesophagi and stomachs of the birds taken in this period contained 100–200 of these larvae. When feeding, eiders dig in a flooded bog with their beak. They swam along the edge of a shore growth or among flooded sedges, submerging their head or dabbling just like Mallard *Anas platyrhynchos*; we did not see them diving that time. Birds fed in pairs or in close groups of two to four pairs together.

In 1960, in the middle of June, many chironomid larvae were found in the eider stomachs (Uspenski *et al.*, 1961). We did not detect them and relate this fact to the peculiarities of the summer season of 1971. We met with extremely few of chironomid larvae in the diet of birds at all, even in ducks so specialized on this food as Steller's Eider and Long-tailed Duck. Moreover, almost no chironomid larvae were seen and collected in lakes and ponds.

At the end of June, a mass of cranefly adults emerged, and the number of their larvae in the bog drastically decreased. From that time till August, caddisfly larvae became the main food of Spectacled Eiders (Table 4). Besides these, eiders consumed in July various invertebrates—mainly aquatic chironomid larvae (Gammaridae, Dytiscidae) but also the terrestrial ones which can be blown onto the water surface (adults of Diptera, Trichoptera, Carabidae, *Lepyrus* sp. etc). At the end of June and beginning of July, eiders fed both on lakes and in delta channels and took their food by diving much deeper than at the courtship time. After 7 July, birds began to feed again almost solely on shallow (20–70 cm) overgrown lakes (Table 5). By the end of the summer, eiders' diet ceased to be diverse, and ducks again ate large quantities of the seeds of *R. pallasii*.

In some stomachs, gastrolites (pieces of gravel 1–5 mm in diameter) were found up to 7 July, i.e. a month after the eiders had been on the sea (there is no gravel in the delta). Seeds of *R. pallasii* which occur intact in many stomachs, may act as gastrolites too.

In general, changes in the diet of the Spectacled Eider during the summer correspond with the seasonal dynamics of abundance of some food items (Figure 5). The larvae of *Prionocera* seem to be probably the most valuable food. Disappearance of males from the breeding grounds as well as decrease in fat of females (including non-breeders) correspond with the seasonal decline of these larvae.

Acknowledgments

We are most grateful to Dr Yu. I. Tchernov for identification of some invertebrates from the digestive tracts of the eiders, and to Dr B. A. Yurtsev for botanical identifications. Dr S. M. Uspenski has kindly placed at our disposal results of the analysis of several food samples collected by him in 1960 and identified by Dr Yu. I. Tchernov.

Summary

Data on the numbers, breeding, and diet of the Spectacled Eider *Somateria fischeri* were obtained in 1971 in the delta of the Indigirka river. This eider breeds in the low tundra with numerous shallow lakes and flooded depressions, most abundantly in the maritime half of the delta (thirty-three to sixty pairs per 10 km^2) and rarely in the inland tundras. There are about 17,000 pairs in spring with a 1 : 1 sex ratio. Eiders nest scattered in the uniform wet tundra or several near one another on lake islets. Nesting in colonies of gulls and terns provides a protection from predators. However, large gulls themselves destroy many eider nests; therefore, only nests within the

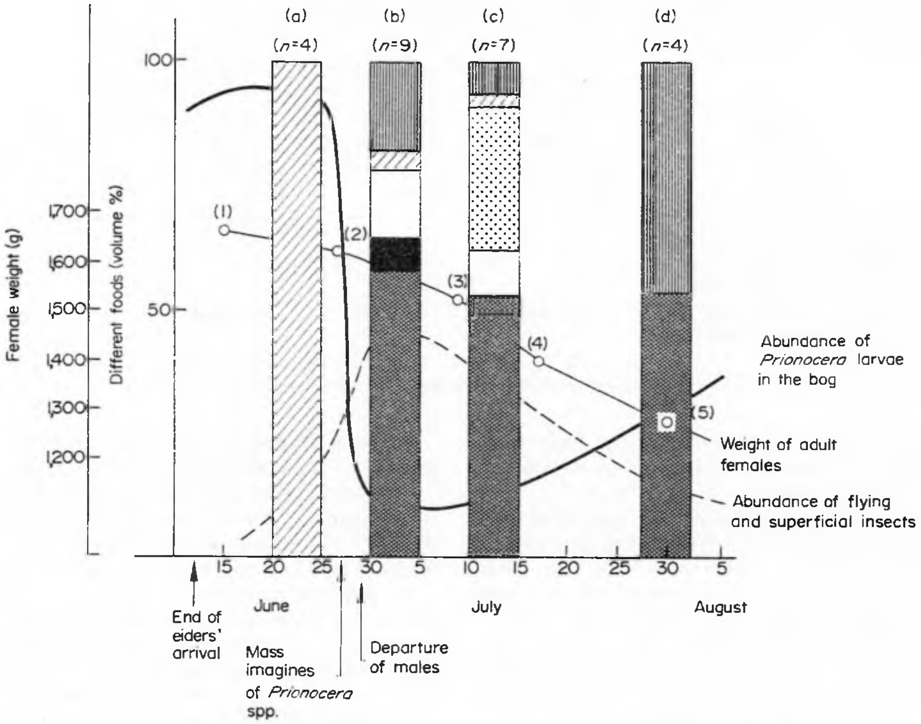

Figure 5. Seasonal changes in the diet of Spectacled Eiders and in abundance of some food items. Volume per cent of the main foods: (a) 24 June; (b) 28 June–7 July; (c) 26 July–25 August. Slant-hatched, larvae of craneflies *Prinocera* spp.; cross-hatched, caddisfly larvae; stippled, chironomid larvae; open, other aquatic invertebrates; solid, non-aquatic insects; vertically hatched, seeds of *Ranunculus pallasii.* 0—0, Curve of female weights: (1) 5–18 June, according to Uspenski *et al.*, 1962; (2) 24–29 June ($n=4$); (3) 4–12 July ($n=10$); (4) 17 July ($n=10$); (5) 26 July–5 August ($n=3$, including data by Uspenski *et al.*, 1962). ——, Relative abundance of *Prionocera* larvae in the bog. ---, Relative abundance of flying and superficial insects.

defended territories of gull pairs have a chance of surviving.

Only drakes in full plumage appear at the breeding grounds. Variations in female plumage (possibly correlated with age) are described. In 1971, nearly 50% of females did not start to breed. There was a great loss of clutches from gull predation. Many ducks had repeat nests but not more than 10–15% seemed to be successful. The first clutches averaged 5·56 eggs; all clutches, including repeated, 3·74. Population increase by the end of summer was unlikely to be more than 15–25%. Non-breeding and unsuccessful females remained during the whole of July. The bulk of the food at courtship time was larvae of crane-flies *Prionocera* spp., and from the end of June till the beginning of August larvae of caddisflies. Many kinds of other invertebrates were consumed in July, and many seeds of *Ranunculus pallasii* on first arrival in June as well as at the end of July and beginning of August. Seasonal changes in eider's diet are probably correlated with the dynamics of abundance of food items.

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Figure 6. The female Spectacled Eider returning to her nest. *A. A. Kistchinski*

The Shelduck population of the Ythan estuary, Aberdeenshire

I. J. PATTERSON, C. M. YOUNG AND F. S. TOMPA

Introduction

The Shelduck *Tadorna tadorna* is a large and conspicuous species whose spectacular moult migration has attracted much attention (Hoogerheide & Kraak, 1942; Coombes, 1950; Goethe, 1961a, 1961b). As one of the territorial ducks, the social structure and regulation of its populations pose particularly interesting problems. There have, however, been few detailed studies of local populations, an exception being Hori's (1964a, 1964b, 1965, 1969) study on Sheppey in the Thames estuary. Here the majority of breeding birds hold territories on freshwater fleets in grazing marshes and nest in hollow trees, haystacks and farm buildings in close proximity to man. The population on the Ythan estuary, Aberdeenshire, contrasts with the Sheppey one in being much further north, with the birds staying throughout the breeding season on a muddy estuary and nesting mainly in rabbit burrows among sand dunes.

The present study was carried out in separate periods by the three authors; in 1962–1964 by C.M.Y., in 1966 by F.S.T. and since 1968 by I.J.P. The aim of this paper is to describe changes in population size over this period and discuss the various population processes which might have contributed to these changes.

Study area

The Ythan estuary, 57°20′N, 2°00W, 21 km north of Aberdeen is well separated from other estuaries suitable for shelduck populations, the nearest being at Findhorn on the Moray Firth 100 km northwest and at Montrose 75 km south. The intervening coast is chiefly rocky with some sandy beaches and

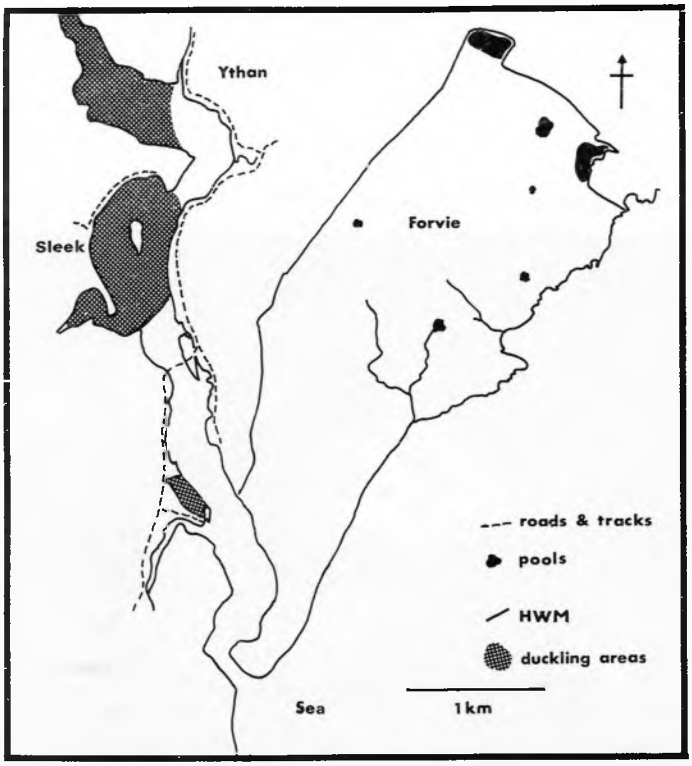

Figure 1. The Ythan estuary and Sands of Forvie National Nature Reserve, showing the areas of the former used by Shelduck broods.

only scattered pairs of Shelduck occurred there during the study.

The estuary is 7 km long and up to 0·6 km wide (Figure 1) with a mixture of muddy shores and bays, sand and gravel beaches and mussel *Mytilus edulis* beds. Roads and tracks run close to the shore along the entire length, so that all parts of the relatively narrow area can be observed easily. On the east (seaward) side is the Sands of Forvie National Nature Reserve, a complex area of dunes. Seven dune ridges are oriented at right angles to the coast stretch from the southern tip of the peninsula to the village of Collieston (Landsberg, 1955; Burnett, 1964). The dunes at the southern end are mobile and sparsely covered with marram grass *Ammophila arenaria*; towards the north there is increasing vegetation cover with extensive heather *Calluna vulgaris*. Rabbits *Oryctolagus cuniculus* were abundant in the dunes throughout the study, their burrows providing most of the Shelduck nesting sites. Temporary and permanent pools occurred in many of the dune valleys.

North and west of the estuary is mixed farmland where a few scattered pairs of Shelduck occurred on lochs and ponds.

Methods

A large part of the study was based on the case histories of individually marked Shelduck. These were caught as ducklings just before fledging by chasing them or by driving them into nets, and as adults in the winter flock by baited funnel traps (Young, 1964). A few were caught on territories and a few females were netted at the nest burrow. Each bird was given a unique ring combination of coloured celluloid (1962–1966) or 'Darvic' rigid P.V.C. (from 1968) rings. Only black, white, red, yellow, green and blue were used to avoid confusion in the field. Since the Shelducks spent much of their time on open mudflats, leg rings were easily identifiable up to 300 m. From 1969, combinations of dye spots on the white parts of the plumage, using 'Durafur Black R' a fur dye kindly supplied by I.C.I. Ltd, allowed identification of birds at greater distances, on water or in long grass.

Other techniques used in particular parts of the study will be described in the relevant sections.

The annual cycle

Most of the Shelducks were absent from the Ythan from early July until March. Recoveries of twenty-one ringed birds during this period were all from moulting areas on the northwest coast of Germany and from the southern North Sea coasts. The first Shelducks returned to the Ythan during November but numbers remained low over midwinter, in contrast with the Thames area where there were large wintering flocks which dispersed to other areas in February leaving only the breeding population (Hori, 1964a, pp. 333, 335). Marked Ythan Shelducks have been seen in wintering flocks on the Eden estuary near St Andrews where the number in late winter greatly exceeded the local breeding populations (Boase, 1959 and personal observations). It is likely that returning moult migrants first assemble in large estuaries like the Eden and later disperse to breeding areas.

Shelducks arriving on the Ythan during winter and early spring formed a loose flock usually centred on the largest mudflat, the Sleek (Figure 1) though sometimes, especially in severe weather, near the mouth of the estuary when the higher salinity nearer the sea prevented the mud from freezing. The flock was usually widely scattered while feeding but the birds roosted at high tide in a dense group on an island in the Sleek. Two Shelducks caught in this winter flock have been recovered in subsequent weeks in wintering areas further south suggesting that some birds may return to the major winter flocks, although records of colour-marked individuals showed that most birds stay continuously once they arrived. In the Sheppey population (Hori, 1964a, p. 336) adults similarly left the wintering area on the Swale channel and dispersed to freshwater pools nearer the nesting area in early spring.

During March, pairs began to leave the Sleek flock and dispersed over the whole of the muddy parts of the Ythan estuary. The establishment of territories has already been described by Young (1970a) who showed that in 1962–1964 a constant number (seventy to seventy-two) of pairs were territorial while the remainder of the population remained in a flock either on the Sleek, or, later, on the upper parts of the estuary. Most of the flock birds were 1- or 2-year-old pre-breeders but some were paired adults which quickly occupied territories when the owners were removed. This contrasts with Hori's study where, after a similar dispersal of adults to territories on freshwater fleets, the remaining flock was made up entirely of immature birds and unpaired adult males.

Concurrently with the establishment of territories, pairs from the Ythan began to visit the Forvie sand dunes (Figure 1). Soon after dawn, single pairs left the estuary and flew or walked around the dunes visiting burrows for some time before usually assembling in groups, as described by Young (1970b). He called these groups 'parliaments' after Coombes (1949) although the latter may have been referring to groupings on feeding grounds. Young (1970b) found that the same individuals were seen at the same place on several occasions over periods of some weeks. Hori (1964a) found similar groups with consistent membership, which he called 'communes', in the nesting area and showed that the association between the pairs persisted throughout incubation; birds which lost their eggs continued to visit the same nesting area until the last pair in the group hatched their brood. Young (1970b) also found that pairs which failed to hatch ducklings were more likely to be seen in gatherings in the nesting area than were successful birds.

During the incubation period the male remained alone on the estuarine territory where the female joined him to feed when she left the nest. Females which lost or deserted their clutches returned to their territories which were maintained for some time before the pairs abandoned them and joined the non-territorial flock. This flock gradually increased until the general departure on moult migration in early July. The flock also contained at this time numbers of 1-year-old birds which arrived during the late breeding season.

Successful pairs took their young directly to the nearest part of the estuary and then swam with them to their feeding area. This was almost always in a different part of the estuary from the former territory site although the parts of the estuary used by broods included many also used for territories (though most of these were abandoned by the brood stage). The parents, particularly the males, vigorously defended an area round the brood against other Shelduck and were also seen to attack Wigeon *Anas penelope*, Redshank *Tringa totanus*, Common Tern *Sterna hirundo* and Eider *Somateria mollissima* as well as potential predators such as the Herring Gull *Larus argentatus*.

Crêches of young Shelduck have been widely reported (Kirkman, 1913; Boase, 1938, 1959, 1963; Coombes, 1950; Gillham & Homes, 1950; Bannerman, 1957; Isakov, 1952; Hori, 1964a, 1964b, 1969). These were also seen on the Ythan, though the group size was smaller (maximum twenty-seven) than at other places. Crêches were detected by the mixing of young at different stages of plumage development within one brood (criteria described by Gollop & Marshall, 1954), and by dye-marking ducklings. Water-soluble food dyes were injected into each egg of selected clutches about 4 days before the expected hatching date, using the method developed by Evans (1951). Ducklings with their down dyed red or blue could be distinguished in the field for at least 4 weeks.

Crêching was seen to occur when broods came together while feeding and as the parents interacted. Afterwards, in many cases, some or all of the young from one brood joined the other parents. Most crêches were seen on areas like the Sleek where several broods occurred at the same time with overlapping ranges. In 1962 four crêches were detected (from twenty-seven broods hatched), in 1963, six from twenty-two broods and in 1964, none from eighteen broods (Table 1). On Sheppey, Hori (1964a, 1969) found that most broods formed crêches

Table 1. Shelduck brood crêches on the Ythan

Date (day, month, year)	Total young	Age groups present			
		Ia	Small Ib	Large Ib	Ic
16.6.62	4	3	1	.	.
20.6.62	5	2	3	.	.
20.6.62	4	2	1	.	1
14.7.62	10	.	3	.	7
1.7.63	19*	.	11	.	8
13.7.63	10	3	10	.	.
22.7.63	5*	.	2	3	.
22.7.63	14*	.	14	.	.
23.7.63	27*	27	.	.	.
25.7.63	18	.	8	2	8

* Included colour-marked young.

with only a few of the parents attending young. The difference may have been caused by the greater concentration of broods on Sheppey, where most young were taken to one area rather than to several as on the Ythan.

After broods mixed, the behaviour of the parents varied; some showed no obvious reaction to the change while others attacked the ducklings by rushing at them and pecking. These attacks were sometimes directed entirely at the strange ducklings, as in the case of one pair with unmarked young which attacked red-dyed ones in the mixed brood. In contrast on 11 June 1969, after two pairs with young of different ages had been forced together by human disturbance leaving one pair with all the young, the male and female attacked both their own and the strange (larger) young indiscriminately for 5 minutes before the other pair, who had flown off, returned. When they called, their own young ran to them. Attacks by parents on their own young as described by Hori (1964a, 1964b, 1969), have not been seen on the Ythan in any brood without evidence of prior mixing.

Parents which lost young by brood amalgamation or disappearance rejoined the flock in early July. Parents with broods stayed until the young were fledged and then migrated in August, leaving only the juveniles which formed a scattered flock until they gradually dispersed. The Ythan was then generally empty of Shelduck during October and November.

Population size

The Ythan Shelducks formed a convenient population unit for study, being over 75 km away from other similar groups at Montrose and Findhorn. However, in such a mobile species there was likely to be interchange between the Ythan birds and those on neighbouring estuaries, as well as a through passage of returning migrants in spring.

The birds were counted by moving systematically up the estuary by bicycle or car from the river mouth, scanning each section. The narrowness of the estuary and proximity of roads made it easy to count these conspicuous ducks. Counts were made at low tide, when the birds were most dispersed, and after mid-morning when few were likely to be in the nesting area. A watch was kept for flying birds moving from the counted to the remaining area or *vice versa*. During the incubation period, the number of sitting females was estimated by counting solitary males on territories. Most of these were individually recognizable by rings or by being consistently at the same spot, but a few single males near the non-territorial flock may have been unpaired birds. In 1962–1964 and 1968, counts were restricted to the estuary but from 1969 the birds in the surrounding area were counted by one person traversing the Forvie dunes and another visiting the known lochs and pools in the farmland while a third counted the birds on the river.

Changes in number were measured both within and between years.

Seasonal changes in number

The total number of adult Shelduck on the Ythan estuary rose rapidly in each year from December to April, after low numbers in November (Figure 2). A fluctuating level through April, May and June was followed

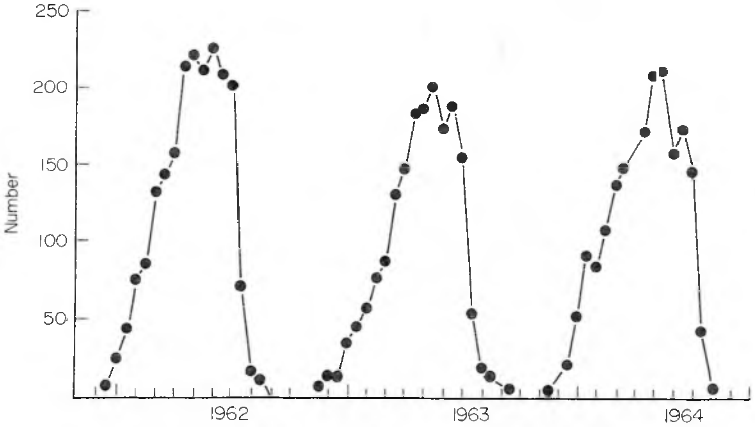

Figure 2. Seasonal changes in the total number of adult Shelduck on the Ythan estuary.

by a very rapid decline with the moult migration in early July.

Shelduck are thus virtually summer visitors to the Ythan, with the whole population present in the area for only 3 months. This contrasts strongly with more southern populations such as that on Sheppey (Hori, 1964a) where the local population, although mixed with wintering birds, appear on estuary shores near the breeding area from early winter. Even in the Forth estuary, only 155 km south, some stocks reach their breeding-season levels of abundance as early as December (Jenkins, 1972).

Changes in population between years

The mean number of Shelduck present in May of each year, when the population appeared to have reached the seasonal peak and to be relatively stable, was used to measure annual changes.

There was a slight but non-significant drop from May 1962 to May 1963 (Figure 3) with only slight recovery in 1964. By 1968 the population had declined markedly. In 1969, the mean number of birds on lochs and pools away from the river made up 12% of the total count; when these are excluded, to make the count comparable with the preceding years, the 1969 total shows a further slight decrease from 1968.

The drop from 1962 to 1963 may have been caused by heavy mortality in the exceptionally severe weather, when large numbers of Shelduck were found dead (Dobinson & Richards, 1964; Harrison & Hudson, 1964). Hori (1964a) also found a decrease between these 2 years which he attributed to the severe weather. No similar winters occurred to account for the decrease from 1964 to 1968. There were reports of poor breeding in at least some of the intervening years but no counts of fledged ducklings were made.

Breeding

Nests

Nest sites were found by watching ducks returning from feeding to resume incubation, and by searching for burrows with traces of down on the vegetation around them. Almost invariably the birds used rabbit burrows with a few nests in natural cavities behind turf overhanging low banks. Most burrows had well-overgrown entrances and the nest was usually about 1 m and rarely beyond 2 m inside. Of thirty-five sites found in 1962–1964, three were used twice (by different birds) and two others showed signs of having been used before, with traces of old down and egg shells below the nest. Shelduck on Sheppey (Hori, 1964a) used sites in hollow trees, haystacks and under isolated buildings as well as burrows, and many of the sites were used every year, often by the same birds. This difference may have been caused by a shortage of rabbit holes in a generally low-lying area of grazing marshes with the water table near the surface compared to the very high density of available burrows in the Forvie dunes, or it may indicate a difference in nesting 'tradition' in the two populations.

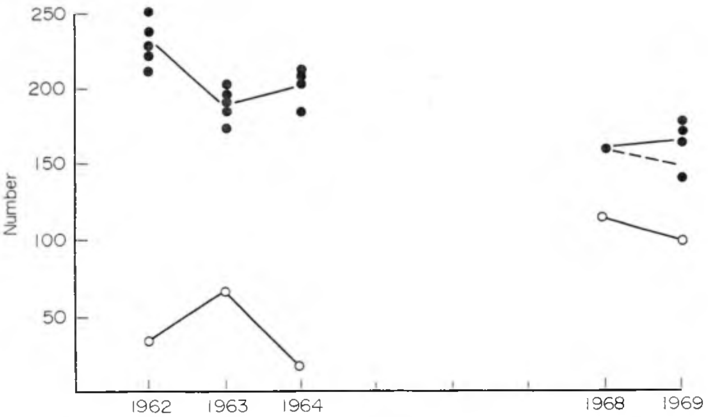

Figure 3. Changes in the Ythan population between years. The points show the total birds present in separate counts in May and the solid line joins the means. The dotted line indicates the 1969 mean total when birds away from the river are excluded. ●, Total adults; O, young fledged.

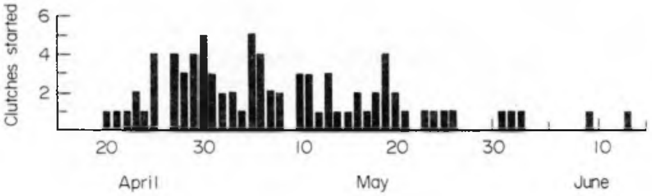

Figure 4. Date of laying the first egg of each clutch.

Laying dates

The date on which the first egg of a clutch was laid was estimated by back-dating. This was straightforward in the few nests where laying was still in progress when the nest was found, since the interval between eggs was 1 day. The incubation period measured in five such nests averaged 28·8 days (26–31) which agrees well with Hori's (1964a) observation of 30 days in six nests and 31 in another. In nests where the hatching date was known, 29 days' incubation plus 1 day for each egg, were subtracted to give the laying date. Some clutches were not detected until after hatching; in these a further 1 day of brooding in the nest (the mean of four nests observed at hatching), plus the estimated age of the young when first seen, were subtracted. There were several errors especially in the last method; young may not have been seen on the day they left the nest, they may have been in the nest for more than a day (Hori, 1964a), their age may have been estimated wrongly, and any losses of eggs or young before being seen would erroneously delay the estimated laying date. Further, the laying dates of the successful pairs, estimated from the appearance of their broods, may have differed from those of pairs which lost their eggs. However, Hori (1964a) found that the distribution of laying dates derived by back-dating from the appearance of broods agreed well with that from direct observation of nests. The results from all the methods have been combined in Figure 4.

The first egg was laid around 20 April in 1962 and 1964, slightly later in 1963, with most clutches started in the first 2 weeks of May. Laying continued up to 12 June (1964), showing a very wide spread of laying date even though there was no evidence of repeat clutches by birds which failed. Hori (1964a) found a very similar laying period of 25 April to 19 June with a peak from 7 to 23 May, showing that the later arrival of Shelduck in Aberdeenshire did not result in later breeding than in the south.

Proportion of the population which bred

The difficulty of finding Shelduck nests in an extensive area of sand dunes with abundant burrows made it impossible to detect breeding directly by finding nests except in a few pairs. Instead, breeding was assumed in pairs where the males were seen alone, with the female appearing only occasionally, since preliminary observation and other studies of Shelduck (e.g. Hori, 1964a, 1969) showed that pairs stay together in all their activities prior to laying and incubation. This method is, however, very sensitive to the frequency of observation. If clutches are lost during laying or early in incubation, the short absences of the female will be detected only by frequent or prolonged observation of the pair and such pairs might be regarded as non-breeders.

Frequency of observation varied between 1962–1964 and 1966. In the first period all the pairs on the estuary were checked at fairly long intervals; in 1966 a sample of 36% of the pairs, those which were particularly easy to observe from roads, were selected and checked at least once daily. In both periods, whenever a male appeared to be alone, the whole adjacent area of shore was searched particularly thoroughly for his female. The possibility of a neighbouring female being erroneously recorded as the mate was reduced by identification of individuals by rings, dye or variations in female facial plumage.

None of the adult males from pairs without territories was ever seen consistently without its mate or accompanying young in any of the 4 years. It is of course more difficult to detect the absence of the female in pairs without a fixed territory and so breeding is less likely to be detected. However, all females seen flying from the nesting area to the estuary joined territorial males and all identifiable pairs which hatched ducklings were known to have been territorial, so it is unlikely that any non-territorial pairs did breed and certainly none was successful.

Among territorial pairs, many more males were seen alone in 1966 than in 1962–1964

Table 2. Proportion of territorial pairs in which the male was seen alone on his territory at least once

Year	Territorial pairs	Male seen only	% seen alone
1962	71	44	62·0
1963	70	32	45·7
1964	72	31	43·1
1966	27*	23	85·2

* Sample selected from the total of seventy-five pairs. χ^2 values comparing each year with 1966: 1962, 4·87; 1963, 12·36; 1964, 14·06; 1962–1964 combined, 11·79: all significant.

(Table 2) and it is important to establish whether this was a real difference or one resulting from the difference in technique described earlier. The results differ in the direction expected; fewer pairs were recorded as breeding in the years (1962–1964) when observation frequently was lower. The efficiency of the method in the two periods can be tested by considering pairs with ringed males which were later seen with ducklings, and finding what proportion of such successful pairs would have been detected before hatching by the 'male seen alone' technique. Since the females would have been absent for much of the time over the whole laying and incubation period of 30–40 days they had the highest chance of being recorded absent. In 1962–1964 just under half of the successful males were seen alone during laying and incubation by the female (Table 3), whereas in 1966 all of the successful males in the selected sample were seen alone at least once. Since the proportion of successful pairs 'missed' in 1962–1964 was similar to the proportion of the total classified as non-breeders, it is likely that the difference in results was due to the difference in method and that all territorial females did in fact lay in all years. However, the one season of more frequent observation may have been unusual, so it would be very desirable to test this method further. Hori (1969), through finding a large number of nests by searching and observation of flight paths of females, also suggested that most or all of the territorial pairs laid.

Table 3. Proportion of ringed male Shelduck, later seen with broods, which were seen alone on territory at least once during the laying and incubation period of the female

Year	Number of successful males	Number seen alone	% seen alone
1962	13	4	30·8
1963	10	6	60·0
1964	8	4	50·0
1966	11	11	100·0

χ^2 values for each year compared with 1966: 1962, 4·06; 1963, 5·30; 1964, 6·97; 1962–1964 combined, 7·45; all significant.

Clutch size

Clutches varied from five to eleven eggs with an overall mean of 8·1 (Table 4). Clutches in 1962 were slightly but not significantly higher than in 1963 and 1964. Two clutches, each of which appeared to have been laid by two females, have been excluded. In one, eleven had been incubated for around 20 days and three others for only a few days; in the other, with seven eggs, a second nest was started in the same burrow and the two clutches became scattered and mixed. These nests were eventually abandoned. Such multiple nesting, in only two out of thirty-two completed clutches examined, was less frequent than on Sheppey where Hori (1969) suggested it in thirty-five out of 128 clutches ($\chi^2 = 6·41$, $P < 0·05$). He used a criterion of over twelve eggs in a clutch as an indicator of multiple nesting, since in sixty clutches over twelve had evidence of more than one female, lacking in sixty-nine isolated nests, all with clutches under twelve. In addition some of the clutches under twelve may have been multiple as seven normal clutches of three to six eggs were recorded. The slightly higher mean clutch size of single clutches (7·6–9·3) on Sheppey might be explained by the generally higher likelihood of multiple nesting there than on the Ythan. This in turn may, with the more frequent re-use of the same nest sites on Sheppey, reflect a more restricted supply of nest sites.

Table 4. Clutch size of Shelduck on the Ythan

Year	Clutches	Range	Mean	SE
1962	13	5–11	8·7	0·4
1963	11	6–9	7·6	0·2
1964	6	7–9	7·7	0·3

Incubation

Visits by the female to the next burrow were recorded by placing in the entrance a treadle switch connected remotely to an electrical pen recorder. Inward and outward movements were distinguished by occasionally watching the female arrive or by checking whether the most recent tracks were entering or leaving the burrow. Incubating females left the nest at any hour during daylight and showed no clear diurnal or tidal rhythm; they were rarely off at night. In a particularly complete example from many similar but shorter records, the bird left the nest three to six times a day for a total of about 4 hours, though this varied even for the same female in successive days (Table 5). Hori (1964a) found that female Shelduck on Sheppey left the nest less often (one to three times, usually twice) and for a shorter total time (3·1 hours) and he emphasized the difficulty experienced by the birds in returning unobserved to nests near human habitation, rarely a difficulty on the Ythan.

Table 5. Frequency and duration of periods off the nest by one female Shelduck

Date (June 1963)	Number of times off	Total time off per day (hours)
5	3	3·25
10	4	4·50
11	5	3·75
12	5	4·50
13	4	3.50
14	3	2.75
15	4	7·00
17	5	4.50
18	5	4·75
19	6	4·25
21	5	4·75
Mean	4·46 ± 0·28	4·31 ± 0·33

Hatching success

Nests were difficult to observe regularly because the females were likely to desert after being disturbed; over one third of the females did not return after the nest was first examined (Table 6). Excluding desertion due to disturbance, 76% of clutches hatched (Table 6). This may well be an over-estimate since the clutches lost by desertion might have been those most likely to fail from other causes. Although the sample was small, there was little variation in the hatching success of clutches between years. It was not possible to calculate the hatching success of the individual eggs since the dye-injection technique used on many of the clutches appeared to cause mortality in a number of eggs. Hori (1964a) found that 69% (1963) to 71% (1962) of all eggs laid hatched successfully, but he regarded this as unreliable and an over-estimate of success. Of the six Ythan nests lost, two were deserted before the clutch was completed, two were associated with multiple nesting (see above) and two were taken by predators, tentatively identified by tracks as Weasels *Mustela nivalis* or Stoats *M. erminea*.

Another estimate of the hatching success of clutches can be obtained from the number of broods of day-old ducklings seen on the river, compared to the number of pairs which bred. This will give a minimal value since some broods may be lost before being recorded. If it is assumed (see above) that all territorial females laid eggs, between 25% (1964) and 38% (1962) of them were successful

Table 7. Hatching success of territorial Shelduck pairs on the Ythan; from counts of day-old broods

Year	Territorial pairs	Number seen with broods	%
1962	71	27	38·0
1963	70	22	31·4
1964	72	18	25·0
1966	75	28	37·3
(1966 sample	27	11	40·7)
1962–1966	288	95	33·0

None of the differences is statistically significant.

Table 6. Hatching success of Shelduck clutches on Forvie; from observation of nests

Outcome of nest	1962	1963	1964
Hatched some young	8	8	3
Deserted after being examined	5	6	3
Clutch not completed	.	2	.
Taken by predators	1	.	1
Involved in mixed clutches, abandoned	1	1	.
Total	15	17	7
Total, excluding those deserted	10	11	4
% of these clutches hatching	80	73	75

in bringing broods to the river (Table 7), a much lower proportion than that suggested by the nest observations (above). The 'brood-count' method probably underestimated success but was likely to be closer to the real value than estimates from nest observations.

Brood size at hatching

The number of ducklings in broods when first seen on the river, compared with the mean clutch size, gives an estimate of losses from successful clutches between laying and appearance of the brood. There are a number of errors in this method; broods may not be seen on their first day, giving an undefined period in which losses are being estimated: broods which are lost before being seen may be different in size from those which survive; and broods may amalgamate before being seen.

The mean brood size varied from 6·4 to 7·1 (Table 8) although none of the differences between years was statistically significant. In each year (1962–1964) the mean brood size was lower than the mean clutch size (Tables 4 and 8) but the largest broods seen (Tables 8 and 9) were larger than the biggest clutches, suggesting that some amalgamation of broods had occurred before they were first seen, so that brood size may have been overestimated. Hori (1969) recorded mean brood sizes between 6·1 and 7·8 (excluding those broods with more than twelve ducklings as being from mixed clutches or broods). Mean brood size on Sheppey was from 0·8 to 2·5 smaller than the mean clutch size in the same year.

Table 8. Sizes of broods when first seen

Year	Number of broods	Range of brood size	Mean brood size
1962	27	2–14	6·4
1963	22	3–14	7·1
1964	18	2–15	7·0
1966	28	2–15	6·6

Duckling survival

Most broods were individually identifiable by having at least one marked parent, or by size, age of ducklings and position on the river. In 1962–1964 the number of young surviving in each brood was recorded at least once in each plumage stage (Gollop & Marshall, 1954) until fledging. In 1968–1969 the broods were not checked in detail but the young were counted just before fledging.

Ducklings disappeared most rapidly in the first 2 weeks (Table 9, Figure 5), and most of those which reached 30 days of age went on to fledge. Very few ducklings were found dead; most disappeared between counts, and the cause is unknown.

Table 9. Size and survival of Shelduck broods on the Ythan in the years 1962–1964

		Age class and (age in days)							
Brood size	No. of Broods	Ia (1–5)	Ib (6–12)	Ic (13–18)	IIa (19–25)	IIb (26–33)	IIc (34–43)	III (44–60)	Flying (60+)
1	1	1	1	.	.	.	.	.	.
2	6	12	8	5	3	1	1	1	1
3	3	9	8	5	5	5	5	5	5
4	8	32	23	7	4	4	4	4	4
5	6	30	14	7	7	2	.	.	.
6	9	54	27	14	13	13	13	13	13
7	7	49	35	15	14	10	7	6	6
8	10	80	58	40	33	14	8	8	8
9	4	36	35	29	29	25	25	25	25
10	4	40	30	29	26	22	21	18	18
11	3	33	14	10	1	1	1	1	1
12	1	12	3	2	.	.	.	.	.
13	1	13	.	.	.	.	.	.	.
14	3	42	39	33	38	35	30	30	30
15	1	15	5	3	.	.	.	.	.
All	67	458	300	199	173	132	115	111	111
1962	27	173	102	65	58	46	35	32	32
1963	22	159	140	97	93	66	65	64	64
1964	18	126	58	37	22	20	15	15	15

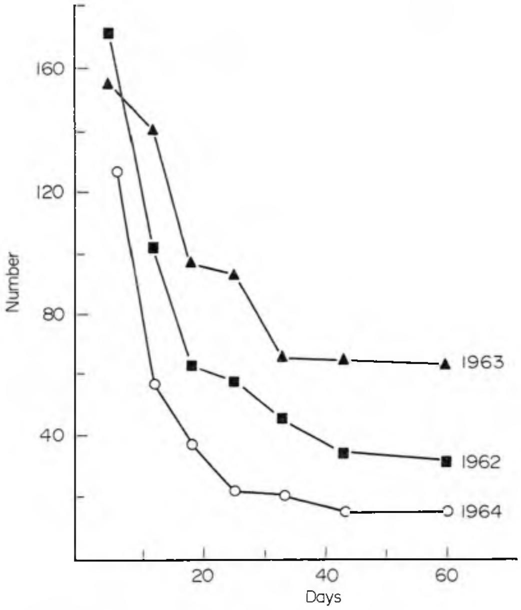

Figure 5. Survival of ducklings on the Ythan. The points show the number of ducklings alive at each age. Dates from Table 9. ▲, 1963; ■, 1962; O, 1964.

In the 1962–1964 period most young were fledged in 1963, when there was a much lower rate of loss over the first 2 weeks of life. The proportion fledging was significantly higher in 1963 than in 1962 ($\chi^2 = 20{\cdot}15$, $P < 0{\cdot}01$) and 1964 ($\chi^2 = 29{\cdot}31$, $P < 0{\cdot}01$); the latter 2 years were not significantly different. The production of fledged young varied from 1·2 to 1·9 per territorial pair with an overall mean of 1·5 per pair. It would appear from Table 9 that the broods of intermediate initial size were the most successful. Thus, 38·6% of the ducklings in broods of six to ten fledged, as opposed to 26·9% in the eleven to fifteen broods and 11·9% in those of one to five.

On Sheppey, breeding was also more successful in 1963 than in the other years of study.

In both 1968 and 1969 on the Ythan the total number of young fledged was considerably higher than in 1962–1964, in spite of the lower total population in the later years. The number of territorial pairs was not determined in 1968–1969 but was probably lower than in 1962–1964, so that production of fledged young per territorial pair may have been much larger. It is not possible to compare these values with Sheppey where the ducklings hid in deep vegetation well before fledging and so the number fledged could not be counted directly (Hori, 1964a).

Mortality

The disappearance of marked birds was used to estimate their mortality rate, although such losses could have included movement of surviving birds to other populations. Evidence of emigration will be considered below but in any case, death and emigration affect the local population in the same way.

To calculate losses for each year, those marked birds which were ringed or recorded on the Ythan between December and July were taken as a sample of birds known to be alive at the start of the season. There may have been some bias in the newly ringed birds, since those marked later in the winter had already survived part of the year being considered.

Of this sample, those birds seen in the next season (or in subsequent years) were known to have survived the 12-month period from the start of one season to the start of the next. The same procedure was used for the 2-year interval from 1964 to 1966 and the 3-year period from 1966 to 1969. Duckling survival was calculated for the period from their ringing date just before fledging until their return in the subsequent season. These estimates of survival are minimal, since some surviving birds may not have been recorded.

The survival of adults varied only from 66·0 to 80·2% between years (Table 10).

Table 10. Survival of marked adult Shelduck

Years	No. alive at start of year a	b	Survival per year (%)
1962(a)/1963(b)	111	89	80·2
1963(a)/1964(b)	163	119	73·0
1964(a)/1966(b)	107	57	73·0
1966(a)/1969(b)	87	25	66·0

Boyd (1962) estimated the mean annual mortality rate of adult Shelduck, over Britain as a whole. to be 20%, which is in agreement with the Ythan estimate.

Only 13% of marked ducklings were ever seen on the Ythan in subsequent years (Table 11), all but one of them being seen first as 1-year-olds. It is possible that more of this age group moved to other populations but so far none has been recovered elsewhere in the breeding season.

Table 11. Survival of marked ducklings

Year	Number of ducklings ringed	Number seen in subsequent year	%
1962	15	0	0
1963	32	6*	18·8
Total	47	6	12·8

*One not seen in 1964 but was seen in subsequent years.

Movement

Immigration into the Ythan population was inherently difficult to detect since very few Shelduck in adjacent populations were ringed. There was some evidence of emigration; on 21 May 1969 twenty-seven Shelduck were seen leaving to the northwest, towards the Moray Firth and a further four left in the same direction 6 days later. Yearlings were seen in both flocks. Several searches of populations up to 30 km beyond Inverness revealed only one Shelduck previously ringed on the Ythan, a male apparently alone on territory near Inverness on 12 May 1970. This bird was ringed as an adult on the Ythan in March 1965 and had not been seen there in the intervening years. It is possible that this bird and those seen leaving, were Shelduck from more northerly populations which stopped for some time on the Ythan in transit. No marked birds which had been resident throughout a breeding season on the Ythan have been recorded alive elsewhere in subsequent years. The only Ythan adult recovered dead in another breeding area in the breeding season was found on 14 June 1963 only a short distance from the Heligoland moulting area and so may well have been an early moult migrant.

Limitation of the population

Although the study so far has been too short for definite conclusions to be drawn about the factors limiting the size of the Ythan population, it is possible to arrive at some hypotheses.

Adult survival was high, and varied relatively little between years even though the population size changed. It is probable that much of the mortality occurred in winter away from the Ythan, so that this factor was unlikely to be important in limiting the local population in relation to its environment.

Immigration and emigration were difficult to study. No Ythan residents were found to have moved elsewhere but it is possible that migrants returning north may stop for some time on the Ythan and thus provide a pool of potential settlers so that this factor must be left for future assessment.

The production of fledged young varied considerably between years and was inversely related to population size in the same year (Figure 6). The study has been too short to show whether breeding output affects subsequent population size but the low survival and return (Table 11) of the small number of young produced in 1962–1964 (Figure 5) was clearly inadequate to replace the annual loss of adults. Although the deficit may have been made up to some extent by immigration, it may have been a cause of the lower population in 1968.

A first limitation on the number of young fledged was set by the number of pairs able to obtain territories, since there was no evidence of breeding by non-territorial adults. The number of territories was strikingly constant from 1962 to 1966 but was probably lower in 1968–1969, raising the

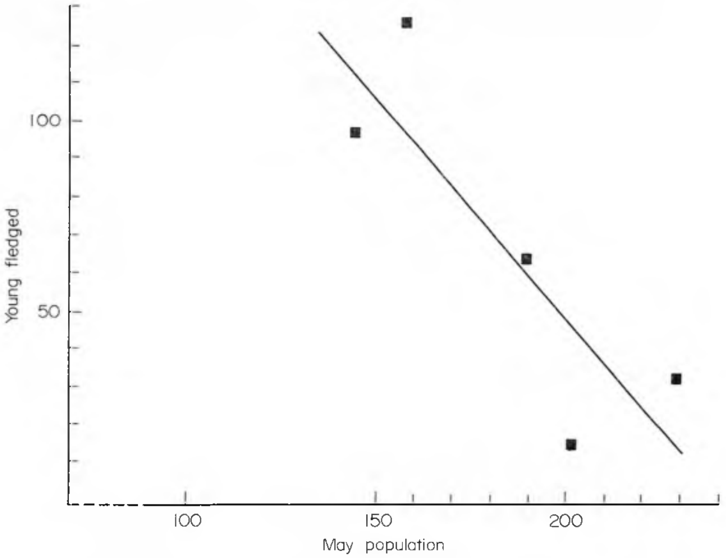

Figure 6. The relationship between the population size in May (river only) and the number of fledged young produced. The line is the calculated regression; $y=274{\cdot}7-1{\cdot}13x$, $r=0{\cdot}841$, $(0{\cdot}10<P>0{\cdot}05)$.

question of the factors limiting the number of territories, discussed by Young (1970a).

Clutch size varied relatively little, either between years or between the Ythan and Sheppey populations. Losses of complete clutches, although also not very variable, were high and accounted for about two thirds of the total loss from egg laying to fledging. The cause of this considerable depression of breeding output is unknown.

Duckling mortality in the first 2 weeks of life was also high and varied considerably and significantly between years. Since losses were correlated with population size in the same year they could potentially regulate the population, although it is not yet possible to show the effects of changes in breeding output on subsequent population size.

Future work must measure changes in population size and breeding over a longer period and determine the cause of the low and variable output, concentrating on the limitation on the number of breeding (territorial) pairs, and on the causes of the high level of clutch loss and the high mortality of ducklings in their first 2 weeks.

Since the number of territories was fairly constant most of the variation in population size was associated with changes in the number of flock birds. The decrease in the number of young fledged with increasing population size (Figure 6) thus suggests an effect of these non-breeding flock birds on the breeding output of the territorial birds. There are several ways in which the two categories might interact, by competition over food, by behavioural interaction on the estuary or nesting area or by direct interference with breeding. These possibilities will be tested in a more detailed study started in 1970.

Summary

The Shelduck *Tadorna tadorna* is virtually a summer visitor on the Ythan Estuary, Aberdeenshire, with most of the local population absent from the moult migration in early July until all have returned in April. The mean population in May dropped from 210 in 1962–1964, to 160 in 1968–1969. Breeding success was low, with 24% of clutches lost and 76% of ducklings lost between hatching and fledging. 87% of fledgelings failed to return after their first year dispersal. This very low recruitment was inadequate to replace annual adult mortality of 20–34%, but there is some indication that breeding output was better in years with a lower May population.

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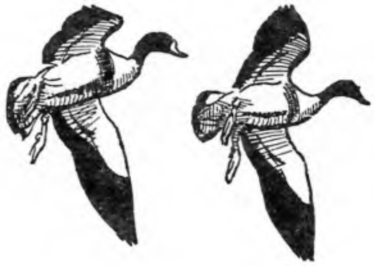

Criteria for ageing embryos of the Eider

MARTYN L. GORMAN

Introduction

It is often important, in the study of wildfowl breeding ecology, to be able to determine how long individual birds have been incubating. This can be estimated by shining a bright light through eggs from the bird's clutch (Hanson, 1954; Weller, 1956). However, the accuracy with which the embryos within can be aged through such 'candling' becomes progressively lower the further incubation is advanced. By opening the egg and examining the external appearance of the embryo much more precise estimates can be made. These require comparisons with a series of embryos of known age, and the necessary descriptions for the Eider *Somateria mollissima* are presented in this paper.

Material and methods

The data were collected during a study of the breeding biology of a population associated with the Sands of Forvie Nature Reserve, Scotland.

The data are from two sources; eggs from nests which had been incubated for a known period; and freshly laid eggs removed to an artificial incubator maintained at 38°C.

The mean length of time to hatch eggs does not differ significantly between eggs in nests and in artificial incubators and thus the rate of development is comparable between the two sets of eggs. In the case of eggs incubated in the nest, development was timed from the date on which the last egg of the clutch was laid. The female remains at the nest after laying the penultimate or prepenultimate egg of the clutch. Proper incubation does not begin, however, until the last egg is laid; in this way all the eggs develop together and indeed usually hatch within twelve hours of each other.

The embryos were carefully removed from the eggs and embryonic membranes and placed in 70% ethanol for 3 weeks. They were then gradually dehydrated in an ascending series of ethanols and finally stored in absolute ethanol. This technique led to some shrinkage of tissues, but it had the advantage of hardening the specimens and rendering them resistant to handling.

Stages of development

Representative stages are illustrated in Figures 1 and 2.

24 *hours*

By the end of the first 24 hours of incubation the head fold is pronounced with the primitive knot about one third of the way back from the anterior margin of the area pellucida. The first one or two pairs of somites are recognizable as cellular condensations on either side of the primitive knot.

48 *hours*

By the end of 48 hours, the first signs of cranial flexure are apparent, the fore-brain lying at an angle to the hind-brain. The rudiments of the eye-lens, optic cup and auditory placode are recognizable. There are up to sixteen pairs of somites. In the live specimen the heart can be seen to be beating.

5 *days*

A superficial auditory pit can be seen. The limbs are apparent, the fore-limbs showing flexion at the elbow. The eye is pigmented, while a ridge of tissue representing the eyelids circles the eyes. The whole embryo is curved with the tail almost in contact with the head.

6 *days*

The auditory pit is deep and obvious. The limbs show signs of digitation, the fore-limb having a protuberance on its leading edge, the future alula. The upper mandible is apparent as a knob-like process.

7–8 *days*

The raised eyelid primordia are beginning to grow over the eye which now has up to eighteen scleral papillae. Digits are clearly defined in the hind-limbs with webbing between them. The fore-limb has two ridges representing the incipient radius and ulna. The primordia of the retrices are clearly defined although feathers are not yet to be

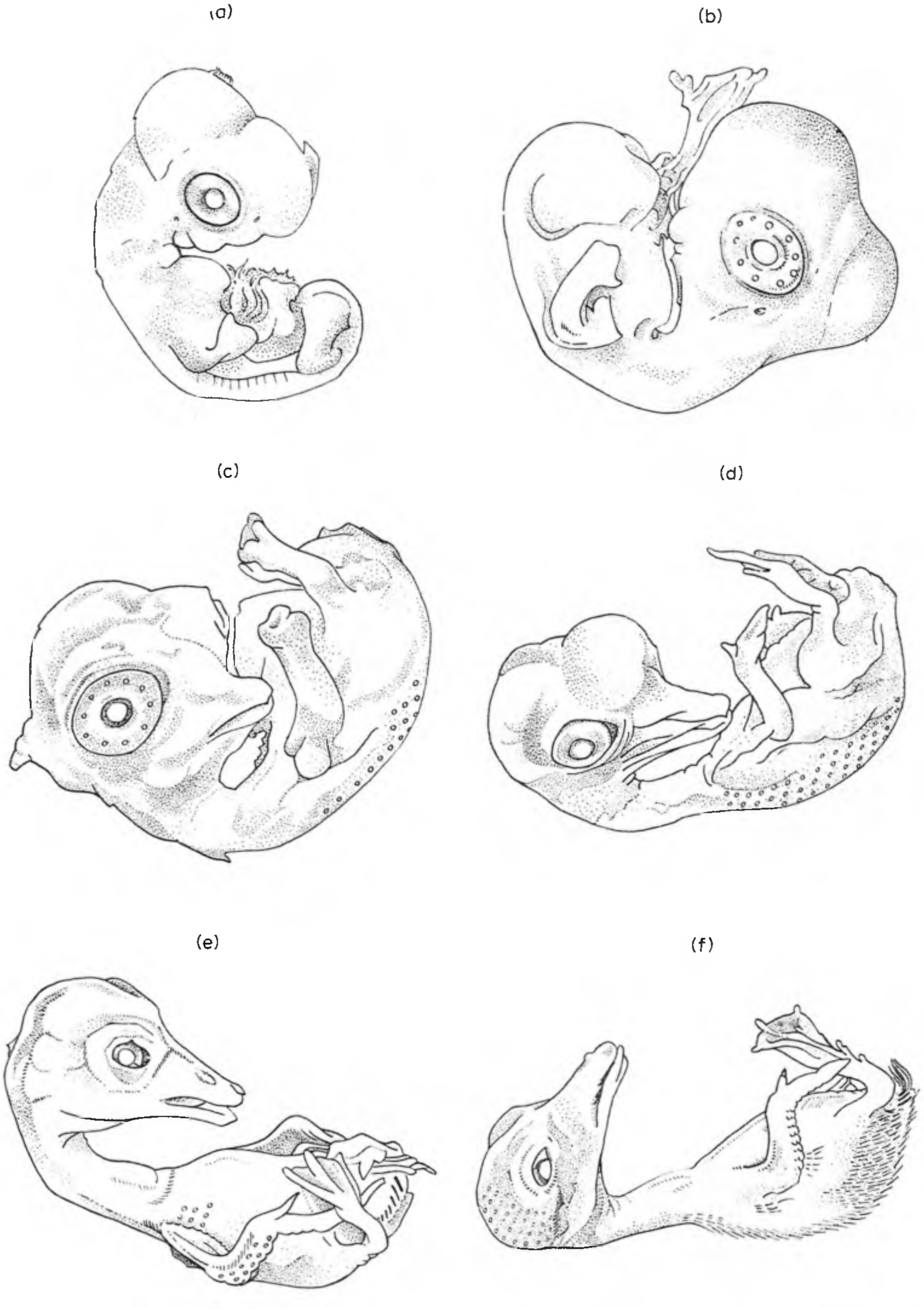

Figure 1. Stages of development. (a) 5 days incubation; (b) 6 days incubation; (c) 8 days incubation; (d) 10 days incubation; (e) 12 days incubation; (f) 13 days incubation.

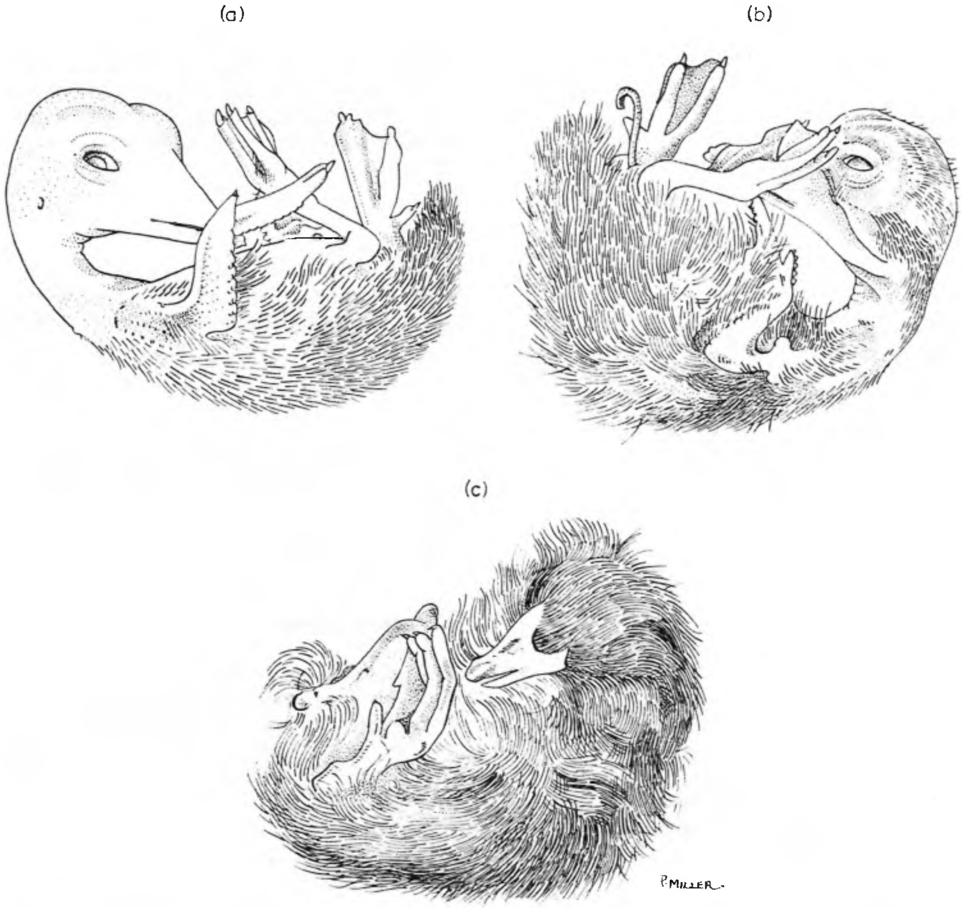

Figure 2. Stages of development. (a) 14 days incubation; (b) 15 days incubation; (c) 18 days incubation.

seen. The cerebral hemispheres and the mesencephalon are relatively less pronounced.

10 *days*

The fore-limb is well differentiated with the alula completely formed. The upper and lower mandibles are extended and form a recognizable beak. The nictitating membrane is apparent, while the eyelids have grown over the eyes to such an extent that the scleral papillae are almost obscured from view. The retrices may be pigmented. Pterylae are situated on the tail, lumbar regions and along the spine.

12 *days*

The nostrils are well developed. The retrices are pigmented and well developed, while pterylae cover the whole body apart from the head. Pigmented feather germs are just apparent on the thighs and lumbar-regions. The egg tooth is obvious. The eyelids continue to grow, the space between them now being oval in outline.

13 *days*

Pigmented feathers are present on the back, thighs and shoulders. Pterylae are visible on the head. The opening between the eyelids is now nearly the normal adult shape.

14 *days*

Growth of feathers continues. The head and neck pterylae show the beginnings of pigmentation. The claws of the hind digits are well developed.

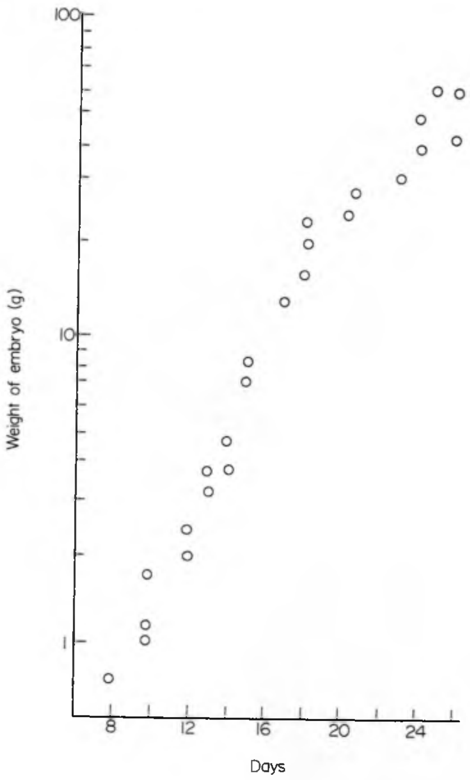

Figure 3. The growth of the embryo. Each point represents the preserved weight of one embryo, without the yolk sac.

15 *days*

The feathers of the head and neck are more highly pigmented and developed. The trailing edge of the wing is feathered although the rest of the wing is still devoid of feathers.

17 *days*

The tip of the beak, which is now obviously 'eider' in shape, is keratinized and distinct. The whole embryo is now covered in down.

18 *days to hatching*

Development from 18 days onwards consists largely of growth, little external change in morphology taking place. During this period age is best assessed from the size of the embryo (Figure 3).

Acknowledgments

This work was carried out while I was a Senior Kilgour Scholar at the University of Aberdeen. I am grateful to the Nature Conservancy for permission to work on the Sands of Forvie Nature Reserve. Finally, I am indebted to Mrs P. R. (Miller) Vander Meer for her excellent drawings.

Summary

Drawings and descriptions of various stages of development of the embryo of the Eider *Somateria mollissima* are presented.

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Brood care, pair bonds and plumage in southern African Anatini

W. ROY SIEGFRIED

In the Holarctic, migrant species of sexually dimorphic Anatini have a bond between male and female breeders that is seasonal only and breaks soon after egg-laying. The male usually deserts his mate and joins other males while undergoing the post-breeding moult. Reports of males of North American ducks accompanying their females with broods are regarded as rare exceptions (Oring, 1964).

According to Kear (1970), pair bonds are of relatively long duration in certain species of sexually monomorphic Anatini, and probably also in a number of near-tropical ones. Weller (1968) noted that those Argentinian species which retain a long pair bond are those in which males commonly attend the broods. A related general comment is that males of monomorphic southern hemisphere anatines regularly accompany their females with broods. However, there is no published account providing quantitative, comparative data on this phenomenon.

This paper summarizes unpublished records and appraises the significance of males accompanying females with their broods in six species of southern African Anatini, viz, African Black Duck *Anas sparsa*, Cape Teal *A. capensis*, African Yellowbill *A. undulata*, Red-billed Teal *A. erythrorhyncha*, Hottentot Teal *A. punctata* and Cape Shoveler *A. smithii*. For these species, there are 360 brood records on file with the African Wildfowl Enquiry. In addition to these data, my own observations cover 435 broods recorded over the last 15 years. The records derive from all parts of southern Africa, taken here as the entire sub-continent south of about 15°S.

The brood records were analysed according to number and age of ducklings, the presence of one or two accompanying adults, and in relation to place and time of breeding (Table 1). Presumably some of the records of two adults in attendance could apply to two females and not necessarily male and female, since in five of the six species only an expert can tell the sexes apart in the field. However, my own records indicate that the incidence of two females accompanying the same brood is rare, and that it is quite in order to regard the two attending adults as male and female parents.

Brood care

It is clear from Table 1 that in the Cape Teal both parents almost invariably accompany their young, and that the male normally remains with the female and the ducklings until they reach flying age. How much longer the pair and parent-young bonds may persist is not known.

The African Black Duck is the only other species, of the five remaining here, in which males have been observed accompanying females with well-grown young. However, the evidence for this is ambiguous, due to the

Table 1. **Incidence of male and female parents accompanying broods. Figures in parentheses represent numbers of broods accompanied by both parents, other figures refer to broods accompanied by females only**

Species	No. broods and age (in weeks) of ducklings				Total no. broods observed
	0–1	1–3	3–5	5–7	
A. sparsa	11	9	7	6	33
	(2)			(2)	(4)
A. capensis	3	4	1	2	10
	(40)	(28)	(15)	(13)	(96)
A. undulata	98	89	57	40	284
	(10)	(4)			(14)
A. erythrorhyncha	18	19	11	7	55
	(8)	(11)	(5)		(24)
A. punctata	5	5	5	2	17
	(1)	(1)			(2)
A. smithii	86	66	46	27	225
	(21)	(8)	(4)		(33)

species' secretive habits, its localized and 'difficult' habitat, and other factors which are responsible for a general paucity of observations and unsatisfactory, incomplete records (Siegfried, 1968). Current work, involving individually marked wild birds, indicates that the African Black Duck has a long-standing or permanent pair bond. It is probable (Siegfried, 1968), that the males temporarily desert their mates with young broods, but remain in the same general area (the permanent home range of the pair) and later rejoin the female.

There is one record of a Cape Teal male moulting wing feathers while accompanying a female with a brood. There are no observations of brood-accompanying males directly helping to care for the young. There are isolated records of brood-accompanying males driving off conspecific males in the Red-billed Teal and the Cape Shoveler, but this behaviour has not been observed in the African Yellowbill and Hottentot Teal. In the Cape Teal brood-accompanying males frequently drive away other males. However, the male's aggressiveness is usually associated with Inciting by the brood female and thus appears to be an expression of sexual behaviour rather than defence of the young. Such parental behaviour as brooding, distraction display, active defence of young and leading them to safety are performed solely by the female. Thus, males which accompany females with broods apparently do so as an extension of the pair bond through the attraction provided by the female, and the presence of the brood itself exerts no extra inducement. Of course the male's attendance could still promote survival of the young through enhanced predator detection.

The Cape Shoveler, Hottentot Teal and African Yellowbill males do not regularly accompany their mates with broods. The Red-billed Teal occupies a position intermediate between these three species and the Cape Teal. In the African Yellowbill and to a greater extent in the Cape Shoveler it is evident that some males do continue, for a limited time, to associate with their mates while their ducklings are young; the incidence of this behaviour appears to be more frequent in these species than in their North American counterparts, the Mallard *A. platyrhynchos* and Northern Shoveler *A. clypeata* (cf. Oring, 1964).

In the Red-billed Teal and Cape Shoveler (the two species with sufficient data for comparison) the parental male's presence appears to be of no advantage to the size of the brood (Table 2); which tends to bear out the contention that in these species selection for the male's attendance has operated mainly for reasons other than increased survival and success of the brood *per se*. Broods hatched early in the season were no more often attended by males than late-hatched ones, but this conclusion is based on inadequate data. The data were insufficient to compare the incidence of male attendance in different geographical areas of breeding. Such comparisons, particularly in the Red-billed Teal, might contribute much towards understanding how and why the male's behaviour varies.

Table 2. Mean brood size in relation to age and parental accompaniment. Figures in parentheses represent broods accompanied by both parents, other figures refer to broods accompanied by females only. Sample sizes are given in Table 1

Species	Mean brood size in relation to age (in weeks)	
	0–1	1–3
A. erythrorhyncha	7·16 (7·12)	6·42 (5·10)
A. smithii	7·00 (6·72)	5·12 (4·42)

Ecological synopsis

Before exploring whether relationships between parent and young can be correlated with morphological and behavioural characters of the various species, it is necessary to report certain ecological features of fundamental importance as selective pressures shaping the species. Synoptical accounts are set out below, based on personal observations supplemented by information taken from the literature. They are substantially correct in outlining the generalized condition applicable to each species, and should be regarded as no more than that. The accounts are compiled from (a) data collected in those parts of the natural range of a species in which it is most numerous, and (b) from populations which are not, or very little, affected by man-made changes to the environment. The main artificial factor, which has a considerable bearing on the ecology of southern African waterfowl, is the ever-increasing multitude of water storage and irrigation schemes; these are most developed in the Republic of South Africa. However, there are still extensive areas of southern Africa which contain pristine wetlands and their populations of waterfowl. The biologist cannot evaluate the survival value nor interpret properly the evolutionary significance of an animal's behavioural (or other) adaptations without recourse to a study of the natural condition. Moreover, recently it has become clear that features of social behaviour can vary considerably within a species, with different populations showing adaptive modifications most effectively appropriate to the ecological circumstances under which they live (Crook, 1970; Watts & Stokes, 1972).

African Black Duck

Temperate zone. Localized and nowhere numerous. Inhabits perennial rivers and streams. Sedentary with a permanent home range. Usually in pairs and never congregates into large groups. A regular, annual, seasonal breeder. Social courtship reduced.

Cape Teal

Temperate zone. Locally common. Most typically inhabits alkaline waters of short-lived nature in arid areas. Nomadic, with long-distance movements. Usually in pairs and small parties, occasionally forms flocks of 100 or more. Irregular opportunistic breeder; breeding varying with erratic and sporadic rainfall. Social courtship occurs.

African Yellowbill

Temperate zone. Wildspread and numerous. Found on most waters including flood-plains, lakes, *vleis* and large rivers in relatively well-watered regions. Resident, with local short-distance movements. Usually in pairs and small parties, though often encountered in flocks of a hundred or more. A regular, annual seasonal breeder. Social courtship occurs.

Red-billed Teal

Mainly tropical zone. Widespread and very numerous—the most numerous of the Anatini in southern Africa. Found on most waters, but especially flood-plains and lagoons in relatively well-watered regions. Mainly resident, with local short-distance movements. Also partly nomadic populations with extensive long-distance dispersal in the dry season. Usually in pairs, or small parties, but often encountered in flocks of a thousand or more. A regular, annual, seasonal breeder in well-watered areas of regular rainfall. Social courtship occurs.

Hottentot Teal

Tropical zone. Localized and nowhere numerous. Found mainly on permanent sheltered waters, but also floodplains in relatively well-watered regions. Resident, with local short-distance movements. Usually in pairs and small parties. A regular, annual, seasonal breeder. Social courtship occurs.

Cape Shoveler

Temperate zone. Locally common and numerous. Inhabits most typically shallow, seasonal *vleis* in areas of dependable rainfall. Suspected migrant with long-distance movements, though part of the population is resident. Usually in pairs and small parties, though often encountered in flocks of a hundred or more. A regular, annual, seasonal breeder. Social courtship occurs.

Pair-bond

The point made by Weller (1968), that the *Anas* males which commonly accompany females with broods are those which have relatively long lasting pair-bonds, only applies here to the Cape Teal. The African Black Duck's riverine habitat provides peculiar condition; a sedentary, anti-social way of life coupled with a long-standing or permanent pair-bond are the species' main behavioural adaptations (Siegfried, 1968). The male usually does not accompany his female with the brood.

Although much of southern Africa is either arid or semi-arid, receiving irregular and unpredictable rains, there are only two anatids typical of these areas—the Cape Teal and the Cape Shelduck *Tadorna cana*. The rest of the waterfowl community tends to be concentrated in the better-watered areas of either the tropical or temperate zones (Siegfried, 1970). In the Cape Teal it is assumed that the long-standing pair-bond is related (though not exclusively so) to the species' need to take advantage of unpredictable breeding opportunities. Non-breeding Cape Teal, paired as well as unpaired birds, gather together on more permanent waters where they take part in social courtship the whole year round. Not only are new pair bonds formed but existing ones are continually tested and reinforced, maintaining the birds in an almost constant state of synchronized readiness for breeding. It is necessary for the members of a pair to travel together and to be ready to establish territory and initiate nesting early in response to the erratic presence of short-lived habitat. This does not, however, entirely explain why the pair bond remains intact once incubation has started.

On a basis of species counts alone, in southern Africa generally, there are at least four times as many potential predators on waterfowl nests than there are in most of the Holarctic region. In the arid and semi-arid areas Cape Teal often construct their nests in a minimum of cover. In addition to predators, flash flooding or rapid drying up of breeding water commonly contribute to the destruction of eggs and ducklings. The Cape Teal, to realize its maximum reproductive potential, must be ready not only to nest early, but, if unsuccessful, to make repeated attempts at breeding and the short-lived habitat may not permit time for renewed courtship, re-pairing and establishment of territory following on nest or brood destruction. The pale grey plumages of adults and downy young blend well with the brine-encrusted saline pans, devoid of emergent cover, which are preferred breeding habitat. Broods are perhaps relatively more vulnerable to predators when feeding along these open shorelines, and the presence of both parents probably improves detection of predators and enhances survival of the young.

In the African Yellowbill social courtship and pair formation tend to occur seasonally (Rowan, 1963). This is more especially true in the Cape Shoveler (Siegfried, 1965). However, casual observations give the impression that the incidence of these behaviour patterns is considerably less compressed in time and less intense in rate of performance than in their northern counterparts, the Mallard and the Northern Shoveler. In the southern species there is opportunity for repeated social courtship and breeding over a relatively extended period.

The prolonged pair-bond appears to be better developed in the Cape Shoveler than in the African Yellowbill (Table 1). Generally, in the food-specialist Shovelers a mated male needs to expend much time and energy in establishing and defending a discrete, exclusive territory to provide his mate with the opportunity to feed unhindered, for building up energy reserves for egg laying and incubation (Seymour, 1971; personal observation). It stands to reason that energy and time savings will accrue to those Shovelers which are already paired when attempting to replace clutches.

In the African Yellowbill, as in the Mallard, feeding is less specialized, the breeding female ranges more widely, and, consequently, the male's role is less important in ensuring opportunities for the female to feed. In the African Yellowbill, and in the Mallard, a proportion of all 'rape-flights' (McKinney, 1965) appear to be initiated by re-nesting females which have been deserted by their mates; the rape-flight culminates in fertilization of the eggs. Rape is rare in Shovelers (McKinney, 1970).

If the preceding arguments are correct in their claims for advantages accruing through extended pair-bonds, what of the opposite? Why are the bonds in the African Yellowbill, Cape Shoveler and Hottentot Teal not as durable as in the Cape Teal? What factors are involved in the termination of the bond? According to Sibley (1957), the males of northern hemisphere Anatini desert their mates early in the cycle because their bright plumage might increase the risk of danger to their females and progeny by drawing the attention of predators. This explanation cannot be invoked for the dull-plumaged, monomorphic southern species. For northern species, Selander (1966) suggested spatial separation of the sexes as a mechanism ensuring adequate food resources for the young. In the north food is abundantly available for a relatively short time. In northern Anatini, selection has operated in numerous ways to both shorten and maximize the reproductive effort: clutches are larger, incubation periods are shorter and growth rates of ducklings are faster than in their southern counterparts (Kear, 1973). Under these conditions, the suggestions made by Sibley and Selander are plausible, and, in addition, selection would favour early termination of the pair-bond so that the annual moult, as an extra-energy demanding process, occurred in the sexes at different times and places before migration.

In those parts of well-watered southern Africa which receive predictable rains the whole reproductive cycle, from start of social courtship through to fledging of the brood, and post-breeding moult, occupies a longer period and the individual's breeding cycle proceeds at a slower rate than in the Holarctic. There are, of course, seasonal periods of food abundance and scarcity, but the extremes of northern climates are absent. Productivity even during the most favourable time of the year is well below that found in the north. Thus, there is relatively less food available at the same time to parents and young in the south, and Selander's (1966) suggestion could apply here as well. However, it seems more likely that selection favours early onset of moult in males, since social courtship commences as soon as the moult is over and because those males which are first ready to commence the new cycle of social courtship will be those which have moulted early. These males presumably have an advantage in obtaining mates; and there is no evidence to suggest that males and females ever occupy separate geographical areas, as is the case in 'wintering' populations of certain Holarctic migrants.

The ecological condition is different for the Cape Teal. The ephemeral breeding habitat can be extremely productive. Presumably, this allows the male to stay with the female and brood and to exercise his final advantage, in terms of his genetic contribution, by enhancing survival of brood, and/or giving him an edge for future breeding attempts. Interestingly, the Cape Teal's incubation period is shorter than those of the other southern African Anatini. The longest belongs to the African Black Duck, which lays the smallest clutch of all, and whose habitat is considered to be relatively poor in producing food (Siegfried, 1968).

So far discussion has focussed on the Cape Teal, African Yellowbill and Cape Shoveler. Besides being the best known of the six species, they represent fairly clear-cut examples of species which have either a long or a short pair bond. Relatively little is known about the Hottentot Teal. The Red-billed Teal has been left until last, because it does not fit neatly into one of the two categories of pair bonding considered thus far. The data assembled (Table 1) clearly indicate that certain birds maintain a long bond and others a short one. Based on casual observations, it appears that broods are accompanied most often by both parents when they occur on waters from which other Red-billed Teal are absent. Using the ecological premise applied to the other species, the Red-billed Teal condition can be explained only if considerable segments of the population are exposed to, and respond to, different environmental pressures. There is ample evidence from ringed birds (Winterbottom, 1964) to indicate that Red-billed Teal wander extensively in the arid and semi-arid areas, where they also breed. Presumably these birds would be subjected to ecological pressures similar to those prevailing on the Cape Teal. It is not known, however, to what extent they comprise a group distinct from the main population inhabiting the well-watered tropical areas. Conceivably, there might be variable behaviour in the same individuals under different environmental conditions.

Plumage

According to Weller (1968), in southern anatids a sexually monomorphic (and usually dull) plumage is owned by those forms which show a tendency towards permanent pairing, an extended period of courtship, reduced migration, and the absence of an 'eclipse' plumage in males. Among southern African Anatini, the Cape Shoveler is the only species with permanent sexual dimorphism in plumage; it also is the only species in which apparently a major segment of the population performs regular migration (Siegfried, 1965). Thus in this case sexual dimorphism in plumage appears to be correlated with migration, and casual observations suggest that the species' social courtship is more strictly seasonal and commences later in the year than that of the resident African Yellowbill in the same geographical area. Since the two species differ little in their local breeding peaks, the Yellowbill a few weeks ahead of the Shoveler (Rowan, 1963; Siegfried, 1965), it stands to reason that the Cape Shoveler has a relatively shorter pair-bond before initiating nesting. Thus if tenure of pair-bond is to be measured from time of first pairing to time of first nesting then the Cape Shoveler fits Weller's (1968) proposition that: 'in fact, strongly migratory segments of duck populations at any latitude may be less prone toward permanent pairing'. The fact that in the Cape Shoveler pair-bond may endure well into and beyond incubation seems of lesser importance in relation to the development of sexual dimorphism. What does seem to be critical, and common to regular migrants, at all latitudes, is that their annual time and energy budgets permit only relatively compressed bouts of courtship tending to be restricted to a short season. Tamisier's (1972) studies on European Teal *Anas crecca* on their wintering grounds point to the need for individuals to balance time spent on courtship against the energy expenditure and predation risks involved; the birds spent relatively little time on courtship, which occurred mainly towards the end of the wintering period.

In the southern African Anatini, taken as a group, courtship commences a new cycle as soon as breeding and the annual moult are completed; and the ecological conditions permit a relatively extended period of social courtship, and probably the formation of longer-lasting pair-bonds, prior to actual breeding. The striking male plumage features of northern birds apparently evolved primarily in response to intense competition for mates, in the relative absence of opposing selection pressures. Conceivably in response to predation, the dull-plumaged Red-billed Teal and Cape Teal are reported to have reduced and simplified their postures and vocalizations in courtship displays (Kaltenhäuser, 1971), and the African Yellowbill and Black Duck tend to perform their courtship activities after sunset (personal observation). It seems likely that sexual dimorphism or monomorphism in plumage will be understood fully only when more is known about time/energy budgets and predation pressures. It is suggested that for many dimorphic Anatini the food and feeding situation affords a short period of intense, elaborate social courtship. In monomorphic forms, predation pressure is heavier and a lower but more sustained level of food permits a longer period for more frequent, less intense, less elaborate social courtship. Males of southern hemisphere anatines at high latitudes, with relatively short periods of high productivity, tend, as in northern migrants, to have bright plumage; this applies to certain species of *Anas* in southern Australia, New Zealand and South America.

It is possible to invoke the same ecological correlates in seeking to explain the evolution of reduced sexual dimorphism and simplified social courtship displays in certain isolated island races derived from mainland *Anas* stocks. An essentially ecological explanation would differ quite radically from the hypothesis developed by Sibley (1957) and advanced further by Johnsgard (1960, 1963, 1965). These authors claimed that conspicuous male plumages are present in those northern Anatini which occur together, and were evolved specifically as a mechanism to avoid hybridization. In presenting their case both authors stressed the island situation in a sort of inverted argument; that since insular populations are separated from closely related species, the chances of hybrid matings are minimal and hence selection for bright male plumage is relaxed. However, more recent studies of *Anas* species have failed to produce evidence that male plumage brightness is a reinforcer for preventing hybridization (Johnsgard, 1967). In addition, those races of *Anas* (e.g. Greenland Mallard *A.p. conboschas*) which inhabit islands with ecological extremes tend to retain bright plumage in males.

Sibley (1957) explained the lack of sexual dimorphism in many southern hemisphere Anatini by speculating that these species were ecologically segregated to a greater degree than species in the north, resulting in decreased chances for hybridization. This argument does not fit the facts, as pointed out by Siegfried (1965) and Weller (1968). In contradistinction to Sibley and Johnsgard, it is submitted that in most northern anatines enhanced sexual selection, as an ecological effect, is primarily responsible for favouring conspicuous male plumage, and that these bright plumages mainly function epigamically (attracting and stimulating females) and intrasexually (competing with conspecific males) in social courtship. It is logical to assume that in the species of Anatini occurring together, selection for isolating mechanisms basically resorts to vocalizations and postural displays (rather than bright colours *per se*), since these signals can be made effective as and when necessary. Most morphological characters, on the other hand, also comprise other adaptations.

Finally, Weller (1968) suggested that loss of the 'eclipse' plumage in Neotropical Anatini might be due to the irregularity of breeding seasons, and that birds constantly in breeding plumage have an advantage in being ready to pair at short notice whenever environmental conditions permit. From the foregoing accounts it is clear that Weller's mould does not accommodate the southern African species, the majority of which are regular seasonal breeders, but, nevertheless, have no eclipse. The eclipse can be regarded as a special cryptic plumage, increasing chances of survival of moulting males which are normally brightly coloured. Predators and other factors, induce moderation and compromise selection for brightness. Thus, the males in a particular population will be as conspicuous as is advantageous within the confines of particular ecological limits. If selection for brightness proceeded from an original state of dull plumage (whether the same as that of the female or not) and went no further than a point beyond which it would be disadvantageous to go, then that bright plumage would always be worn since at no time would it be especially disadvantageous to the individual. If, however, the degree of brightness is such that its continued presence is disadvantageous to the individual during its most vulnerable period (the moult), then selection for a special cryptic plumage for that period could be expected. In this regard, the shovelers present an interesting case. There are four species, the Northern Shoveler, Cape Shoveler, Australian and New

Zealand Shoveler *Anas rhynchotis* and Red Shoveler *A. platalea*, with male plumage ranging from most bright in the Northern Shoveler to least bright in the Cape Shoveler. The Northern Shoveler has an eclipse; the Cape Shoveler lacks a special eclipse and is permanently brighter than the female. The Australian and New Zealand Shoveler is considerably brighter than the Cape Shoveler and has an eclipse plumage (Frith, 1967).

In concluding this discussion, much of which is speculative, it is desirable to emphasize the modern view (e.g. Crook, 1970; Orians, 1971) that ecological factors are intrinsic in determining the evolution of mating and spacing systems of animals. In the final analysis, it is likely that food and feeding ecology, with attendant energy budgeting, will prove of fundamental importance to our understanding of social systems in the Anatini. Study of the ecological origins of waterfowl behaviour has been neglected; and these studies are needed as much as the psychological and phylogenetical ones.

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Summary

The incidence of males accompanying females with broods is compared in six *Anas* species: African Black Duck *A. sparsa*, Cape Teal *A. capensis*, African Yellowbill *A. undulata*, Red-billed Teal *A. erythrorhyncha*, Hottentot Teal *A. punctata* and Cape Shoveler *A. smithii*. Males accompany females with broods in those species which have extended pair-bonds. Length of pair-bond is influenced by ecological factors which shape a species' social behaviour as well as features of its morphology. It is suggested that plumage brightness in males evolved as a result of sexual selection. In migratory forms the ecological conditions, regulating time and energy budgets, afford a relatively short period for elaborate, intense social courtship. Regular migrants have sexually dimorphic plumage. Most residents and nomads are monomorphic; this is attributed to heavier predation pressure and a lower but more evenly sustained productivity of food, permitting a relatively extended period for less intense, less elaborate social courtship.

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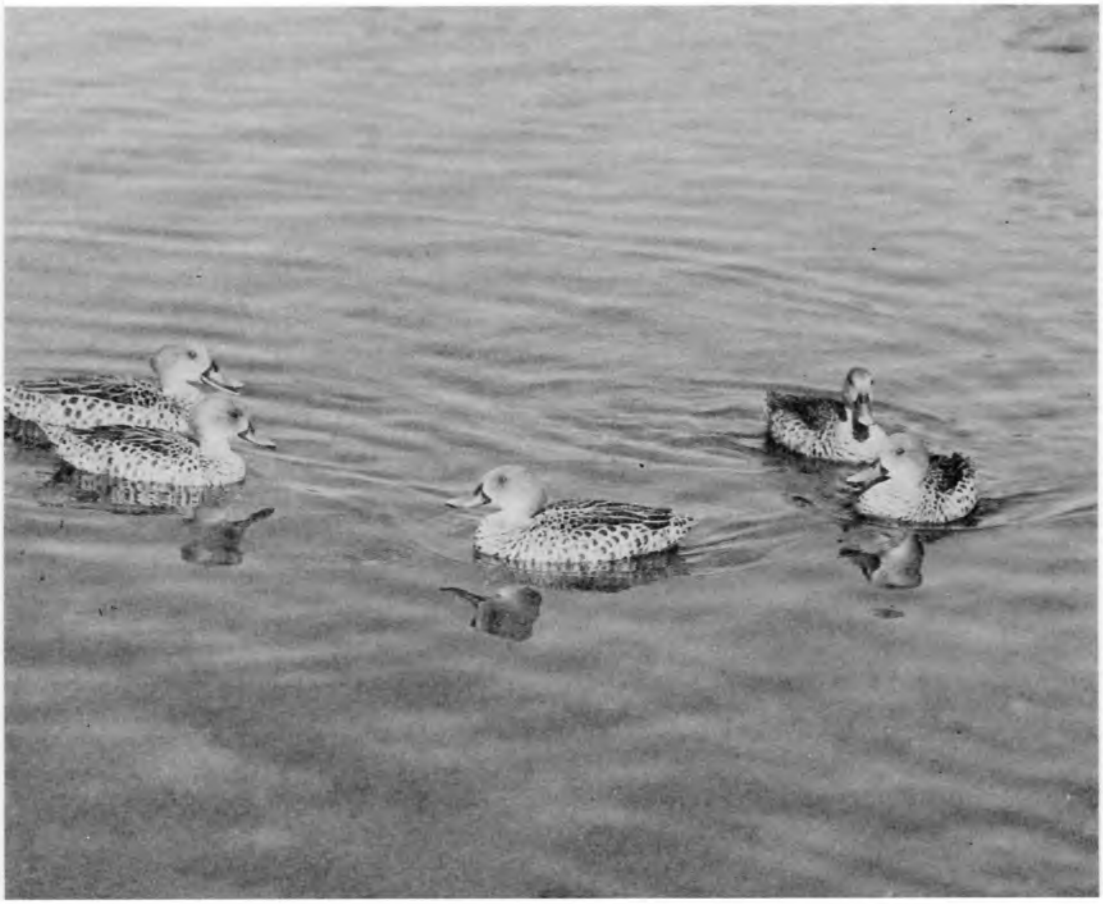
A group of Cape Teal *Anas capensis* displaying.

Joe B. Blossom



The survival of broods of the Egyptian Goose in Uganda

S. K. ELTRINGHAM

The Egyptian Goose *Alopochen aegyptiacus* nests in a variety of places. Mackworth-Praed & Grant (1952) stress its tree-nesting proclivities but Pitman (1965) believes that most nests are on the ground and that it is only the prominence of the tree nests that has led to the belief that a tree is the preferred nest site. It is true that incubating birds are rarely seen except in such prominent places as the disused nests of other birds of which

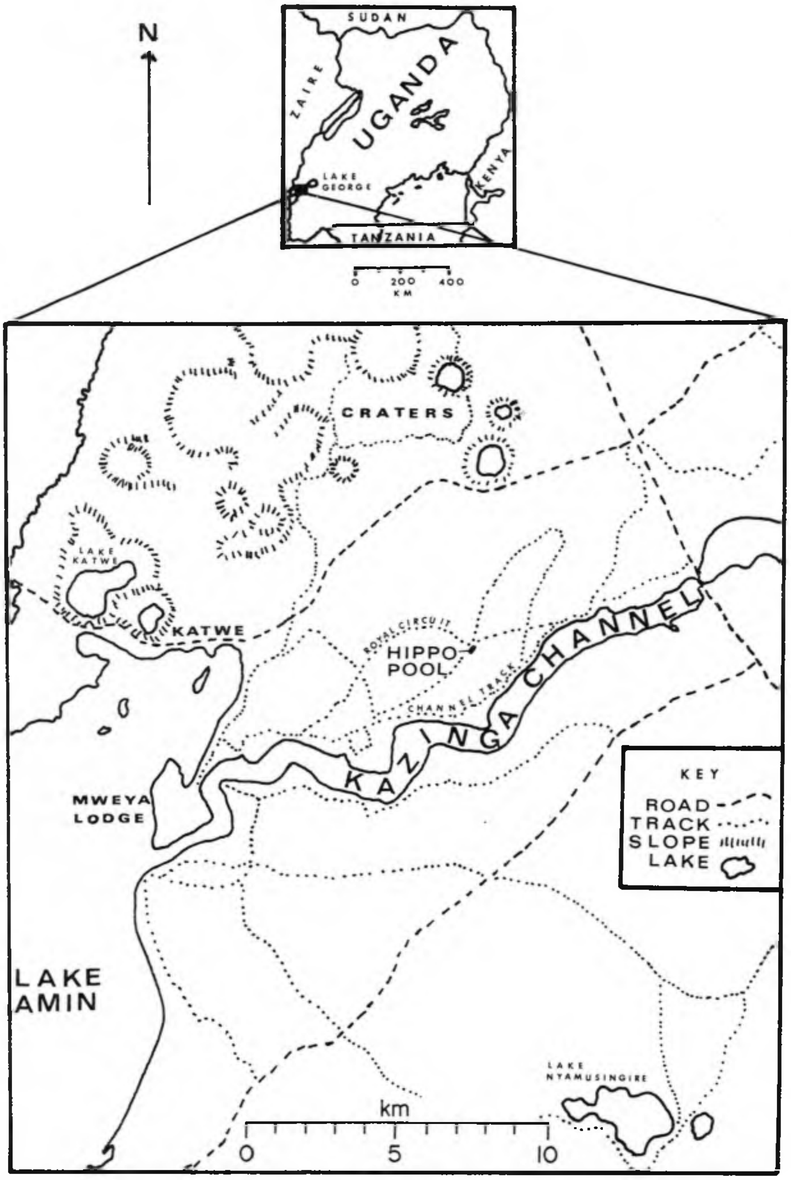


Figure 1. Map of part of the Ruwenzori National Park in western Uganda showing the location of the Hippo Pool where the study was made.

the Hammerkop *Scopus umbretta* is especially favoured, but the Egyptian Goose seems to prefer holes which are plentiful throughout its habitat. Whatever the nesting site, the young are called out of the nest by the parents soon after hatching and led to water. Both parents remain with the brood until the young birds are fully grown. During this period, the goslings are subject to considerable mortality but its extent has not previously been estimated. An opportunity to do so occurred when it was noticed that a large hippo wallow in the Ruwenzori National Park (formerly the Queen Elizabeth National Park) in western Uganda was a favoured nursery for broods of Egyptian Geese. The survival of the broods on this wallow was followed from April 1968 until June 1972. Some preliminary observations began in February 1968 to examine the feasibility of the work but the fate of the broods seen then was not followed in detail and the data have not been included in the results.

The hippo wallow in the Ruwenzori National Park is situated near the track known as the Royal Circuit at latitude 0°09′S and longitude 29°59′E (Figure 1). It is roughly oval in shape about 500 m long, about 230 m wide and about 0·01 km^2 in extent. The wallow carries a varying number of adult Egyptian Geese with an average population of 167 birds (Eltringham, 1973). Twelve other species of wildfowl have been recorded on the wallow but not in great numbers. Exceptionally, as many as 139 White-faced Whistling Duck *Dendrocygna viduata* and forty-eight Red-billed Pintail *Anas erythrorhyncha* have been counted on the wallow but numbers are normally very much less. During the period of study, the wallow was visited by flocks of palaearctic migrants with peaks of up to 750 Garganey *Anas querquedula* and 250 Pintail *Anas acuta* during the northern winter. In May 1972, the wallow was covered within a few weeks by floating plants of Nile Cabbage *Pistia stratiotes* so that no open water was left. The Egyptian Geese no longer brought their young to the wallow and the study was, therefore, terminated.

Methods

The wallow was visited on average about six times a month and circled in a landrover which was stopped whenever a brood was seen. On each visit between 16.00 and 17.00 hours, the location of the broods as well as the number and size of the young were recorded on a sketch map which was drawn from a vertical air photograph. Observations were facilitated by the use of a pair of 10 × 50 binoculars. The broods were easily recognized from their location and from the number and size of the goslings. No geese were marked because of the problems of catching in an area frequented by hippopotamus and other dangerous large mammals including elephant, buffalo and lion. The data given below refer to sixty-two broods which were first recorded when the goslings were very small. Partial data from a further eleven broods which appeared on the wallow after the goslings had developed beyond the newly hatched stage have not been used here because the original sizes of the broods are not known.

Results

Copulation

Copulation was observed only twice but as copulation in this species is imperfectly known (Johnsgard, 1965), it is worth recording the details. The first copulation took place at about 16.00 hours. When first seen, the birds were standing in shallow water and dipping their heads to the surface. The female crouched while still in the water and the male at once mounted and poised on the female's back for about a second before coition took place. The whole process took only 4 or 5 seconds before the male dismounted. Both birds then preened behind the wing while one, believed to be the male, chased other geese and was in turn chased by a third. The second copulation was at about the same time of day and also took place in shallow water near the shore. The female was already crouching when the pair was seen and coition took place immediately with no pause. The female began to call during copulation and the male probably did so too. As before, copulation was followed by preening behind the wing.

The number of breeding birds

The approximate location of each brood when first seen has been plotted on a map (Figure 2). It is clear that these plots are grouped. Each group presumably represents the successive progeny of a single pair, the period between the dispersal of one brood and the appearance of the next being compatible with the time required for nest building and incubation. There are a few

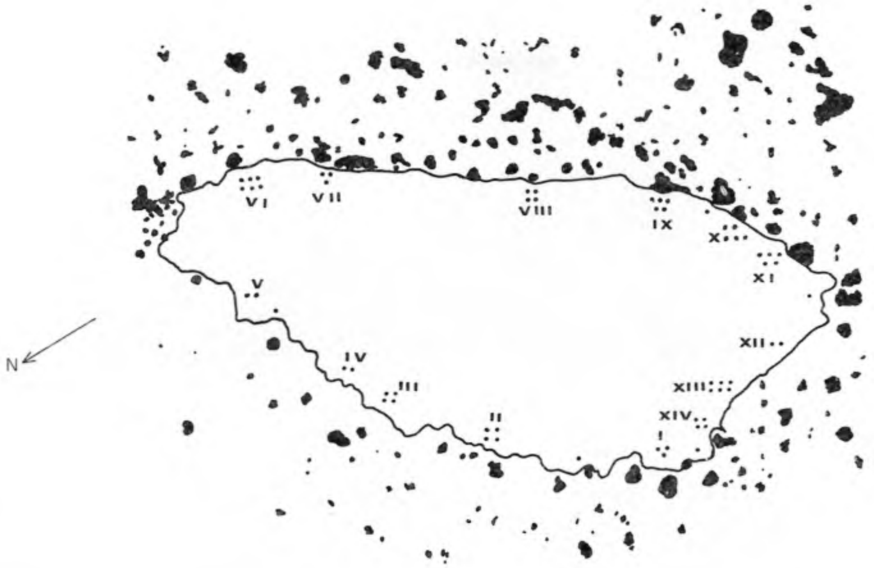


Figure 2. Map of the Hippo Pool showing the approximate location of broods of Pairs I to XIV. Each dot within the outline of the wallow represents a brood. The black shapes represent bushes. Drawn from an aerial photograph.

isolated broods which may represent pairs which took their young on to the wallow on that one occasion only. Apart from these, there appear to be fourteen resident breeding pairs, each presumably holding part of the shore line of the wallow as a territory. The pairs were spread fairly evenly along the shore but there was a marked tendency for them to concentrate in areas with the greatest cover, which affords protection against aerial predators. Only Pair V occupied an area that was relatively open. The broods spent much of their time on land and were usually some distance from the shore when sighted. They invariably rushed towards the water, accompanied by their clucking parents, whenever the land-rover approached and swam rapidly out towards the centre of the wallow for a distance of 20 or 30 m before slowing down.

On the whole, each brood was in the same area each time it was seen, but occasionally they were found some distance away from their usual haunts. For example, Pair VII was once seen with its brood on the opposite shore between Pairs IV and V. It is clear from the number of broods found with each pair over the 4 years that some geese nested twice in the year.

Brood size

The brood size at hatching is not known. There is always the possibility that some goslings were lost on the journey or before they were first seen on the wallow. The figures given here are, therefore, minimal. Details for the 5 years 1968–1972 are given in Table 1 from which it can be seen that the average brood size over the whole period

Table 1. Brood size of Egyptian Geese when first seen on Hippo Wallow

Year	Total no. of broods	Total no. of young	Average brood size	Standard deviation	Range
1968	14	80	5·7	1·841	2–12
1969	18	128	7·1	2·133	2–17
1970	13	76	5·8	1·649	1–11
1971	14	97	6·9	1·958	2–14
1972	3	21	7·0	2·550	2–12
Total	62	402	6·5	3·524	1–17

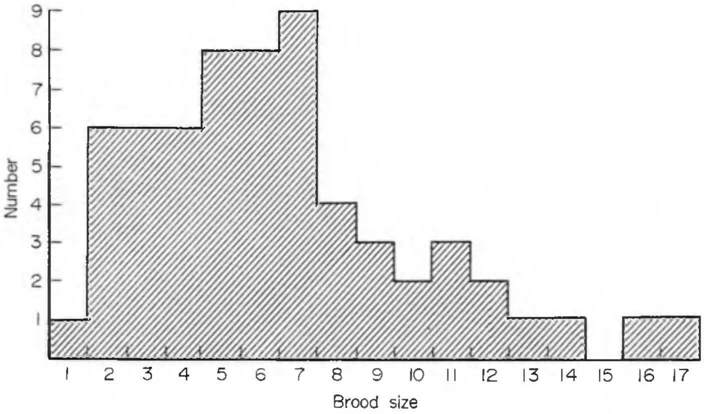


Figure 3. Frequency distribution of the brood size for sixty-two broods of the Egyptian Goose.

was 6·5 with a range of from 1 to 17. There is no significant difference between the brood sizes each year ($\chi^2 = 3{\cdot}303$; $0{\cdot}90 > P > 0{\cdot}50$). Figure 3 shows that the brood size distribution was markedly skewed with an abrupt cut off after a brood size of seven. Only eighteen broods (29%) were larger and it is possible that some of these resulted from amalgamation of broods or multiple laying in a nest. No brood was ever with more than two adults and usually both birds, presumably a mated pair, were present. There is, therefore, no evidence of crêche formation as is seen in the closely related Common Shelduck *Tadorna tadorna.* The only evidence for amalgamation was a brood of fourteen, first seen when the young were of medium size, in which six goslings were distinctly bigger than the rest.

Brood survival

Sixty days from the first sighting the goslings are of adult size, but not necessarily weight Siegfried (1967), and some begin to take up an independent existence at this point. Consequently, Table 2 shows the survival of the goslings up to the age of 60 days from first sighting. The overall survival was 60·4% but there were considerable variations each year which are statistically significant ($\chi^2 = 14{\cdot}663$ for 1968–1971 and 29·776 for 1968–1972; $P < 0{\cdot}001$ in each case). Apart from 1972, when the number of broods was too small to be significant, these differences are due to a year of poor survival in 1970 and one of good survival in 1971. For several months in 1971 the wallow dried up to a considerable extent but it is difficult to see why this should have been advantageous. There was no notable event in 1970 likely to be responsible for the poor survival. Meteorological conditions as recorded at a station about 10 km to the south west, were not markedly different each year. Rainfall, at 871 mm in 1970 and 958 mm in 1971 respectively, was only a little higher than the average of 839 mm, while sunshine hours were not very unusual at 1,887 hours in 1970 and 2,028 hours in 1972; the average being 2,095 hours. The high proportion of broods reared without loss was the factor mainly responsible for the good survival figure for 1971.

The survival at 5-day intervals is shown in

Table 2. Survival of the broods of Egyptian Geese 60 days after first sighting

Year	No. of broods	Initial no. of young	No. of young at 60 days	Survival (%)	No. of broods with no survival	No. of broods with 100% survival
1968	14	80	51	63·8%	4	2
1969	18	128	80	62·5%	4	6
1970	13	76	33	43·4%	5	1
1971	14	97	78	80·4%	1	5
1972	3	21	1	4·6%	2	0
Total	62	402	243	60·4%	16 (26%)	14 (23%)

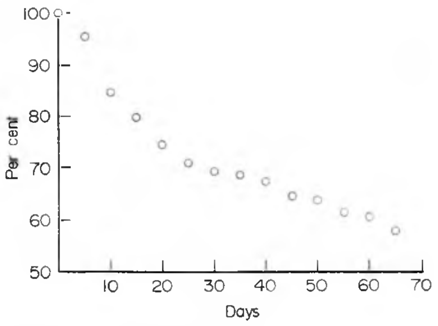


Figure 4. The percentage survival of 402 goslings of the Egyptian Goose at 5-day intervals.

Figure 4. For the first 25 days, there is a uniform mortality rate but subsequently the curve flattens out and continues again at a constant rate, until after the 60th day when there is a sudden drop. However, it is likely that this decline in brood size is due not to mortality but to dispersal of the young. The goslings are then fully grown and lack only the adult's black spot on the chest and brown colouration around the eye. Birds in this juvenile plumage were often seen in the non-breeding flocks near the wallow and had obviously just left their parents. Not all young leave the brood, however, even though they are fully independent. The average period during which at least one gosling remained with the parents was nearly 82 days for the forty-six broods which survived beyond the 60-day stage. The maximum was 145 days. About 20% of these broods remained complete throughout the time they were seen with their parents. No evidence of agonistic behaviour on the part of the parents towards the grown young was noticed and it is probable that the latter leave on their own volition. No doubt many broods of large goslings are simply abandoned when the parents leave to renest. The possibility that the survival varied according to the original size of the brood was tested. Table 3 suggests that goslings survived better in the larger broods but the trend is not significant ($\chi^2=4{\cdot}419$; $0{\cdot}50>P>0{\cdot}10$). The average size of the fourteen broods which suffered no losses was, at 4·8, not significantly different from the value of 5·0 for sixteen broods in which all the goslings were lost ($0{\cdot}50>P>0{\cdot}10$).

Table 3. Survival in Egyptian Goose goslings in relation to the initial size of the brood

Initial brood size	Initial no. of young	No. of young at 60 days	Survival
0–3	31	17	55 %
4–6	112	58	52 %
7–9	122	74	61 %
10–12	77	51	66 %
13–15	27	21	78 %
16–18	33	22	67 %

Seasonal appearance of the broods and productivity

Figure 5 shows the average number of new broods appearing on the wallow and the average number of young in these broods for each month of the year. The figure also includes the average number of these goslings which were successfully reared to 60 days after they were first seen. The production of broods is obviously seasonal and related to rainfall, with the period of maximum numbers of broods lagging a little behind the seasonal rise in rainfall. No broods are found in January, one of the driest months, and very few are seen in February and March. Only three of the sixty-two broods appear in the first 3 months of the year. Although there is a fall off in the

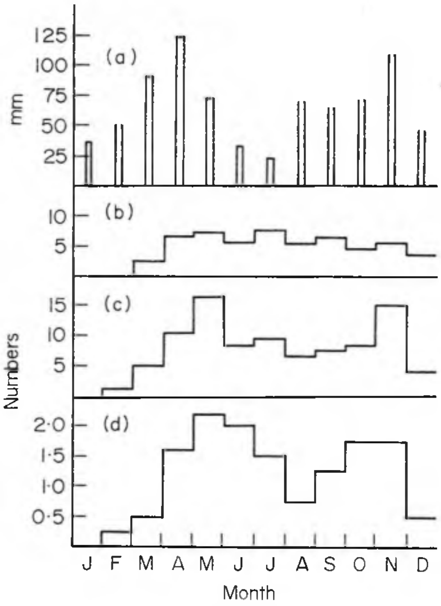


Figure 5. Productivity of the Egyptian Goose on the Hippo Pool. The figure shows (d) the average number of broods produced each month, (c) the average number of goslings hatched each month, and (b) the average number of goslings hatched each month which were reared to the 60-day stage. The average rainfall (a) at Mweya for an 8-year period up to 1971 is included.

number of broods after the second dry season in June and July, the decline is not so great nor does it last for so long as it does earlier in the year. The dry season is a period of deprivation, akin to a palaearctic winter, for grazing animals such as the Egyptian Goose. Rather more rain falls in the first wet season than in the second. During the early part of a rainy season, the grass grows vigorously and is much richer in protein. It is likely that the improved quality of the food is the proximate factor that stimulates breeding. Nesting and incubation are maximal when rainfall is at its height and most broods are, therefore, brought on to the wallow towards the end of the wet season.

Fluctuations in the average number of goslings produced each month tend to follow those of the broods but the two wet season peaks are more sharply defined due to seasonal differences in the brood size. However, when the number of goslings from these broods which survived to 60 days is considered, the data lose most of their seasonality. The productivity in the sense of the number of birds joining the adult population is more or less constant after the first 3 months of the year.

Productivity of individual pairs

Table 4 shows the contribution made by each pair to the total productivity and includes the broods brought by 'casual' pairs which appeared only once on the wallow. The greatest number of broods produced during the 4 years of the study was six from Pair VI and this pair also produced the greatest number of goslings—forty-nine—but it was less successful in rearing them. The largest number of goslings surviving to 60 days belonged to Pair III which was a very successful pair altogether. Although they only produced four broods, the average brood size was large and the survival good and their contribution to the total number of goslings reared was as high as 12%. A few pairs were not very successful. Thus Pair II produced only eighteen goslings from four broods and of these eleven (61%) did not survive. Pair VIII had much the same lack of success. Pairs with high and low productivity seem to be scattered randomly about the wallow. It is likely that the successful pairs were those which were older and more experienced in looking after the young. It is not necessarily the pairs which produced the most broods that had the highest productivity. There is not, in fact, a significant correlation between number of broods and number of young reared ($r = 0{\cdot}437$; $P > 0{\cdot}1$).

Discussion

There is not much published information on the breeding biology of the Egyptian Goose. Pitman (1965) gives some figures for the clutch size but no mean. He mentions the complement as being in the range of six to ten with one clutch of fifteen eggs of which two were infertile. He gives the brood size on reaching the water as seven to eleven

Table 4. Comparison of breeding success in individual pairs of Egyptian Geese

Pair no.	No. of broods produced	No. of broods failed	No. of broods successful	Average brood size	Initial no. of young	No. of young reared	Survival
I	3	0	1	3·7	11	8	73%
II	4	2	2	4·5	18	7	39%
	4	0	1	9·0	36	29	81%
IV	2	0	1	5·0	10	9	90%
V	2	0	1	6·0	12	7	58%
VI	6	2	1	8·2	49	23	47%
VII	3	0	2	8·0	24	23	96%
VIII	4	2	1	4·8	19	8	42%
IX	5	2	0	6·8	34	17	50%
X	5	1	0	5·0	25	12	48%
XI	5	1	1	6·2	32	21	68%
XII	2	0	0	10·0	20	16	80%
XIII	6	2	0	6·5	39	20	51%
XIV	4	1	1	6·8	27	20	74%
Casuals	7	3	2	6·6	46	23	50%
Total	62	16	14	6·5	402	243	60·4%

which is a little higher than the mean number found in the present study. Mackworth-Praed & Grant (1952) give a range of five to eight for the clutch size. No comparative data of the survival of goslings in other areas are available but the overall survival of 60·4% is not exceptional compared with other species of wildfowl. Baker (1970) reports a 56% survival in the Wood Duck or Carolina Duck *Aix sponsa* from observations of web-tagged birds in 1968 and of 52% from direct observation of seventy-seven broods in 1969. Most of the mortality (74%) occurred in the first 2 weeks after hatching. Odom (1970) found that the brood size of the same species had been reduced by nearly two-thirds at the 4–7-week age class.

The causes of mortality amongst the goslings can only be inferred as no death was ever witnessed. However, there is no shortage of potential predators in the area. Birds of prey are plentiful. It is unlikely that the large eagles would bother with small goslings and they are more likely to be taken by Black Kites *Milvus migrans*, which are particularly numerous, and other medium-sized raptors. The adult geese were several times seen to defend their broods vigorously against kites, a fact which suggests that these birds feed regularly on the goslings. Protection against aerial attack is probably the reason why breeding pairs tend to favour a shore line backed by thick bushes as these provide escape cover. Broods may well be kept off the water to a large extent as a kite could easily snatch a gosling from the surface. While on the water, the broods are also vulnerable to predation from Monitor Lizards *Varanus niloticus*. These reptiles reach a length of about 1 m in the Ruwenzori Park and are often seen at the hippo wallow both on land and in the water. Although primarily scavengers and egg stealers, the Monitor will take any small animal it can catch. The hippo wallow is too shallow and lacking in oxygen to support ordinary fish but it is possible that lung fish *Protopterus* occur and if they do, they would certainly take young goslings. The hinged tortoise also occurs in the wallow and might take some of the very small goslings as may snakes, particularly on land.

Mammalian predators are probably unimportant. Genets *Genetta tigrina*, Civets *Viverra civetta*, Ratel *Mellivora capensis* and various species of mongoose have all been seen in the region of the wallow but, with the exception of the Banded Mongoose *Mungos mungo*, these are nocturnal predators. It is not known where the broods roost but it is probably on the bank near the shore so that they can slip into the water if disturbed.

Many species of storks and herons occur at the wallow and although the major food items appear to be frogs and insects, they would no doubt take any gosling separated from its parents.

Finally goslings may become separated from the rest of the brood and lost. Normally, the young keep close together but sometimes, while feeding on the algae or other underwater vegetation, they become rather spread out. If they were to be attacked at such times, one or more goslings might well become separated from the brood in the resulting mêlée. No direct evidence of this was obtained but sometimes the brood scattered madly when surprised by the landrover and the reaction to predators is probably similar. In 1971, a gosling of Pair VII left its brood and joined another belonging to a casual pair, remaining with it until fully grown. It is possible that the young bird had become separated from its siblings during some disturbance. Presumably the exchange took place when Pair VII, as mentioned above, crossed over the wallow to a point between Pairs IV and V. Incidentally, the geese and the hippos tended to ignore one another. It was amusing to see the tiny goslings swimming sedately through a school of these huge mammals. Only on one occasion, was a hippo seen to react when it threatened a brood by opening its mouth. The resulting tidal wave caused more consternation than the threat.

It is not possible to use the data collected in this study for a full assessment of the population dynamics of the Egyptian Goose since the birds present at the wallow probably form only a part of a wider grouping. Eltringham (1973) made regular counts of the geese at the wallow at the same time as these observations were carried out and found that an average number of 167 geese were present over the 4-year period. However, the deviations from this mean are very great. Until the home range of the geese is known, there is little point in estimating such parameters as recruitment and mortality for the population. Such data would have required more time than was available in a spare-time undertaking.

Taking the young away from the nest to water soon after hatching occurs widely in the Anatidae. Duck and geese do not take food to the young which have, therefore, to go out and get their own. However, it might seem that they could do this without going to water yet it appears that open water is essential. The wallow lost its attraction as a nursery as soon as its surface became covered with nile cabbage, suggesting that it is not simply a supply of drinking water that is required but sufficient water for bathing and swimming.

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Summary

Details of sixty-two broods of the Egyptian Goose *Alopochen aegyptiacus* on a hippo wallow in western Uganda were collected over a 4-year period between 1968 and 1972. Fourteen pairs used the wallow regularly while a few other pairs appeared sporadically. The average size of the broods when first seen was 6·5 with a range of 1 to 17. Of the goslings, 60·4% survived for a period of 60 days or more after first sighting but there were significant differences between the survival in certain years. Mortality was greatest in the first 25 days. There was no significant correlation between survival and brood size. A greater number of broods appeared on the wallow during the wet seasons than during the dry but there was little seasonal variation in the number of young reared to the 60-day stage except that very few, if any, young were produced in the first 3 months of the year. Some pairs were more successful than others in producing or rearing young. Possible mortality factors are discussed and it is concluded than avian predators are probably responsible for many deaths.

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Territorial behaviour of wild Shovelers at Delta, Manitoba

NORMAN R. SEYMOUR

Territory typically refers to 'any defended area' (Hinde, 1956) and this usage is adhered to in this paper. The status of territory in breeding ducks is less clear than in most other birds. Hochbaum (1944) considered it to be present in all dabbling ducks, but Sowls (1955), Dzubin (1955) and Lebret (1961) did not agree.

In the Shoveler *Anas clypeata*, published accounts are conflicting. Hori (1963) concluded from his studies of wild Shovelers in Kent, England, that they were non-territorial. Poston (1968) also found little evidence for territorial behaviour near Strathmore, Alberta. However, McKinney (1967), in agreement with Hochbaum (1944) and Sowls (1955), presented evidence, based mainly on intensive studies of captive birds, that territorial behaviour can be well developed. Detailed data relating to this behaviour in wild populations appears to be lacking. The present study was designed to obtain such quantitative data on the manner in which areas are defended, and the extent to which such defended areas, as opposed to the undefended portions of the home range, are used by pairs of Shovelers. Data were also collected on the types and frequencies of hostile male behaviour involved in territorial defence.

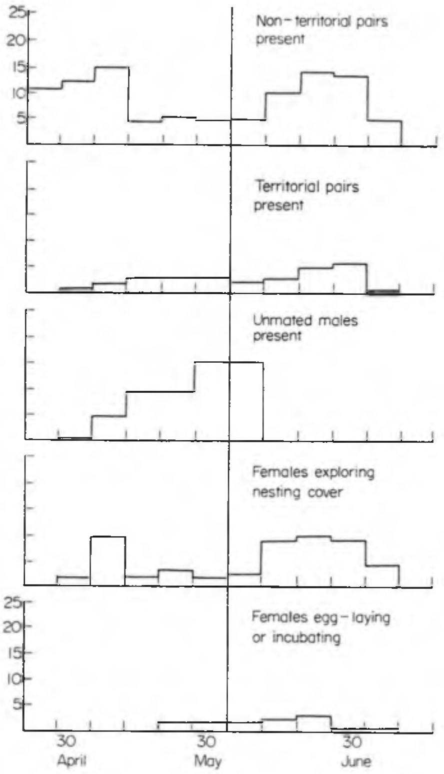

Figure 1. Number of Shovelers present and engaged in different activities during successive weeks during breeding period (20 April–10 July).

Study area

The study area lay 2·4 km south of Delta, Manitoba, and was a roadside ditch, 1·9 km long and 10–20 m wide, together with portions of adjacent meadows. The general features of the area in 1970 were essentially unchanged from a description given by Sowls (1955). A 12-week period of observation, 20 April to 10 July 1970, encompassed all known Shoveler breeding activity on the area (Figure 1).

The ditch and water on the adjacent east meadow were connected during the first 8 weeks of observation. The meadow water decreased progressively, however, from 26·8 ha (67 acres) during week 1, to 0·4 ha (1 acre) during week 8. The ditch proper, which became distinct from the drying meadow during week 9, contained water throughout the summer, and was crossed by four small dykes.

Vegetation of the flooded meadow began to emerge during week 5 and covered much of it by week 7. Except for 0·2 km at the north end, the ditch was never clogged with vegetation, although *Typha* sp., *Scirpus* spp. and *Phragmites* sp. did appear in discontinuous patches along the sides of the ditch throughout the summer.

Methods

Seventeen males were trapped by placing a hand-reared captive female in a clover trap of the design described by Lincoln & Baldwin (1929). They were marked with nasal saddles (Bartonek & Dane, 1964) and released at the trap site. Mated males were caught by placing the trap at the male's major loafing spot on the ditch; unmated males were captured in the meadow. In addition, three females were caught on their nests, similarly marked and released.

A car was used to observe the area at the northern and southern limits of the study area, a 6-m observation tower near its centre. Wooden strips were placed at 30-m intervals out from the major loafing spots of males, and at 90-m intervals on the meadow, to enable the location of males to be estimated.

The first count was normally made as soon as the birds could be seen (approximately 05.00 hours) and lasted for 30 minutes. Subsequent counts of the same duration were done at 2-hour intervals, the last being just prior to dark (approximately 22.00 hours). This schedule was followed for 4 or 5 days each week, except the first and last, when it was reduced to 3 days.

In addition, weekly aerial transects of the marsh were made from 6 May to 13 July and intensive checks of the water areas at the periphery of the marsh were made every 2 weeks from 1 May to 1 July to determine where Shoveler territories occurred.

Breeding chronology

Paired Shovelers began to use the flooded meadow during week 1. These pairs were non-aggressive upon arrival and often sat within 1·5 m of other pairs. Poston (1968) also found that newly arrived Shoveler males showed little hostility. Male threat display increased during week 2, being based on a 'moving territory' (Dzubin, 1955), in which the male defended the mobile female. During week 3, aggression increased further and pairs became isolated from each other.

Unmated males arrived during week 2 (Figure 1). They courted and chased mated females and made jump flights as described by Lebret (1961) and McKinney (1970). From one to seven unmated males would harass a pair, whose male threatened and chased the intruders. During week 3, of seventeen pairs under observation, twelve began searching for nest-sites on the ditch. Unmated males remained on the flooded meadow at that time, rarely harassing pairs which were using the ditch.

Figure 1 also indicates the number of pairs on the study area that were considered 'territorial' and 'non-territorial' on the basis of evidence presented below. Twelve different pairs resided on the study area over the 12 weeks, the last pair having established themselves during week 10. Non-territorial pairs, apparently searching for suitable breeding sites, were present for periods ranging from 2 days to 3 weeks. There was an influx of non-territorial pairs in weeks 8, 9 and 10 (Figure 1). During week 10 and 11, all but one nest on the study area was destroyed by predators and most pairs left the area. No new territories were subsequently established.

Aggressive behaviour and territorial defence

Direct observations of localized aggressive behaviour concerned, primarily, ten marked, paired males. Additional supporting evidence for territoriality was provided by observations of 'ritualized fighting' (McKinney, 1967), mainly at the apparent boundaries of defended areas.

Aggression in Shoveler males includes 'hostile pumping' (threat display), 'ritualized fighting', 'chasing', and 'three-bird flights' (see McKinney, 1967, 1970 for descriptions of these behaviours). The last named are referred to throughout this paper as pursuit flights.

'Hostile pumping' and associated calls were elicited in a resident male when an intruder approached the defended area. If the intruder continued into the territory, 'hostile pumping' was followed by 'chasing', then pursuit flights if the intruder did not immediately leave the area. 'Hostile pumping' and calling were also noted, in the apparent absence of other Shovelers, when the male returned to the defended area after pursuing intruders. At these times, he typically sat in the ditch near his loafing spot for 5–10 minutes or longer, often vocalized, and then went to the loafing spot. 'Hostile pumping' was also seen when a male approached a neighbouring territory whether or not the resident male was there.

'Chasing' was done primarily by territorial holders, who typically rushed over the water with the neck outstretched and bill slightly upward, often open, and pointed at the other male. The latter, usually unmated, showed little hostility toward the chaser and generally left the area quickly. 'Chasing' usually gave way to 'ritualized fighting' between holders of contiguous territories (see below).

In the Shoveler pursuit flights appear in part to function in driving away intruders, and hence do seem relevant to territorial defence.

Aggressive interactions were highly localized, occurring mainly in the vicinity of the loafing spot. Table 1 indicates the frequency of male sightings and of aggressive behaviour of resident males in relation to the loafing spot during the entire laying and incubation periods. There were significantly more sightings and hostile encounters close to the loafing spot (0–30 m) both for the com-

Table 1. **Location of marked territorial males on their territories and of aggressive interactions between these males and intruders relative to the major loafing spot used**

	Distance from major loafing spot		
	30 m	31–60 m	61–90 m
Location of spot sightings of 10 males (481 sightings)	399 (83%)	34 (7%)	48 (10%)
Location of males during bouts of observation (126 hours)	117 (93%)	6 (5%)	3 (2%)
Location of aggression (threat, chasing, ritualized fighting) of 10 males	257 (73%)	89 (25%)	8 (2%)
Location of boundary conflicts	5 (16%)	24 (71%)	4 (13%)

bined data on nine males ($\chi^2 = 88$, $P < 0{\cdot}001$) and for an additional single male ($\chi^2 = 212$, $P < 0{\cdot}001$).

The male was most visible to, and best seen by, intruders from either the prominent loafing spot or from the unbroken expanse of ditch. Most intruders approached along the ditch and rarely from the meadow behind. Almost all (95%) hostile displays occurred either at the loafing spot or in the ditch, suggesting that the water area rather than the meadow area was being defended. Prior to pursuit flights, the pursuer was usually on or near the loafing spot. After 264 (99·2%) such flights, the pursuer returned to the territory, usually within 30 m of the loafing point, which further indicates that aggression was territorial in function. Pursuing males whose mates were at the nest returned to the territory on 188 (95·5%) occasions, suggesting that the behaviour is related to the physical site and not just the position of the female. Vocalizing by the female at the nest was not detected during or after pursuits but this may have occurred and influenced the male's return.

Hinde (1966) indicated that, 'along the boundary between territories is a narrow no-man's land where prolonged skirmishes take place and actual combat is rare, such skirmishes being practically limited to the boundary region'. 'Ritualized fighting', which appears to be an example of such skirmishes, was used by McKinney (1967) to indicate the location of Shoveler territorial boundaries. As indicated in Table 1, most 'ritualized fighting' in the present study occurred in the area of 45–60 m from the loafing bar ($\chi^2 = 25{\cdot}7$, $P < 0{\cdot}001$).

Males on contiguous areas appeared to recognize common boundaries. They were to be seen sitting, relatively inactive, for as long as an hour within 3–6 m of each other, each bird on its own territory. 'Hostile pumping', 'chasing' and occasionally 'ritualized fighting' occurred primarily when one male approached more closely to the other or crossed the common boundary. Such interactions by males with laying or incubating females typically occurred immediately after he had accompanied his mate to the nest-site and returned to the ditch. However, most boundary interactions occurred during the pre-laying period, the time of territory establishment. After the initial boundary interactions, the neighbour's territory was rarely entered whether or not the owner was present. Where boundary conflict had initially been intense, territorial males did not enter contiguous territories even after the neighbouring male had deserted.

Extensive observations (96 hours) of four neighbouring males which established territories at approximately the same time, provided additional information about territorial boundaries. The territories of these males (A–D) during the pre-laying period are illustrated in Figure 2. Although it is difficult to define exactly the location of boundaries where actual conflicts were not seen, the dashed lines delineate them approximately, on the basis of disputes that were seen (dots in Figure 2) combined with the almost exclusive use by the resident male of the remaining area. More than 70% of encounters at the northern boundary of the territory of male A and southern boundary of the territory of male B involved unmarked males, presumably attempting to establish territories. Over 90% of encounters occurred on the ditch itself, apparently because most intruders landed there.

Pursuit flight endings are also included in Figure 2. They indicate that pursuits typically ended near, but outside the territory as defined by boundary conflicts *per se*. Pursuit

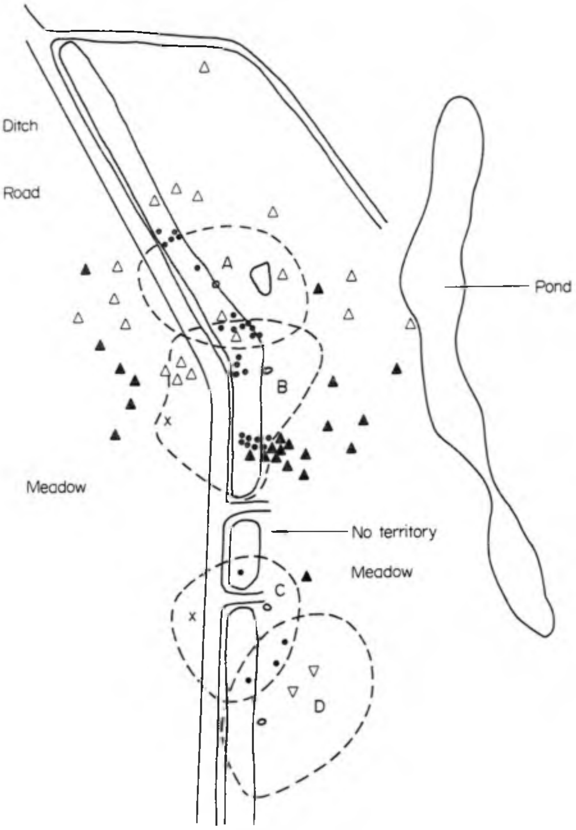

Figure 2. Coincident territories of four Shoveler males (A–D) along a roadside ditch. – – –, Limit of area intensively used and defended; ●, disputes between Shoveler males; ×, nest of resident female; O, loafing spot of resident male; △, ▲, ▽, end of pursuit flights made by males A, B, C, respectively.

flight behaviour between males A and B provided further evidence that neighbouring males recognize and observe a common boundary between their contiguous territories. These flights typically involved reversal of roles, the pursuer becoming the pursued, when crossing above the boundary line in the ditch.

Territory size

Estimates were obtained of the maximum space defended, actually only a very restricted portion of the total home range used by the pair (Dzubin, 1955). This was illustrated by territorial males which at times range far on pursuit flights.

As shown in Table 1 all defence during the laying and incubation periods occurred within 90 m of the loafing spot, thus making the maximum effective size of the territory approximately 0·9 ha (Table 2). There was also a vertical component to territory size. Defending males would threaten intruders at more than 90 m (height estimated by comparison to power line poles) but rarely gave chase unless the intruder indicated the intention to land.

Dzubin (1955) observed that territories in the Mallard *Anas platyrhynchos* and Blue-winged Teal *Anas discors* may be larger during the early periods of nesting. A significant difference ($\chi^2 = 13{\cdot}0$, $P < 0{\cdot}001$) was also found in the mean area used by Shovelers before and after the onset of egg-laying (Table 2). Observations of three Shoveler males whose mates retained eggs for a considerable time revealed that defence was strong until it ceased abruptly during late incubation.

Territorial males ranged farther from the loafing spot during the early-morning (05.00–10.00 hours) period, apparently because aggressive interactions, particularly pursuit flights, were triggered at this time by the

Table 2. Comparison of maximum size (hectares) of territories between the pre-laying and laying/incubation periods of ten Shoveler pairs

	Pre-laying	Laying/incubation
Mean area	2·9	0·9
Median area	3·2	0·6
Range in area	1·3–5·0	0·1–1·5

increased movement of non-territorial pairs. When non-territorial pairs were active later in the day, the same phenonemon was observed. Despite the temporal variations in aggression, territories did not change significantly in size as a function of time of day. Dzubin (1955) again reports a similar result for the Mallard and Blue-winged Teal.

There was no significant size difference between four territories established before 8 June and five later territories, despite the fact that the concentration of both territorial and non-territorial pairs on the study area was then greater. This suggests that territorial males do not occupy the largest possible area when pressure from other pairs is low. However, the concentration of pairs on the study area was not sufficiently great to determine this point conclusively.

Stability of territories

Major changes in boundaries did not occur when adjacent territories were abandoned due to nest failure. Stability was also maintained despite frequent hostile encounters between the territorial Shovelers (19% of all encounters observed), and between non-territorial Shovelers and the incumbents. Poston (1968) similarly noted that once established, Shoveler pairs were not displaced by other pairs.

Certain areas were used by successive pairs, rather than being occupied continuously by a given pair throughout the entire breeding season. One striking example of successive use of a portion of the study ditch by three males is indicated (Table 3) in relation to egg laying and nest losses. Duration on the territory was based on first and last sightings of the male or female of the pair; duration of a male's dominance was based on his success in excluding others.

The importance of the nest was suggested by the almost immediate reversal in dominance between males 2 and 1 following nest loss by pair 1. Dominance may also alter prior to nest loss, however, for male 3 assumed dominance over male 2 about 10 days prior to the loss of the latter's nest, when the pair-bond was weakening and male 2 was spending much less time on the territory.

The use of the territory by the female may be severely restricted by the hostile behaviour of encroaching males. Female 2 did not forsake the territory for at least 6 days after her mate deserted her, but she was extremely secretive when off the nest, staying primarily in the vegetation in the ditch edge, and using only a few square metres of water opposite the nest for feeding. Female 3 also used the territory after her mate deserted her, but loafed and fed within a smaller area, approximately 15 m in radius, than she used before her mate's departure. A similar restricted radius of activity was also noted for the only other two females whose nests were still viable when they were deserted by their mates. These observations suggest that the male is essential in maintaining the territory for the female.

Use of territory

In agreement with Poston's (1968) work on wild Shovelers, I found that pairs spent much of their daylight hours on the territory. During the pre-laying period, when the territory was being established, ten pairs spent from 2 to 4 hours on the territory (usually in the period 05.00–09.00 hours) when other pairs searched for nesting sites. They were not on the study area at other times. During late laying and incubation, males of ten pairs observed spent an average of 73·5% (range 55–90%) of the daylight hours on the territory, thus making use of the area by other pairs virtually impossible.

Table 3. Use of the same portion of the ditch by three Shoveler pairs at different times

	Duration of pairs on territory	First egg to nest destruction	Period of dominance
Pair 1	27 Apr.–27 May	15 May–22 May	27 Apr.–23 May
Pair 2	15 May–17 June	1 June–16 June	24 May–6 June
Pair 3	6 June–9 July	12 June–9 July	8 June–9 July

Females spent all of the daylight period on the territory, even in the absence of their mates. Hochbaum (1944) suggested that females may not have observed territorial boundaries at such times, but their activities were none the less localized, usually around the loafing spot. Such females were rarely harassed by territorial or non-territorial males presumably because these males still associated the area with a hostile territorial male.

Discussion

Since Hochbaum (1944) reported territorial behaviour in ducks, several authors have criticized aspects of Hochbaum's conclusions while others state that territorial behaviour does not occur in the Mallard and Shoveler (Lebret, 1961; Hori, 1963). These differences of opinion are considered by McKinney (1965) to be due primarily to the dearth of evidence for defended areas. However, for the Shoveler and some other species, McKinney (1965) and Siegfried (1968) state that the concept of territoriality is valid and widely accepted. In agreement with McKinney's (1965, 1967, 1970) work on captive Shovelers, my observations of localized activity (Figure 2) including intraspecific hostility (Table 1) and exclusiveness of the localized area, all show that Shoveler males in a wild population may defend an area which is often contained within reasonably well-defined limits.

Poston (1969), working in a prairie pothole habitat where the concentration of breeding pairs was low, found home range size of Shovelers to be 73 acres (29·2 ha) while Gates (1962), who worked in habitat similar to that found at Delta, measured home ranges of not greater than 20 acres (8 ha). Mean territory size during the laying and incubation periods in the present study, 2·3 acres (0·9 ha), closely resembles Poston's (1969) estimate, based on two pairs, of 1·5 acres (0·6 ha) for the corresponding 'core area'. It seems likely that this confined area, which is not readily reduced by aggressive behaviour of intruders, must be considered the portion of the home range most crucial to reproductive success.

Functional significance of territory

Gates (1962), working with the Gadwall *Anas strepera*, and Poston (1968), working with the Shoveler, discounted hostility, a component of territorial behaviour (Tinbergen, 1957), as a mechanism limiting density of breeding pairs on their study areas. McKinney (1965), however, believed that hostility in the form of aerial chasing, as is seen in the Shoveler, served to produce some degree of dispersion of pairs. In agreement with McKinney, my data indicated that Shoveler pairs at Delta were spaced both in time, as seen in the nesting delay of non-territorial pairs (Table 3), and in space as a result of territorial behaviour.

Several hypotheses to explain the function of spacing in ducks have arisen. Hochbaum (1944) theorized that it ensured successful copulation, while McKinney (1967) suggested that it was probably an anti-predator device (see also Errington, 1946; Tinbergen, 1939). Hochbaum, McKinney and Ward (Delta Seminar, 1969) also stressed the importance of food to breeding ducks, as did Geyr (1924) for the Mallard and Siegfried (1968) for the Southern Black Duck *Anas sparsa*.

In the Shoveler, although territorial behaviour does appear to ensure protection for the female from aggressive males, this may be little more than a secondary consequence of territory, as discussed by Hine (1956). Spacing to reduce predation (McKinney, 1965) seems reasonable and cannot be ruled out by the present data. Some resource essential to reproductive success may be defended, thereby justifying the considerable expenditure of energy by the resident male in maintaining the territory. Broods of dabbling ducks are very mobile (Evans & Black, 1955), and presumably feed little or not at all on the territory. However, the adult female may feed there exclusively during the later stages of laying, and for the entire incubation period because they spend little time off the nest (Ward, 1969). Certainly the laying and incubating female Shovelers in the present study fed for much of their time off the nest. The territory then appears to provide a measure of protection for the contained food resource and allow the female to utilize it undisturbed. If so, this would seem to be a reasonable functional explanation for the extended and well-developed territorial behaviour and pair bond of this species.

A further possibility is that an extended pair-bond and associated territorial behaviour might be especially important to Shovelers during re-nesting. Competition for territory sites was keen at this time because of drying of habitat and influx of new pairs. Those which were able to establish territories nested quickly, whereas the females of two non-territorial pairs did not nest at all.

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Summary

The territorial behaviour of wild Shovelers *Anas clypeata* was studied on a 1·9-km long roadside ditch at Delta, Manitoba, Canada. Most of the data used was derived from observations of seventeen marked males and three marked females. Breeding activity on the study area spanned 12 weeks and twelve different territorial pairs were observed. Breeding activity ceased late in the season partly as a consequence of widespread nest predation.

Aggressive behaviour of territorial males took several forms and contributed to the establishment and maintenance of territories. Such behaviour occurred primarily within 30 m of the focal loafing spot and was not noted further away than 90 m.

Boundaries were well defined only where there were frequent interactions. Defence was primarily of the water area and not the adjacent meadows. There was a vertical component to the territory. The area used by pairs became significantly smaller (0·9 ha) after the onset of egg-laying. Territory size did not significantly change later in the season despite an increased concentration of pairs.

Territories were remarkably stable and no pairs lost territories as a result of hostility. However, stability may break down when the pair-bond weakens with advance of incubation or when the nest is destroyed. Certain areas were occupied by as many as three successive pairs.

Pairs spent virtually all their time on the territory after egg-laying was well advanced. Females still used the territory after dissolution of the pair-bond although their activities were restricted to the area around the loafing spot.

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On the behaviour of the White-headed Duck with especial reference to breeding

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Introduction

The White-headed Duck *Oxyura leucocephala* is one of the rarer Eurasian ducks, with a total world population of around 15,000. The main wintering areas are in Turkey, Tunisia and Pakistan. A few nest in southern Spain, North Africa and Turkey, but breeding appears to centre on Kazakhstan in the Soviet Union.

Remarkably little was known about this duck's breeding behaviour in the wild and it had only once been kept for any time in captivity (Duran, 1961). These birds did not breed, despite a mistaken reference in the Zoological Record (Lassaletta, 1963). Attempts were therefore made to establish a breeding group at the Wildfowl Trust, Slimbridge. Mr Christopher Savage caught flightless moulting birds on Lake Khabbaki, Pakistan, and after several attempts three males (A, B, C) and three females (D, E, F) were established. A, C, D, F arrived on 16 January 1968, B and E on 13 December 1969.

Courtship display was observed in 1970, and over the next two summers a general picture of the display patterns was built up. However, activity petered out towards the end of each June. While in S. Africa Mike Lubbock, the Curator, had noticed the related Maccoa Duck utilized disused nests of other waterfowl. Also there were Soviet reports (e.g. Dementiev & Gladkov, 1952) of Whiteheads using old nests of coots and diving ducks. He therefore provided seven potential nest-sites in June 1973. Two were actual disused Coot *Fulica atra* nests. The others were constructions of bamboo and reeds on wire-netting bases staked out over the water.

The strategem was a success and on 24 July one female was found to have laid. Observations, which had been stopped when two males had lost the blue of their bills, were resumed as intensively as possible. The study continued piecemeal, no full-time ethologist being available. Attention was concentrated on the incubation behaviour and on the behaviour of the subsequent young, but other activities were noted, particularly the feeding behaviour. Thus a general picture of daily routines emerged, albeit related to one period of the year, July to October.

The scene of observations

The birds, pinioned when brought into captivity, lived on a pond 60 × 30 m. The water varied from shallows barely awash, down to 2 m. The bottom was muddy, but most of the edge was rough-concreted to prevent erosion. Clumps of vegetation were scattered along the margin but the water itself was open. The pond and surrounding grassy paddock of 0·7 ha were shared with a score of European species of ducks and geese, mostly also pinioned and totalling some seventy individuals.

The Whiteheads seldom left the water and did not become hand-tame for food as did many other species. Rather, they were indifferent to humans. This meant that the natural behaviour patterns were likely to be relatively unmodified. Observations could be made without any hide, the birds often being within 5 m and seldom as far away as 30 m.

The adult individuals were easy to tell apart at such close quarters. Savage (1965) had already remarked on the individual variability in the species. Of the males, A had many white feathers in the black crown and his bill was still blue; B had distinct black spots on the white cheeks; C had black bars extending down from crown to the eyes. Of the females, D had a large splodge of white above the cheek stripe; E a much smaller, V-shaped mark; F no additional mark at all.

General activities

An estimate of the time spent in various activities was arrived at simply by noting at intervals what each individual was doing. These 'activity 'snapshots' were scattered throughout the day and the intervals were not less than 15 minutes. For the three males and the one female (F) which did not nest, 311 snapshots were collected, giving the divisions of activity shown in Table 1. The middle of the day was largely spent in sleeping, the birds being more active during the early morning and late afternoon. When awake (i.e. not resting with the bill tucked back among the scapulars) the commonest activity was preening. This may have been particularly intense because the moult was in progress. Nevertheless, casual observations at other seasons indicate that these are

Table 1. Division (%) of activities of four adult White-headed Ducks throughout the day (311 behaviour snapshots)

Time	Sleeping	Preening	Diving	Swimming	No. snapshots
Before 09.00 hours	35	27	12	26	21
09.00–12.00 hours	55	29	10	6	121
12.00–15.00 hours	64	22	9	5	49
After 15.00 hours	45	25	10	20	120
Overall	51	26	10	13	311

Table 2. Division (%) of day-time activities in four adult White-headed ducks (311 behaviour snapshots)

Bird	Sleeping	Preening	Diving	Swimming
A	43	33	11	13
B	56	22	10	12
C	52	27	9	12
F	56	23	8	13

noticeably 'itchy' ducks and spend a great deal of time and effort on re-arranging their close-packed plumage. Quite often the Whiteheads came to the pond edge to preen, particularly their bellies. They then stood near-upright with no sign of leg weakness such as in grebes. The Whiteheads stand firmly and steadily, one individual for over half an hour. On a few occasions the birds walked for short distances, stomping along, penguin-like, without indications of strain.

One male (A) spent more time preening than the other adults (Table 2). Again this may be related to the state of moult, as he was still blue-billed.

Feeding behaviour

Food for the collection birds (mainly barley, but with some biscuit crumbs) was strewn along one stretch of shore and into the water there, at about 08.30 hours and 16.30 hours. From Table 1 it will be seen that the Whiteheads' diving bouts were not tied to these artificial feedings, but evenly scattered throughout the day. They did not gather in the feeding area when the food was thrown, as did most of the other species. While they clearly make some use of this bounty, they also spent a lot of time feeding in other parts of the pond. What the Whiteheads were feeding on is uncertain, as food was always swallowed under water. There was no floating or emergent vegetation; some seeds might fall from the trees and other vegetation on the steep little artificial hill at one end of the pond. Soviet studies speak mainly of vegetable matter, especially seeds, in the guts of shot birds. A single specimen examined by Savage contained seeds. Possibly the Slimbridge birds were also collecting animal matter, such as chironomid worms known to abound in the detritus.

Rather few studies have been made on the diving of any ducks (e.g. Dewar, 1939; Willi, 1970) so data on this aspect of behaviour was collected; twelve hundred dives, 200 for all of the six adults. Table 3 gives the maximum and mean dive lengths and a measure of the variability of dive-length, the coefficient of variation, (i.e. standard deviation divided by the mean and multiplied by 100). The lower the coefficient, the closer lie the diving times about the mean. The coefficients for the four adults were similar, but male C consistently made longer dives than the others, although feeding in the same parts of the pond. (D and E were timed the next April/June).

Feeding occurred in long bouts, as many as fifty dives in succession being noted. A smaller sample of times spent on the surface between dives during a bout was noted and showed more difference between individuals and also more variability (Table 4). Maximum times on the surface are not relevant, the arbitrary upper limit (30 seconds) being imposed to decide that one diving bout had ended. Male B, which made the shortest dives, did spend the shortest time on the surface. Inspection of the full data showed there was also a general tendency for short dives to be followed by the shorter pauses, and the long dives by longer pauses. However, the relationship is by no means straightforward. Clearly, physiological limitations are not

Table 3. Diving times (seconds) of adult White-headed Ducks, 200 dives per bird

Bird	♂A	♂B	♂C	♀D	♀E	♀F	All
Maximum	33	34	40	34	34	33	40
Mean	18·8	18·5	25·0	23·1	22·6	19·0	21·9
Variation	31	29	29	27	31	31	32

Table 4. Times (seconds) on surface between dives in adult White-headed Ducks

Bird	♂A	♂B	♂C	♀D	♀E	♀F	All
Number	122	105	63	131	144	35	600
Mean	6·4	5·8	8·8	7·9	8·7	9·5	7·6
Variation	65	45	48	37	44	54	5·1

deciding the length of the shorter dives, and the pause after a longer dive may have had as much to do with taking a general look around, and possibly getting more food down the gullet, as with regaining the breath.

The dives themselves appeared almost as effortless as a grebe's, the bird heading under with a barely perceptible kick. In most cases the dive was so deep that no eddies appeared on the surface as evidence of the bird kicking down below.

Social behaviour: courtship

The other main division of activity, swimming, covered not only casual movements between bouts of sleep, preening or feeding, but also directed activities of a social nature. Aggression towards another member of the species was usually in the sexual context. Typical was *open-bill threat*, with the head thrust low, the body hunched and scapulars raised (Figure 1). The posture was sometimes held with the bill closed while the bird swivelled round to follow a moving opponent. Often a *hunched-rush* (Figure 2) across the water followed, head pulled into shoulders and scapulars raised. The opponent usually escaped by diving. The attacker then often gave a *side-ways shake* of the head, sometimes with the bill in the water to produce a splash. Actual physical contact was rare and seldom lasted more than a few seconds. Females attacked males as well as *vice versa*, but the females were more prone to give a simple *open-bill threat*. On the whole, however, the Whiteheads went about their daily business without getting involved in fights. There were no indications of territorial defence by the males, in contrast to the Maccoa Duck (Clark, 1964). The nesting females did defend the nest and its immediate surrounds.

The initial form of courtship appeared in late March with the development of *flotilla-swimming*. Males and females swam in close formation at considerable speed, about 1 m/second, up and down the pond for as much as an hour at a time. Positions within the formation changed, but often a female was in the lead, with its *head-high*, the tail at 45° or flat in the water. *Sideways-flicks* of the head appeared to be flight intention movements and sometimes led (in these pinioned birds) to scutter-rushes across the water. In unpinioned birds these would presumably have developed into group flights like the *ringing-rush* described in other *Oxyura* (Johnsgard, 1967). Generally *flotilla-swimming* birds were silent, but a female sometimes uttered a very soft *gek* and a male a harsh grunt. Several ritualized movements occurred in *flotilla-swimming* (as well as in other contexts). *Dip-diving*, the body being very briefly immersed in a down-up movement, and *cheeking*, the head rubbed on the shoulder, derive from body-care movements. *Wing-shuffling*, the folded wings raised and lowered rapidly, is possibly a thermoregulatory movement, according to Siegfried (1973a). *Dab-preening*, the bill rapidly and repeatedly jabbed into the breast feathers, has probably given rise to the mistaken impression of field observers that the Whitehead has a *bubbling* display like the Ruddy Duck *O. jamaicensis* (e.g. Dementiev & Gladkov

Figure 1. Open-bill threat by female D.
Mary Evans

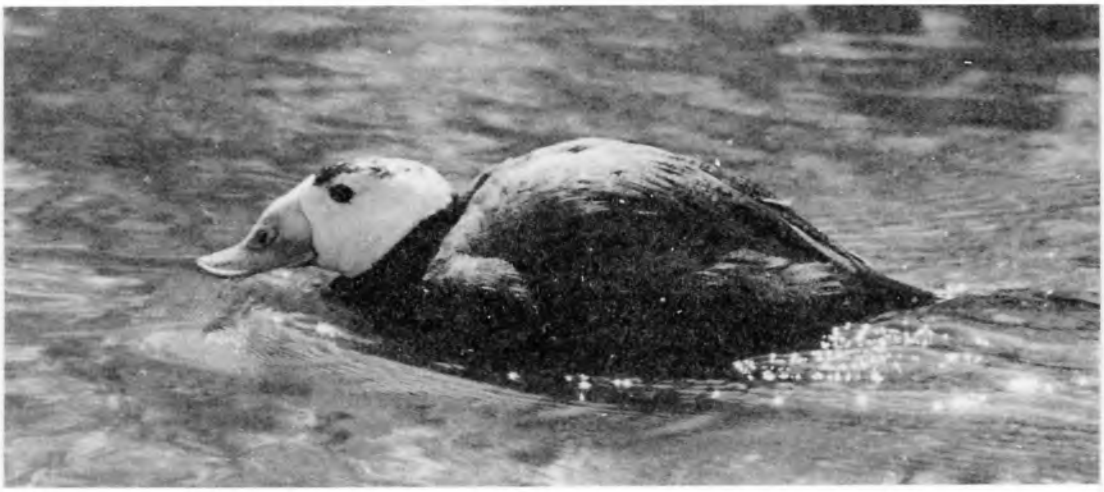

Figure 2. Hunched-rush. *Philippa Scott*

1952; Mountfort, 1958). However, the *dab-preen* was not accompanied by any inflation of the air-sacs nor any mechanically produced sound (or vocalization). The tracheal structure in the male Whitehead, undescribed according to Johnsgard (1967), is simple, there being no bullae or other protruberances. A similar *dab-preen* movement has been described in the Australian Blue-billed Duck *Oxyura australis* (Johnsgard, 1966). Since *dab-preen* frequently appeared after a *hunched-rush* at another male, it may be a ritualized displacement behaviour deriving from conflicting tendencies of attacking and fleeing.

More elaborate group displays appeared next. The males swam rapidly in various directions making a *tickering-purr*. This is somewhat reminiscent of the rattle of the male Garganey *Anas querquedula*, but softer and more continuous. Analogy has also been made with the rapid bouncing of a ping-pong ball on a table. Certainly the rather delightful impression of a clock-work toy results.

A male would *hunch-rush* first another male, then, rather less aggressively, a female. It then swung broadside on to the female, in a *sideways-hunch*. Both the head and the tail, spread in the water, were twisted towards the female (Figure 3). The *tickering-purr* continued, the tail was vibrated and the legs paddled rapidly. The male then swam away and, if the female did not follow, *hunch-rushed* back to do another *sideways-hunch*.

Figure 3. Sideways-hunch. *Philippa Scott*

The series of *sideways-hunchings* might peter out or give rise to an explosive movement, the *kick-flap*. The male's bill, and sometimes the whole head, plunged vertically into the water, the folded wings were jerked upwards and the legs kicked vigorously, often both at the beginning and end of the movement. There would seem to be elements in this display common to the *sousing* described by Johnsgard (1966) in the Australian Blue-billed Duck, but there was no inflation of the neck. After the *kick-flap* there followed a high intensity version of the *sideways-hunch*, *sideways-piping*. The bill was opened and pointed at the female and a series of high, bi-syllabic, reedy cries made. In timbre these resembled the sound produced by the male Black Scoter *Melanitta nigra*. The tail was twisted towards the female, fully spread and strongly vibrated between each double pipe; the folded wings were also slightly raised and lowered. Half a dozen pipe-pipe/tail-vibrate/pipe-pipe/tail-vibrate sequences might follow before he subsided.

The male then performed the *head-high-tail-cock*. The head was raised, with the bill horizontal, and the *closed* tail (*contra* Dementiev & Gladkov, 1952) cocked until it just passed the vertical (Figure 4). The head and tail raisings were synchronized and rather slow and deliberate as if they were being pulled up by puppet-strings. If the tail was in the water at the start, however, it flicked into the upright position more rapidly. The posture was held for a few seconds and then both head and tail were lowered, again quite slowly. Although looking very like the Ruddy Duck at the start of its *bubbling* display, the Whitehead does *not* beat its bill on the breast, the neck does not appear inflated, and no sound is produced. Again, the Whitehead does not insistently manoeuvre itself in front of the female, exposing to her its white under-tail coverts, as does the Ruddy. Once a Whitehead male doing the *head-high-tail-cock* was observed to have its penis protruding stiffly as the tail flicked up. Apart from this evidence of excitement, the *head-high-tail-cock* may well be a low-intensity movement. We shall see later that the downy young takes up a similar posture when agitated, as when separated from its mother. The *head-high-tail-cock* tends to come at the end of more intense display movements, as after a series of *sideways-hunches* peter out, or even when the male has not for some time been engaging in overt displays. In such circumstances as many as nine *head-high-tail-cocks* have been observed in succession, with intervals of up to 10 seconds between them. There is a variant of this posture in which the tail remains cocked but the head is lowered, and then raised again.

The female reaction to even the most intense male displays in the spring was minimal. There might be *open-bill* threat against an importunate male; if she followed him, the feathers on the top of her head might be slightly erected. There seemed to be no greeting behaviour between male and female. Indeed, no definite pair-bond appeared to be established for the birds were not seen to separate off in pairs. Copulatory behaviour was not observed. In other stifftails it is brief and unspectacular. No nest-showing behaviour was seen. Curiously enough, in September, after breeding and with all the birds in eclipse plumage, bouts of group courtship activity occurred and the females then indulged in male-like behaviour, producing *sideways-hunching*, with open bill but only a wheezy sound emitted, *kick-splashes* and *head-high-tail-cocks*. The movements were not to be distinguished from those of the males (which had then also lost their *pipe-pipe* at this time). Some fascinating conjectures about hormonal balances must be held in check until many more displays have been observed.

Nest building and egg-laying

When it was discovered on 25 July that laying had started in one of the Coot's nests, female D already had five eggs. Two more were laid in the following 2 days, but three were kicked out of the nest on 30 July. These, and one other, were removed and incubated artificially, leaving her with three to incubate. Female E was seen to enter this nest on 25 July (opening a doubt whether all the eggs therein belonged to D). However, E thereafter became more interested in the second clump containing another Coot's nest and was seen sitting there, making *sideways-passing* nest building movements on 26 July, and driving other birds away from it the next day. More nest-building and defence were observed on 31 July and 4 August. On 9 August the nest-site was inspected early in the day and found to have two eggs. Two more had been laid by the morning of 11 August and the clutch was complete, at five, by 13 August. It would thus appear that eggs are laid at daily intervals. This is quite a prodigious performance in view of the large size of the eggs; a sample of ten gave an average weight of 97 g. Thus a clutch of seven represents about 100% of a female's body weight.

The third female, F, was observed on another nest clump-site on 19 September, making several bursts of nest-building movements. She had then completed wing and tail moult. Several further bouts of nest-building occurred in the next few days but no structure was formed, and this bird was considered to be a non-breeder. However, when she died 5 months later (27 February 1974), avian tuberculosis being diagnosed, the oviduct was found to be expanded, as if egg-laying had occurred, and a finger-nail-sized piece of egg shell was extracted. What happened to the egg(s) she produced is not known, but obviously she should have been classified as a failed-breeder.

Another behavioural oddity that came to light was nest-building by a *male*, B. He was first observed doing this on 14 August, in a nest-clump not favoured by any of the females. He seized vertical reeds, pulled them

Figure 4. Head-high-tail-cock. *Philippa Scott*

to him and then *trampled* them under (a difficult manoeuvre with the legs mounted so far back). He even tried to pull down the bamboo rods supporting the nest-clump. Reeds in the water were picked up and *sideways-passed* in typical fashion. On this occasion persistent and unmistakable nest-building movements continued for 17 minutes and a photographic record was obtained (Figure 5). Similar activity was seen several times during the next two weeks and a distinct platform became visible. Indeed it is probable that this behaviour is to be considered on a par with the pre-breeding platform-building described in both sexes of the Ruddy Duck by Siegfried (1973a). However, the thermo-regulatory function therein proposed (the platform enabling that essentially southern species to get out of the cold water) can hardly apply at this season. Again, we resist the temptation to speculate on hormonal balances (the bird being well into the eclipse moult) that could lead to sexually ambivalent behaviour.

Incubation behaviour

Although the nest and eggs have been described in the wild (summary in Bauer & Glutz, 1969) no ornithologist had ever seen the female sitting on the nest. This, coupled with a report of eggs hatching after being kept at room temperature for a week, led to the legend that they required no incubation by the female, except perhaps for the first few days. We were now presented with the opportunity to check reality and watches were maintained as often and as long as possible once incubation began. Close investigation was impossible as no disturbance of the birds was acceptable. Female D was only partly visible when on the eggs, E wholly hidden.

In the 25 days between clutch completion and hatching, D's nest was watched on 21 days in thirty-three sessions totalling 49·7 hours, and timed between 06.46 hours and 21.00 hours. In the comparable period E's nest was watched on 16 days in twenty-nine sessions totalling 67·3 hours. D was seen off the nest on twenty-five occasions, E on twenty-three. The time spent off the nest varied from 2 to 38 minutes. Several minutes prior to the departure from the nest D would become restive. Both birds when they appeared at the ramp leading down to the water, made some *sideways-passing* and other nest-building movements. They would then slip into the water and dive, reappearing well away from the nest. Feeding dives were of rather briefer duration than normal (Table 3). Much of the time off the nest was spent in preening and bathing. The nest would then be approached cautiously, in a series of dives, until the foot of the ramp was reached. As the bird climbed out it would briefly repeat the *sideways-passing* nest-building movements. Female D could be seen pulling down surrounding stems to form a canopy while on the eggs. The females did *not* line the nest with down (*contra* Dementiev & Gladkov, 1952). Only a few flecks of down were found in the nest at the end of incubation, such as could have been accumulated by chance.

Figure 5. Nest- (or platform-) building in an eclipse male. *Mary Evans*

The frequency of absence by D from the nest increased as incubation progressed (Table 5). Thus she left the nest about once every 3 hours during the day in the first half of incubation. E left rather more frequently and for longer periods. In the second half of D's incubation the frequency of exodus was nearly doubled although the length of absence was similar. Watch on the second half of E's incubation was not extensive enough to give comparable figures. There is thus some support for the contention that the embryos become more self-sufficient as incubation progresses.

The eggs hatched with startling rapidity. Thus none of D's showed any crack when examined late in the afternoon of 19 August but the one young was on the water by 08.35 hours the next morning. Those hatched in incubators did so in little more than 12 hours from the appearance of the first crack. Weights of those raised artificially were on the first day 57, 58, 59, 60, 64, 65 g. In all cases the incubation period appeared to be 25 days.

Mother/young behaviour

The single young hatched by female D had a rather abrupt entry into the outside world. It was kicked on to the water when its mother attacked a full-winged Red-billed Whistling

Table 5. Incubation activity of female White-headed Ducks

Female	Incubation period	Observation		Times off	Mean duration	Observation time per exodus (minutes)
		Days	Minutes			
D	Days 1–13	10	922	5	13·4	184
E	Days 1–13	12	3494	22	18·5	159
D	Days 14–25	11	2060	20	12·3	103

Duck *Dendrocygna autumnalis* that poked into the nest. The mother then returned to the nest, apparently not noticing her loss. The duckling swam vigorously, high in the water and with both head and tail held up, looking very large for its size. It approached any duck it saw, but they shied away. The male A approached and did several *sideways-hunches* at it (perhaps analogous to male Ruddy Ducks giving the *bubbling* display to newly hatched young). Female F approached, gave the antagonistic *open-bill* display, shied away and dived. The duckling also dived, for 5 seconds, and that after only 7 minutes on the water. It then approached Red-crested Pochards *Netta ruffina*, Common Eiders *Somateria mollissima* and White-eyed Pochards *Aythya nyroca* but these either avoided or poked at it. Finally at 08.53 hours the mother came off the nest, went straight to the young, dived in front of it and led it back on to the nest at 09.00 hours. They both came off for 9 minutes at 09.40 hours and for at least four other short excursions during the day.

The two ducklings left with E had a less traumatic emergence on 9 September, remaining until 14.30 hours, although E had briefly emerged, by herself, at 09.05 hours. They were then eased on to the water by a warden inspecting the situation. One duckling dived for 2 seconds after 7 minutes, and up to 7 seconds within 14 minutes. They were on the water for 97 minutes before the mother led them back to the nest, apparently for the rest of the day.

Both females, on this and the next 2 days, were several times seen to approach a duckling with the bill slightly open and scapulars smoothed (as if in low intensity threat) and to touch it lightly and briefly on the head (Figure 7). This *head-touching* presumably served to strengthen the family bond. The female also produced a low *rattling-purr* especially when the duckling had strayed. For their part the latter have a bi-syllabic *whit-whit* call in this situation and the head and tail were sometimes raised in a facsimile of the *head-high-tail-cock* of the adult. There was also a distinctly different low *twitter*, apparently a general contact, contentment call between the young themselves.

On the 2nd day D's duckling was on the water for at least three periods, one more than an hour, returning for prolonged sojourns on the old nest. The female still made building movements when leaving and returning to the nest. Use of the nest continued into the 4th day, when it became difficult because of a temporary (artificial) lowering of water level. Other clumps were used on the 5th to 7th day, but with the restoration of the water level the original nest site was used again, mainly only at night, until at least the 12th day. Thereafter it became trampled, by other birds(?), and waterlogged and had been abandoned by the 20th day. This duckling fledged successfully. It was able to fly by the 58th day.

The ducklings of E spent more time on the water during their second day, including bouts of sleeping. One water-borne session lasted over 4 hours before the nest was re-entered. This nest remained in good condition for much longer and was still being used for resting, at least at night, until the end of the 23rd day. One of the two ducklings was picked up dead on the 7th morning. The other continued in apparent good health for nearly a month. But its growth then began to fall behind in comparison with its three siblings being reared artificially. Possibly, as

Figure 6. Female E on nest ramp, with young.
Mary Evans

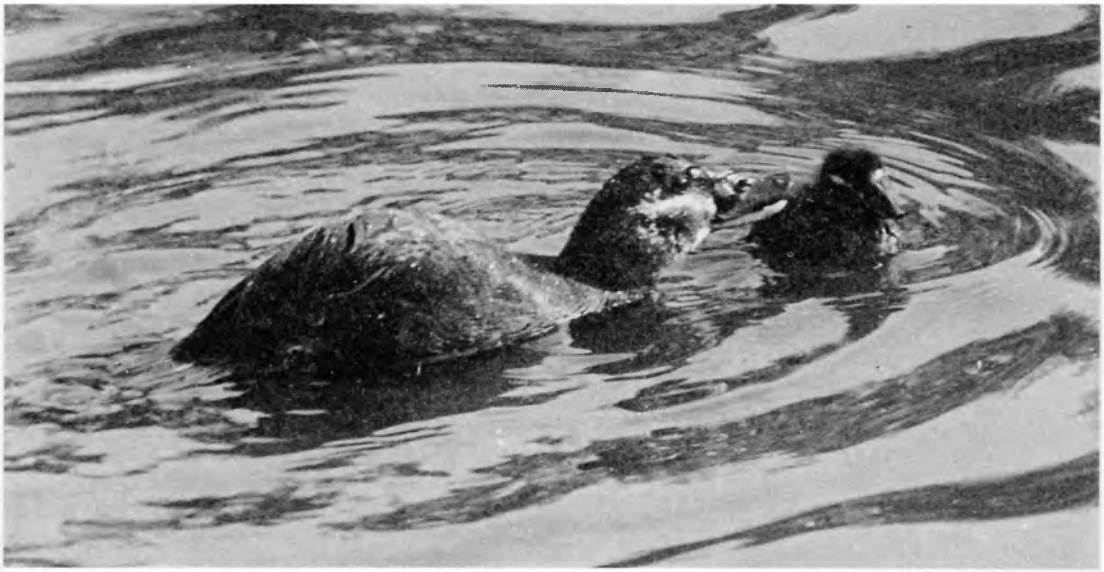

Figure 7. Head-touching by female E to young. *Mary Evans*

it was now mid-October, the natural food (perhaps chironomid larvae) was increasingly difficult to obtain. It was not seen after the 37th day.

Both females proved to be excellent mothers; having only one young apiece may have eased their task. They defended their young against all comers, driving off birds as large as Greenland White-fronted Geese *Anser albifrons flavirostris*. *Open-bill threat* (Figure 1) frequently sufficed, but *hunched-rushes* and actual physical attacks were seen. The mother remained within a few yards of the young for the first 2 weeks, spending more time diving (Table 6) but making much shorter dives than usual (Table 7). Thus in the 1st week the average dive length was about half that which the individual would do when by itself. Occasionally full-length dives would be made, greatly increasing the coefficient of variation. In the 3rd week the chick was left more and more on its own and the mother's diving times lengthened. By the 5th week they were virtually independent of each other.

None of the males paid any attention to the chicks, except for the one immediate post-hatching instance already noted.

An *Oedipus*-like behaviour was observed in the duckling of D. This bird, subsequently

Table 6. **Division (%) of day-time activities of two female (Ad) and two young (Y) White-headed Ducks, post-hatching**

Period	Sleeping		Preening		Diving		Swimming		No. snapshots
	Ad	Y	Ad	Y	Ad	Y	Ad	Y	
Day 1/2	61	62	8	8	11	13	20	17	71
Day 3/7	43	40	11	10	22	38	24	12	122
Week 2	36	46	22	11	22	38	20	5	65
Week 3/4	36	39	20	12	13	40	31	9	111
Week 5/7	42	40	18	17	6	23	34	20	98

Table 7. **Diving times (seconds) of two adult female White-headed Ducks, in relation to family responsibilities (cf. Table 3)**

Condition	Incubating		Accompanying young					
			1st week		2nd week		3rd + week	
Bird	D	E	D	E	D	E	D	E
Number	15	35	63	246	47	135	177	73
Maximum	28	25	22	25	30	26	33	27
Mean	18·7	15·1	9·9	9·1	12·3	15·0	22·4	18·0
Variation	28	21	50	52	47	43	24	31

checked as a male by its cloaca, was apparently stimulated by an outburst of courtship activity in the adults to go through a series of sexual movements, clearly directed at its own mother. This was on its 32nd, 33rd and 42nd days. The duckling produced very definite, if slightly sketchy, *sideways-hunches, kick-flaps, sideways-pipings* (but with only a wheezy sound) and *head-high-tail-cocks.* Female D, for her part, responded, even more astonishingly, with all these typically male movements, looking very much as if she were 'teaching' them to her offspring. One can only speculate about the psycho-physiological states of mother and child that produced these remarkable antics. Fortunately they were captured on ciné-film and sceptics can be convinced at leisure.

Maturation of diving ability in the young

With such readily observable birds the attempt was made to follow closely the development of diving ability. The aim was to record at least fifty dives for each life-day up to 7 weeks. In the event nearly three thousand dives were timed and in the first 6 weeks only the 10th day is without data. In the 7th week data was obtained on the 46th, 48th and 49th days. When dives of the two ducklings were compared at the same ages, no significant differences emerged and the material is therefore lumped together. The second duckling only contributed data up to the end of the 4th week.

The results for the 1st week are set out in Table 8. The rapid occurrence of the first dive after leaving the nest has already been mentioned, but in the 1st day dives were infrequent. The young spent some time dibbling along the water's edge, and this feeding method was also in evidence during the 2nd day. Thereafter nearly all the food was obtained by diving. The dives were slightly longer on the 2nd day, but the main improvement came on the 3rd day when both maximum and average dives reached a level maintained through the rest of the week.

The subsequent increase in the diving times was a slow process and setting out the data day-by-day would occupy too much space. They are therefore lumped by weeks in Table 9. In the 2nd week there was little improvement. The 3rd week saw an increase which was maintained through the 4th. Another step-up was clear by the 5th week and again this was maintained during the 6th. By the end of the 7th week the duckling had a diving performance not very dissimilar from those of the adult males A and B (see Table 4). In the following spring 200 dives by this young bird gave the following data: maximum 32 seconds, mean 20·1, variance 20.

It will be seen from Table 6 that, after the initial 2 days, diving was the major activity of the ducklings' day. This continued until the surviving young became feathered (weeks 5/7), but even then it was doing about twice as much diving as the unattached adults (Table 1). Its preening activity was then also approaching the adult level.

The newly hatched young obviously had difficulty in plunging its downy body through the water and had to take a distinct leap up and over, when immersing. This leap, and the twin water jets kicked up, were still noticeable well into the 4th week. There was also typically a slight water splash after the duckling emerged from the dive, produced by a sideways flick of the bill and probably disposing of water in the gullet. By the 6th week, with the feathers now well developed, the duckling was diving almost like an adult, with hardly any forward leap. Indeed it is clear that changes in bodily proportions as

Table 8. Diving times (seconds) of two young White-headed Ducks in the 1st week of life

Day	1	2	3	4	5	6	7
Number	22	129	189	95	101	141	68
Maximum	11	12	17	16	16	15	15
Mean	5·9	7·7	11·8	12·5	12·1	12·2	11·5
Variation	40	26	18	11	9	18	13

Table 9. Diving times (seconds) of two young White-headed Ducks in the first 7 weeks of life

Week	1	2	3	4	5	6	7
Number	745	495	557	426	387	306	85
Maximum	17	17	19	22	28	30	28
Mean	10·9	12·6	14·2	14·9	17·1	17·5	18·1
Variation	25	17	14	23	20	21	24

Figure 8. Female E and young, preening. *Mary Evans*

well as feather development govern the development of diving ability, but a much more detailed study is required properly to relate these factors.

Although making shorter dives than the adults, the young spent more time on the surface between dives (Table 10). There was also less variability than in adults and even less relationship to the length of the preceding dive. Presumably while under the care of the mother they do not have to spend time looking around for danger. The tightness of the diving times around the means (Tables 8 and 9) also suggests that the young birds were diving near their physiological limits. (Next spring 144 pauses by D's averaged 8·4, variation 51.)

Table 10. **Times (seconds) on surface between dives of young White-headed Ducks**

Birds	D's	E's
Number	303	227
Mean	8·9	10·7
Variation	36	26

Artificial rearing

Of the three birds left with their mothers, one was reared. All four eggs taken from female D for artificial incubation were hatched but the ducklings were not reared. One newly hatched young and two near-hatching eggs were taken from female E. All three were successfully reared. The diet consisted of protein-rich 'Pro Nutro' and some duckweed and millet. The rearing compartments were modified to provide a large deep water tank right from the start. Their average weights, taken at weekly intervals, increased from 58 to 75, 146 and 243 g. This rate of growth was similar to that obtained with Ruddy Ducks (Siegfried, 1973b)

Taxonomic considerations

Johnsgard (1967), summarizing the information then available on the behaviour of stifftails, proposed a dichotomy within the *Oxyura* group. On the one hand were the Ruddy Duck *jamaicensis* and White-headed Duck *leucocephala*, while on the other were the southern stifftails, the African Maccoa Duck *maccoa*, the Argentinian Ruddy Duck *vittata* and the Australian Blue-billed Duck *australis* (the Masked Duck *dominica* appeared rather separate). Our present observations suggest that *leucocephala* has more in common with the southern group. The *dab-preen* appears similar to that of *australis* and the *kick-flap* has elements of *sousing*. *Bill-dipping* and *water-flicking* was also seen in *leucocephala* and the *ringing-rush* would probably occur in full-winged birds. The *bubbling* of the *jamaicensis* is absent, as was calling during *head-high-tail-cock*. There appeared to be no inflated neck display, either using the oesophagus or air sacs.

One can argue taxonomics indefinitely and not to much avail. Perhaps it is best to say that radical divergences within the group do not appear to be indicated by these further behavioural studies.

Acknowledgments

This study would have been impossible without the initial determination of Christopher Savage that a captive group should be established at Slimbridge. Tommy Johnstone, former Curator, got the birds settled, and Mike Lubbock, present Curator, showed the avicultural brilliance that started breeding off. We are grateful to Tim Appleton and to Dr Janet Kear for information on the artificial rearing and to Dafila Scott and many members of staff for casual observations on the behaviour of the birds on the pond. Dr C. Violani very kindly let us use data he accumulated during two periods of study at Slimbridge. Professor F. Bernis clarified the captivity record in Spain.

Summary

The first breeding in captivity of the White-headed Duck *Oxyura leucocephala* at Slimbridge enabled studies to be made of courtship, nesting, incubation and mother/young behaviour. Many undescribed courtship movements are reported. Two females nested in disused Coot *Fulica atra* nests. Nest building movements were observed in a female which failed to breed and also in a male. Incubation was for 25 days, the females only coming off the nest for short periods during the day. They made excellent mothers. An Oedipus-like display of a duckling to its mother was observed, and adult females occasionally showed male courtship gestures. The males took no part in rearing the young and no definite pair-bond appeared to be established. One duckling was reared to maturity by its mother, and three others artificially.

The diving ability of the adults, and its maturation in the ducklings, was examined in detail, over 5,000 dives being timed. There is a brief discussion of taxonomic considerations.

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Postscript

In 1974 both females laid earlier, D starting on 30 June (6 eggs), E on 8 July (5 eggs). Both clutches were removed to incubators on 15 July. Second clutches were started, by D on 31 July (4 eggs), by E on 24 July (7 eggs) after an interval of only 9 days and still producing an egg a day. All 22 eggs were successfully incubator-hatched and 20 young reared.

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The development of rank order and aggressiveness in a group of juvenile Greylag Geese

BRITT-MARIE STAHLBERG

Introduction

The 'triumph ceremony' appears in all species of true geese (Heinroth, 1910; Lorenz, 1935, 1963; Klopman, 1961; Fischer, 1965; Fabricius & Radesäter, 1971).

The triumph ceremony in its most typical form is schematically presented in Figure 1 from Fischer (1965). Numbers 1–4 show the first part of the ceremony—*Rollen*—in which the male of the pair attacks a real or an imagined enemy. When the attack is over, he returns to the female loudly trumpeting with his neck upwards. Numbers 5–6 show the second part of the triumph ceremony—*Schnattern* is the 'greeting'. Here the birds meet each other with a cackling sound and with low protruding necks which are directed past each other. This part of the ceremony has an ontogenetic precedent in the youngster's vi-sound with neck protruding, while *Rollen* appears in adulthood without any earlier stage in its ontogeny (Fischer, 1965). According to Lorenz (1963) the cackling ceremony functions as a bond to keep individuals who know each other together.

Heinroth (1910) found no social hierarchy nor disagreement within a goose family. Similarly, Lorenz (1935) wrote: 'a rankless tolerance is kept until the late autumn. Then at first the unity of the family group disappears and is replaced with a hierarchy'. Fischer (1965) and Lorenz (1963) think that there is no aggression and therefore no pecking order between goslings in such a group in the Greylag Goose *Anser anser*. In contrast, Fabricius & Radesäter (1971) and H-B. Rodemar and R. Larsson (unpublished) have observed lively fights, with an obvious hierarchy, between brothers and sisters of the Canada Goose *Branta canadensis*. Collias & Jahn (1959) have also observed fights between goslings of the Canada Goose. Fabricius & Radesäter (1971) and B. Wasstorp (unpublished) have even seen aggressiveness with a hierarchical arrangement in the Greylag.

The main endeavour of the present work is to see whether or not there exists a rank order between the goslings in a family group of Greylag goslings, and to investigate the relationship of aggression to rank order.

Materials and methods

This investigation was made at the Zoo-

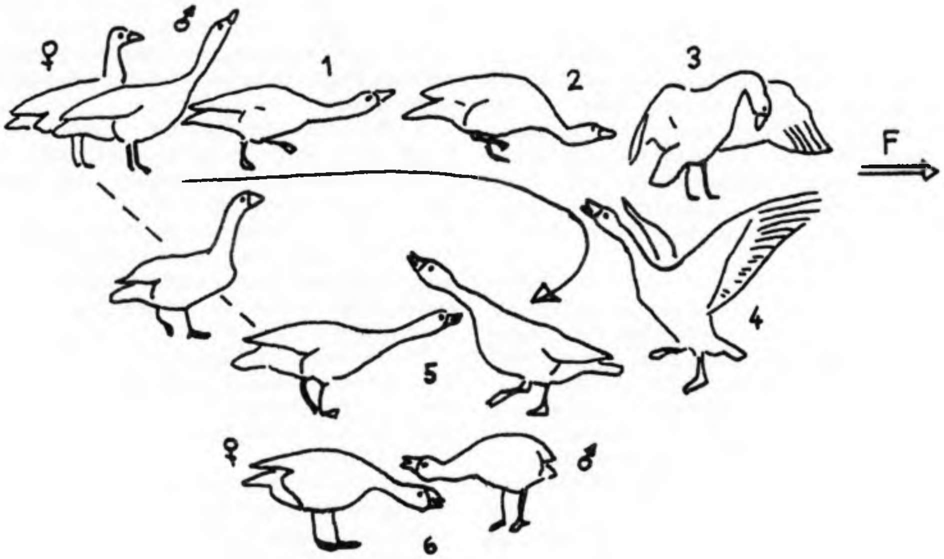

Figure 1. The triumph ceremony of the Greylag Goose schematically illustrated (from Fischer, 1965).

logical field station Öster-Malma, 100 km south of Stockholm, 5 May–26 June 1972.

The group consisted of five Greylag Geese from eggs taken from nests belonging to a wild breeding population in Kalmarsund on the south-east coast of Sweden. The eggs were hatched in an incubator, and the goslings marked with coloured plastic leg rings.

The time for the hatching varied between the daytime of 7 May and the night time of 9 May. Observations began on the 4th day, i.e. 12 May.

White-Blue died on the 4th day and was replaced by a new gosling hatched the night of 8 May.

After the hatching the goslings were moved to another, drying, incubator. They were taken from this machine at age 20–24 hours for 'imprinting' to me as their foster-mother. They were placed at my feet one by one. I moved forward, with a constant repetition of the sounds 'come-come-come'. This procedure was repeated once or twice and then the imprinting was done twice again with the whole group together.

For 9 days the geese were kept in a box furnished with a warming lamp. Then they were moved to a room with a water basin and connected with a fenced area outside. They were fed with growth pellets, given in a crushed form for the first week. They were able to graze all kinds of herbs and grasses during the day. Some vitamins were added to the drinking water.

All types of activity of the goslings were noted along with the time of every movement during 4–6 hours each day. The observations were made out of doors except on a few occasions when the weather was too bad.

This study primarily investigated behaviour showing aggression, inferiority and dominance. Aggressiveness refers to behaviour with definite pecks against an antagonist. Inferiority was indicated by a 'facing-away', and dominance by the lack of this movement. The activities were filmed with a super 8 cine camera, and a motor-driven slide-camera.

Most of the material deals with spontaneous activity. A very small part arises from experiments in which two siblings were placed about 10 m from each other. Usually they then run towards each other and their reactions in respect to each other, and towards the others in the group were observed. These artificial confrontations were done every day from the time that the goslings were between the ages of 7 and 14 days. After that they seemed so accustomed to the situation that they no longer reacted to each other.

Results and discussion

Some of the important developments in the ontogenesis of the Greylag Geese are given below.

First day: any form of disturbance in the environment elicited a characteristic greeting-call 'vi-vi-vi'. The sound was high intensity followed by a neck-protruding. This greeting was very seldom directed towards the stimulus. Just before they fell asleep, they made a high soft buzzing sound. A contact call, elicited during imprinting, was distinguished from the greeting call by having a higher degree of continuity and slightly shorter syllables. Its function seemed to be to keep the group together. If any of the goslings moved away from the group, he uttered a shrill screaming peep of abandonment. During such a scream the lonely gosling ran about until he found his brothers and sisters, whereupon the greeting calls were followed by contact calls.

Second day: greetings were directed towards the stimulus, usually another gosling, which usually answered the greeting. The goslings bit each other's bills and pecked eyes and claws. These seem not to be aggressive acts but more resulting from curiosity and interest in contrasting, obvious objects.

Third day: the first aggressive behaviour was observed. When real bites were given between the goslings, a facing away or a flight from the place of contact resulted.

Fourth day: greetings with evident facings away appeared.

Fifth day: 'buffing' and pushing movements were made in the group when they were going to sleep. This behaviour probably represents the attempts of normally raised goslings to get under the warming plumage of the mother.

Seventh day: the goslings raised their heads and looked around when alarmed.

The frequency of the sleeping calls was much higher during the first week. This is probably partly due to the temperature being lower then and so they huddled together to keep warm and went to sleep. The primary cause could be that they needed much rest in their first week of life.

The threshold releasing the abandonment peep became remarkably higher as the birds became older, paralleling the successive disappearance of the imprinting both to me and to the siblings.

Greetings of the goslings directed towards me (the mother) were both the most common and the most intense. Often, brief 'greeting-orgies' broke out when something alarming happened to the goslings. This happened, for

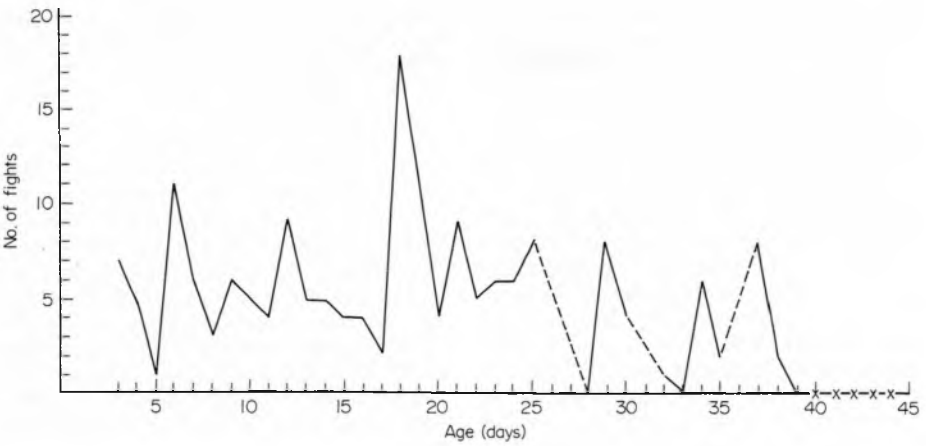

Figure 2. The number of fights during 4 hours per day.

example, when I had been away just for a few minutes and then returned to the goslings.

During the third day of life actual aggressive fights appeared. Stress seemed to be a factor that promoted irritation and aggression. In addition, the fights were released in connection with greetings. The fights appeared nearly as often just before a greeting as after a greeting. A fight finished either when the subordinate bird was forced to turn its head away because of bites from the dominant bird, or when it escaped. The number of fights is shown in Figure 2. The peak when they were 18 days old was due to unusually stressed circumstances, involving exposure to many unknown people. Otherwise the number of fights was distributed rather equally throughout the observation period. It is remarkable that for these Greylag Geese fights went on until the 38th day of life. In the Canada Goose fights occurred only until about the age of 20 days (Fabricius & Radesäter, 1971) and according to Radesäter (personal communication) it should be the same even for the Greylag Goose. Fischer (1965) has, during 10 years' studies on the Greylag Goose, only noticed fights between siblings on five occasions. An important difference is that Fischer's Greylag Geese were living in normal goose families, whereas mine have been imprinted on a human. It seems very likely that a real goose mother, just by her presence, obstructs the aggression of her goslings. A human foster-mother probably does not have such a great influence on the goslings as she cannot be with them permanently. It would have been desirable to have had a natural group as a control to an imprinted one.

Rank order may be established later among my Greylag Geese than among the Canada Geese, but the later fights may have had nothing to do with the rank order but were dependent upon stress factors. Figure 3 shows that after 15 days the geese obviously have composed a rank order, for in nearly 100% of aggressions a facing away by the subordinate bird was elicited, thereby ending the fights.

The facings away, with learning and individual recognition, changed from just a protective measure to an appeasement signal. According to T. Radesäter (personal communication), goslings always turn their heads

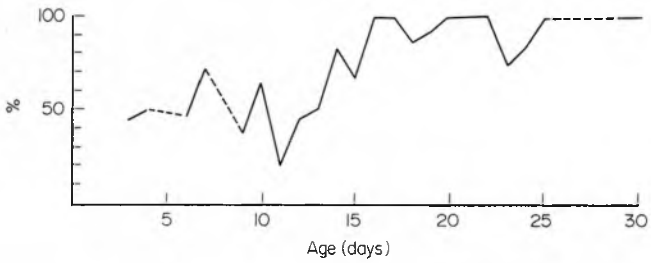

Figure 3. The development of facing away during fights. The ordinate axis shows the percentage of the total number of aggressions where one can immediately observe dominance and subordinance.

away in exactly the same manner, indicating a genetically determined basis. It is possible that both learned and innate movements are involved in the development of a facing away.

A similar turning away of the head described in Canada Geese (Klopman, 1961; Fabricius & Radesäter, 1971). Lorenz (1963) and Fischer (1965) described another form of appeasement signal in Greylag Geese, called redirection, thought to be completely innate and appearing between the 20th–60th day of age. This has also been confirmed by isolation experiments made by B. Wasstorp (unpublished). Both Fischer and Lorenz described and explained the redirection in the following way: the aggressiveness of the goslings increases perceptibly towards strange geese between 20–60 days (paralleling the development of the contour feathers). Since the neck posture in threat and greeting ceremonies is practically identical, these two expressions can easily be confused among the siblings. It is during such 'misunderstandings' (seldom observed by Lorenz) that aggressions in a group can appear. A bite caused no counterblow but rather an eager greeting ceremony. The attacked bird did not then direct its neck straight against the partner, but laterally away from it. This caused the attacker to act in the same way, ending aggression. The re-directed movement, together with deeper vi-sounds (due to the breaking of the voice), Fischer (1965) called *Schnattern.*

It is odd that both Fischer and Lorenz so seldom observed fights in a group of siblings, since both their descriptions of the genesis of the redirection start with fights. It may be that our definitions, which are necessarily subjective, are not the same.

Lorenz (1963) is of the opinion that the greeting (*Schnattern*) has developed from threat behaviour by redirection and ritualization. The early neck-protruding with the following vi-vi-vi-sound is the preliminary stage to both the threat behaviour and the second part of the triumph ceremony. Lorenz says also that it is only during a short period in the ontogeny when the inhibiting functions of the redirection are clear. In a fully developed triumph ceremony there is no aggression and it is activated by an independent drive.

If there is demonstrably a completely innate signal, the function and the meaning of the early fights with the facing away and the resulting rank order may be questioned. Neither Heinroth (1910), Lorenz (1935) nor Fischer (1965) have seen any rank order between the siblings in a brood.

However, there is no reason to doubt the existence of the rank order between the members of my brood, at least until the time for the appearance of the redirection movement. The value of the rank order, as a factor that prevents and diverts outbursts of aggression, is obvious. In my geese the redirection movement was developed gradually, not suddenly. Even when it had appeared, facing away and the rank order was still noticeable,

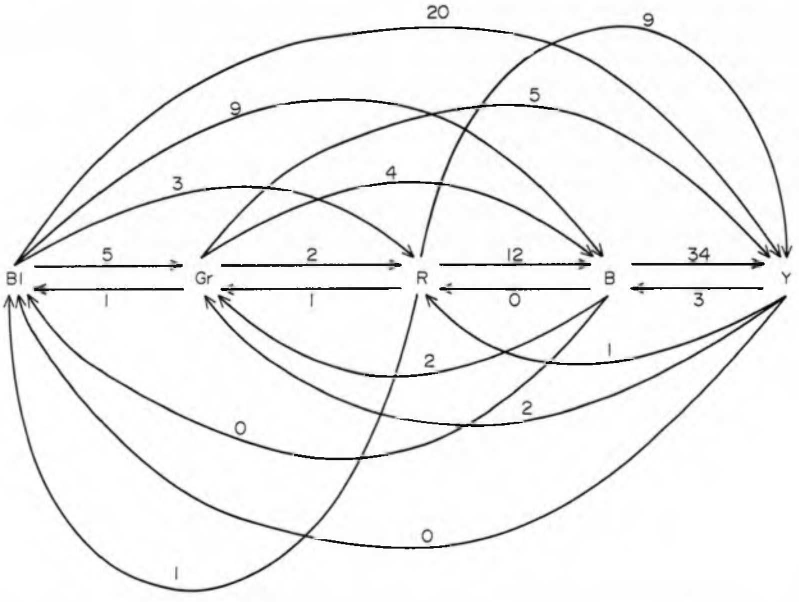

Figure 4. Rank order during fights of five Greylags (Black, Green, Red, Blue, Yellow).

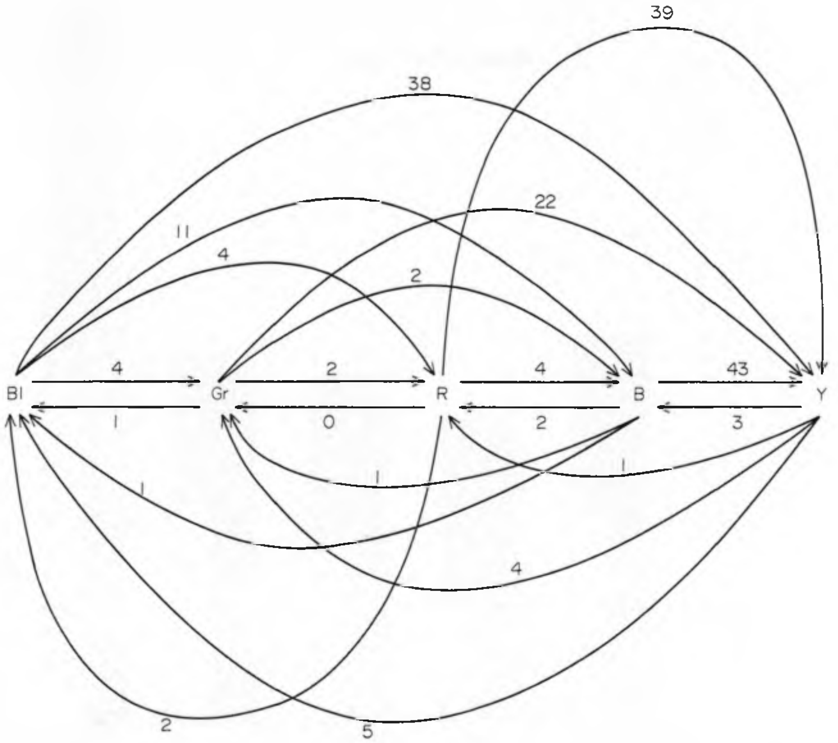

Figure 5. Rank order during greetings of five Greylags (Black, Green, Red, Blue, Yellow).

but slowly diminished. It seems likely that the fights, due to learning, hastened the development of the redirection. Facing away also began already on the 4th day to appear in the greeting ceremonies.

The dominance in fights and in greeting ceremonies resulted in a clear linear rank order: Black-Green-Red-Blue-Yellow, as illustrated in Figures 4 and 5. These are based on all data for the 4th–30th day. Various shorter periods were investigated to attempt to follow the establishment of the rank order, but the data were then too few to allow any definite conclusions to be drawn.

The rank order was demonstrable only in connection with fights and greeting ceremonies. It had no place in feeding, even when the opening to the food container was made so small that only one bird at a time could insert its beak. Nor was there correlation with the rank order when following the foster-mother, the sequence changing all the time. There appeared to be no correlation between the weight of the goslings, at any time, with their place in the hierarchy. The sex of the individuals was not determined.

T. Radesäter (unpublished) found that the gosling of the highest rank received the most greetings and delivered the fewest, while the one of the lowest rank received the fewest and delivered the most. From Figure 6 it is clear that this inverse relationship did not hold in my group. However, Yellow, the lowest ranking bird, ran nervously among its siblings and created, in this way, more opportunities for greeting, leading to an overall higher total.

Greetings can be (1) mutual, (a) with, or (b) without a facing away, or (2) non-mutual. About 50% of the greetings were of type 1(b), 30% were of type 1(a) and the remainder of type 2. The total number of greetings was 628. That as many as half the greetings were of type 1(b), is probably due to the fact that the redirection movement developed at an age of about 25 days.

The second type of greeting appeared to have some connection with the rank order in that the bird in the lowest rank most often performed the greeting while the one of highest rank was the one that did not answer (Figure 7).

A third type of greeting was directed out into the air and not towards any individual. It had the highest frequency during the earliest period of the goose's life and was entirely eliminated at an age of about 25 days and replaced by greetings to the stimulus.

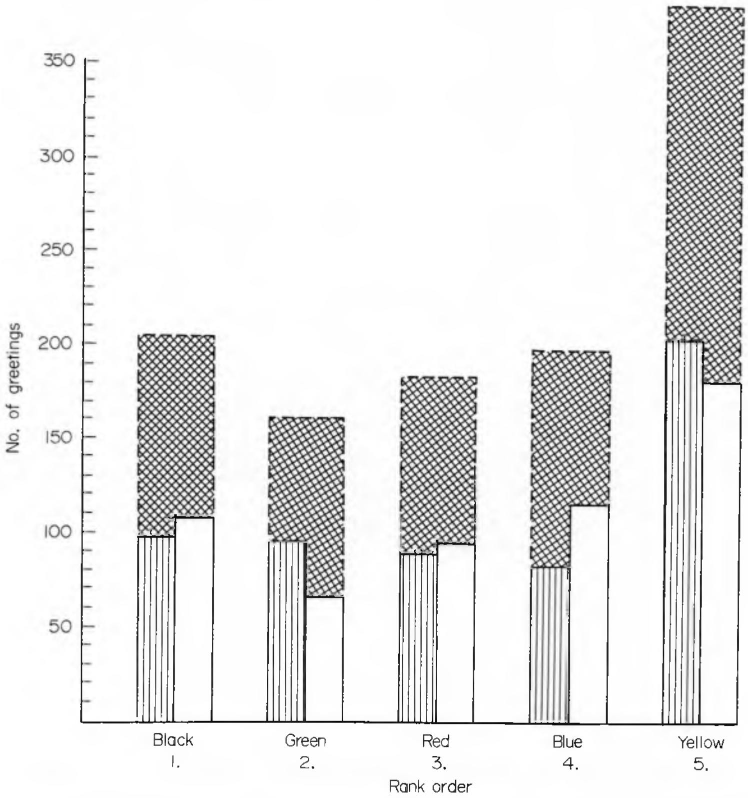

Figure 6. The relationship between received and delivered greetings and the rank order. Age: 4–30 days. Hatched columns, delivered greetings; open columns, received greetings; cross-hatched columns, the total number of greetings/individual.

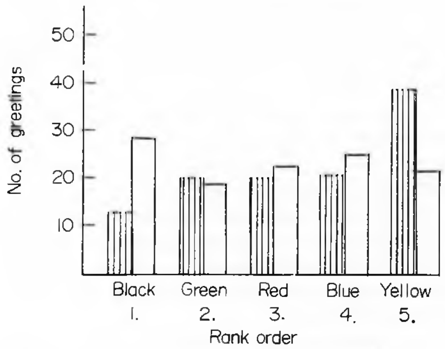

Figure 7. The relationship between the number of non-mutual greetings and the rank orders. Hatched columns, delivered greetings; open columns, received and not returned greetings.

Greetings were elicited by some form of disturbance or uneasiness in the group, as when one gosling was some distance from the rest. At the reunion, an eager greeting ceremony appeared that had the impression of welcoming and of giving assurance that everything was in order again.

Summary

In a group of five incubator-hatched goslings, which were human-imprinted, fights were fairly common and a linear rank order was established. Greeting, appeasement and redirected behaviours are described. Different results obtained in other studies are discussed.

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An Egyptian Goose *Alopochen aegyptiacus* with its goslings. *E. E. Jackson*

Climbing ability of ducklings of some cavity-nesting waterfowl

W. ROY SIEGFRIED

Introduction

A little over 60 years ago Heinroth (1910) published the first of his classical papers pioneering the study of waterfowl behaviour. In that paper an account is given of the remarkable ability of newly hatched American Wood Ducks *Aix sponsa* to climb up the often vertical and sometimes almost smooth inner walls of nest-cavities. Normally a highly competent observer who interpreted his observations with a great deal of insight and clarity, Heinroth stated that in order to succeed in its climb the Wood Duckling is provided with needle-pointed claws which can effectively catch on to the climbing surface, and, further, the duckling is able to climb up a perpendicular or even an overhanging face, like a woodpecker but without the aid of the tail.

When a newly hatched Wood Duck is examined an obvious feature is the relatively long and stiffened caudal down. These special natal tail feathers were noted and described by Beebe & Crandall (1914) who, however, made no attempt to explain their function.

The Wood Duckling does not normally dive for its food, so why should it have a tail very different to that generally possessed by ducklings of other surface-feeding anatids whose young also frequent ponds and other placid waters? Apart from differences in agility, Wood Ducklings forage similarly to downy young of Mallard *Anas platyrhynchos* and other dabblers (Beard, 1964). The answer is that the newly hatched Wood Duck uses its tail in climbing up vertical faces, and, contrary to Heinroth's (1910) statement, the specialized tail actually functions as a brace, somewhat as in woodpeckers.

Once having established that Wood Ducklings used their tails in climbing, I extended my observations to measure the climbing ability of the species and other cavity-nesting waterfowl.

Material and methods

Newly hatched young of the following species were used in the tests: Wood Duck *Aix sponsa*; Mandarin *Aix galericulata*; American Goldeneye *Bucephala clangula*; Hooded Merganser *Mergus cucullatus*; Mallard *Anas platyrhynchos*.

Goldeneye and Mallard eggs were taken from wild birds nesting at Delta, Manitoba, and those of the other species came from the Niska Waterfowl Research Station near Guelph, Ontario. There were three separate clutches of Wood Duck eggs, three of Mallard and one each for the remaining species. Hatching of the eggs occurred in an incubator. Each clutch was incubated separately and hatched as a separate brood to maintain normal sibling relations. As soon as the ducklings were 'dry' they were taken straight from the incubator and placed in a high-sided, darkened carton, where they were kept for 24 hours. Thus, all had had a minimum of visual experience—similar to that which they would have had when hatching in a hole deep in a tree. The carton was kept in a semi-darkened, constant-temperature room.

The testing apparatus was a chimney (Figures 1, 2), built of three hollow cement bricks (known to the building trade as 'breeze-blocks', which are formed from a mixture of lime mortar and coarse sand). Ducklings were introduced, singly, into the chimney. Their responses were observed from a vantage point above its opening. A screen made it possible to observe the ducklings without disturbance. Since the bricks had been made of coarse sand, the chimney's internal walls were just rough enough to provide 'claw-holds' for the ducklings. The tower of three bricks sloped at an angle of 10° from the vertical, and was so placed that light from an electric bulb above penetrated part of the way down the chimney. Thus, when at the bottom of the chimney, a duckling was exposed to a more or less unidirectional source of light—resembling that which it would have seen when looking up at an entrance hole above the gloom of a natural cavity.

At the end of 24 hours in the darkened carton individual ducklings were transferred directly to the testing room, which was effectively sound-proofed. The duckling was placed on its own at the bottom of the chimney and its responses noted during a 5-minute period, after which it was removed from the test-room. Each of its siblings was then tested in the same way—in isolation. Immediately after the conclusion of this

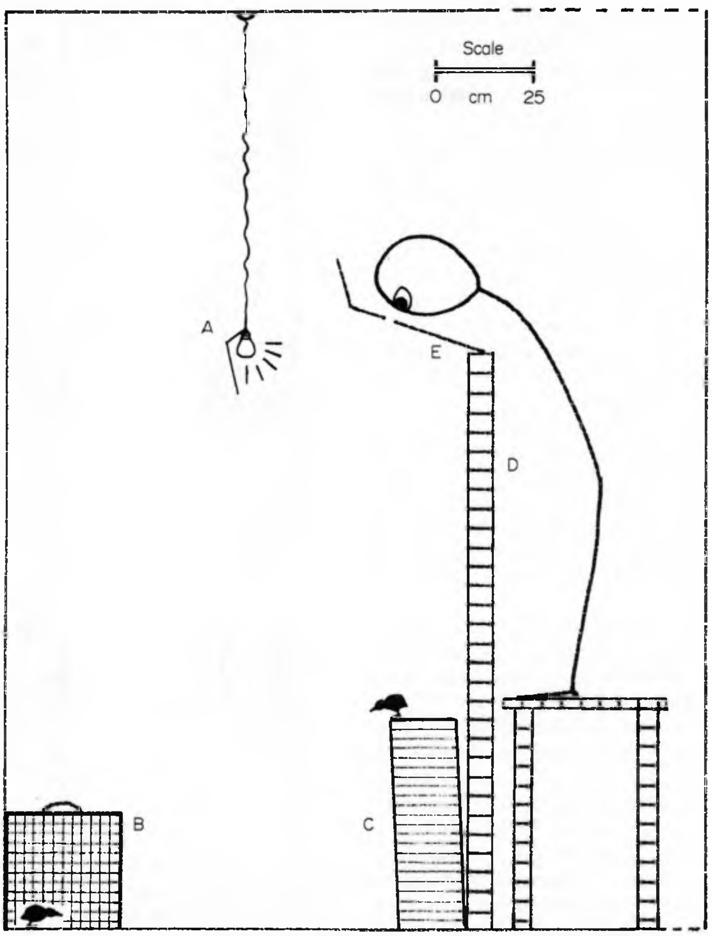

Figure 1. The experimental set-up. A, electric light bulb; B, wire cage containing ducklings when test individuals were permitted vocal contact with their siblings; C, chimney having internal dimensions 11·5 x 9·5 cm. D and E, screens.

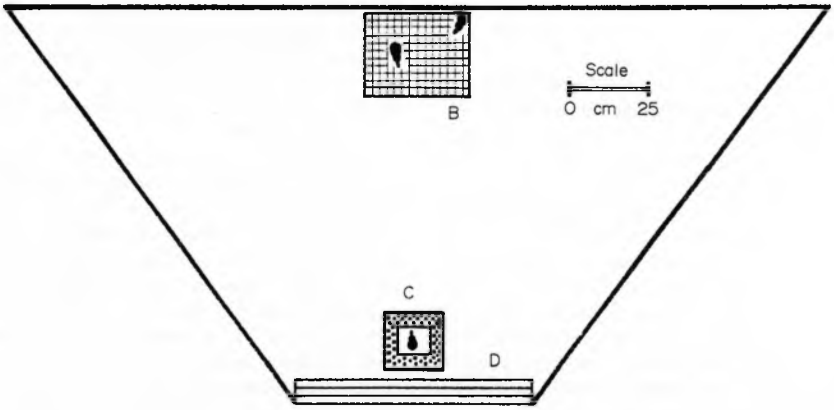

Figure 2. Ground plan of testing room and experimental set-up. B, C and D as in Fig. 1.

series, a second series of trials was started in which the bird in the chimney could hear the calls of its siblings kept in a wire-netting cage near the base of the tower (Figures 1, 2). Thus, every duckling was subjected to two trials. The time before each duckling initially vocalized, the time before it initially climbed, and the total time spent climbing while in the chimney were recorded. Also noted was the number of separate attempts (jumps initiating climbs) made by an individual duckling. Series of trials were operated alternately over a run of test-days. Between test-days, the ducklings were kept in a heated brooder room; they had free access to food and water.

Motion pictures of the climbing activities of Wood Ducklings were taken at sixty-four frames per second; and frame-by-frame tracings were obtained. The ducklings were photographed while climbing the vertical sides of a rigid container made from panels of fine wire gauze, normally used to screen small insects.

Three 1-day-old specimens of each species were X-ray photographed, to facilitate the measuring of skeletal parts. All linear measurements of bones were taken between their articulating surfaces. Functional limb: trunk ratios were computed after the method of Spring (1965). The angle of curvature of the claw on the middle tow was determined by the method of Engels (1940). Values for length and width of the shafts of caudal down were obtained as follows: the lengths of all shafts on the tails of three specimens were summed and then divided by the total number of shafts; measurements of the width of the two central shafts were taken at five standard points between the base and distal end of each shaft, and the results averaged for each species.

Results

Figure 3 illustrates a 1-day-old Wood Duckling's mode of progression up a vertical surface. It is clear that the duckling progresses by a series of leaps, rather than by a foot-over-foot climb. The bird leaps upwards against the vertical surface, to which it clings with the aid of the claws on its toes. The hooks on the wings provide no assistance to climbing. When clinging, the bird's body is placed between its legs and feet which generally are splayed outwards with toes fully spread. From a stationary clinging position, the next stage upwards proceeds by an inwards pulling, or hitching, of the body followed by an upward lift, retaining the body's long axis in a vertical plane. This movement is aided by the bracing effect of the stiffened caudal down, pressed against the climbing surface. At the zenith of the body-lift, the feet are released and the wings are swung outwards and upwards and then inwards. The tail is generally kept in contact with the surface throughout this part of the climbing motion, and is only flipped outward in the last phase of the upward movement when the feet, extended upwards, make new contact and purchase.

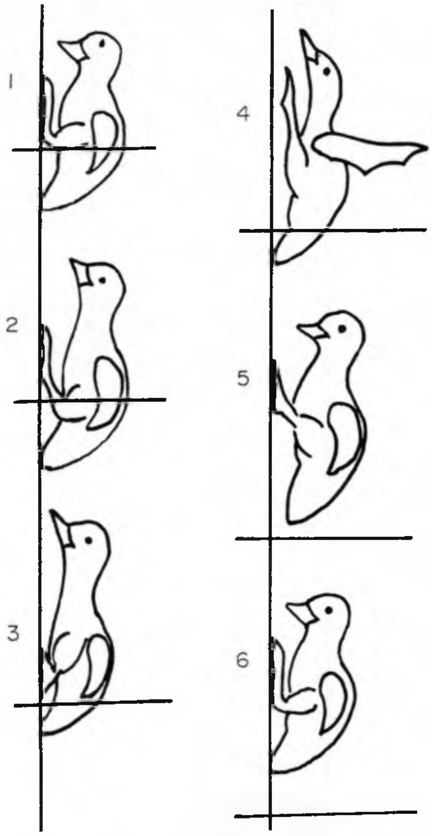

Figure 3. Climbing in 1-day-old Wood Ducks, drawings traced from cine film. Numbers 1–6 denote sequence of progress.

It is apparent that, in a number of aspects the Wood Duckling's climbing strategy, particularly the way in which the tail is used, resembles, and functions similarly to, the method employed by woodpeckers in climbing vertical surfaces. Bock & Miller (1959) and Spring (1965) discuss the gravitational forces acting on woodpeckers. The longer gravitational component passes from the centre of gravity of the bird through the tail feathers to a point where they make contact with the climbing surface. The shorter

Table 1. Average linear dimensions and toe-claw curvature in 1-day-old ducklings. All measurements in millimetres except caudal down shaft-width (epu) and toe-claw curvature (degrees of arc)

Species	Culmen	Hook on wing	Femur	Tibio-tarsus	Tarso meta-tarsus	Total leg length	Middle toe	Claw length	Claw curvature	Caudal down shaft Length	Caudal down shaft Width
Wood Duck	14	Yes	14	27	19	60	25	3·3	89	18·2	23
Mandarin	15	Yes	15	30	17	62	25	4·0	102	17·9	17
Hooded Merganser	17	No	16	31	27	74	25	4·0	107	17·4	18
Goldeneye	17	Yes	20	30	21	71	25	3·9	110	17·7	20
Mallard	20	No	16	30	19	65	24	3·3	94	9·1	15

Table 2. Average functional limb-trunk ratios in 1-day-old ducklings. Ratios computed after the method of Spring (1965)

Species	Femur	Tibiotarsus (4 TV)	Tarsometatarsus (4 TV)	Total leg length (4 TV)	(4 TV)
Wood Duck		165	323	223	711
Mandarin		200	407	227	834
Hooded Merganser		229	443	393	1,065
Goldeneye		286	429	300	1,014
Mallard		254	462	292	1,008

4 TV = four thoracic vertebrae.

component is directed at right angles to the first and tends to pull the bird outward. The first component is effectively countered by anteriorly directed toes and minimal slippage of tail, and the second by laterally directed toes orientated at right angles to the trunk. In the upward lift, hitching inwards of the body decreases that gravity component tending to pull the bird off the trunk. If the bird is able to maintain this position, with the help of the tail, until the feet are extended upward, there will be a minimal tendency to fall outwards while the feet are moving to a new purchase point. Short leg bones increase the efficiency of fixation while the bird is pulling its body toward the climbing surface. Also, short bones generally increase the effective power of muscles inserting on them.

Based on the data contained in Tables 1 and 2, it appears that, comparatively speaking the Wood Duckling has relatively short legs; strongly decurved toe-claws; and, relatively long and broad caudal down shafts.

The main findings of the climbing trials are summarized in Tables 3–7. The data are intended to do no more than suggest trends. Refined analyses are unwarranted in view of the small samples; in particular the availability of only one brood of each of three of the species tested.

Table 4 shows the degree of success that ducklings had in climbing out of the chimney. The Wood Duck was consistently most successful, followed by the Goldeneye. Mandarins and Hooded Mergansers were less successful, and all Mallards failed the test. Wood Ducklings were consistently lighter than ducklings of the other species (Table 3). The heaviest ducklings were Goldeneyes, yet generally they were more successful at climbing than the lighter Mandarins and Hooded Mergansers. Ducklings usually fared best when between 2 and 3 days old. All species were more successful then than when first tested at 1 day old. Exempting the Wood Duck, after 3 days an increasing

Table 3. Average weights in grams of ducklings, and numbers of ducklings tested and successful at climbing out of a chimney

	Day 1			Day 2			Day 3			Day 4		
Species	Weight	Birds successful	Birds tested	Weight	Birds successful	Birds tested	Weight	Birds successful	Birds tested	Weight	Birds successful	Birds tested
Wood Duck	22	5	7	24	6	8	35	7	7	38	13	13
Mandarin	26	2	8	29	5	8	36	1	8	46	2	8
Hooded Merganser	31	3	11	34	3	9				44	1	4
Goldeneye	36	3	16	43	10	14	48	9	14	54	4	14
Mallard	29	0	10	31	0	12	34	0	12			

Table 4. **Climbing success (number of individuals which climbed out of chimney as a percentage of number of ducklings tested), and average time (and S.D.) in seconds taken by successful ducklings in climbing (sample sizes as in Table 3)**

Species	Day 1		Day 2		Day 3		Day 4	
	Success	Climb	Success	Climb	Success	Climb	Success	Climb
Wood Duck	71	78±64	75	80±71	100	32±13	100	68±65
Mandarin	25	132±152	62	120±87	12	254	25	
Hooded Merganser	27	135±76	33	116±103			25	
Goldeneye	19	199±27	73	145±70	64	113±85	29	158±78

Table 5. **Climbing success and the climbing performance of older successful Wood Ducklings**

	Day 5	Day 6	Day 7	Day 8
No. birds tested	17	19	17	16
Percentage successful	100	79	59	25
Mean weight (g)	39	45	52	62
Mean climbing time(s)	60±60	60±31	111±38	194±53
Mean no. jumps	9·1±11·2	8·2±6·0	17·0±7·5	32·2±16·8
Mean no. jumps/minute	8·1	7·0	6·8	9·1
Mean time before call (s)	24±25	47±67	29±27	21±17
Mean time before jump (s)	33±27	62±76	44±29	40±25

proportion of ducklings failed to get out of the chimney. The Wood Ducklings' climbing performance started to decline sharply after 5 days (Table 5). Thus, they sustained their relatively high rate of success longer than the other species.

Amongst the Wood Ducklings which were successful in their climbing, older birds generally made most attempts (number of jumps), and remained longest in the chimney. Older and heavier ducklings were less adept at clinging on to the sides of the chimney; they fell back repeatedly and had to make renewed starts. Wood Ducklings which failed the test performed on average 7·0 jumps per minute as against 7·9 recorded for successful ducklings of the same age and tested in the same manner. Thus for the Wood Duck, at least, it seems as if the successful birds were those which were most persistent in their efforts.

In comparison with the other species, Wood ducklings tended to make fewer starting jumps before emerging from the chimney. This suggests a superior climbing ability. However, climbing (or escape) tendency, as measured by number of jumps by successful birds per unit time, did not differ much between the four cavity-nesting species (Table 6). It is of interest that day-old Mallards made relatively many more jumps (on average 17·1 jumps per minute) than any of the other species; 2-day-old Mallards, by contrast, made fewest attempts (on average 4·1 jumps per minute) at getting out of the chimney. Table 7, again based only on successful birds, shows the ducklings' initial response to the experimental situation. With

Table 6. **Average number of jumps, taken before initiation of a successful climb, and rate of jumping (mean number of jumps per 60 seconds) performed by successful ducklings (sample sizes as in Table 3)**

Species	Day 1		Day 2		Day 3		Day 4	
	No. jumps	Jumping rate	No. jumps	Jumping rate	No. jumps	Jumping rate	No. jumps	Jumping rate
Wood Duck	7·4±3·8	7·1	11·5±10·1	7·6	9·4±8·7	8·3	9·4±8·7	8·1
Mandarin	15·0±18·3	5·7	13·5±10·8	7·1	25	5·9		
Hooded Merganser	47·0±54·0	9·7	9·0±7·5	7·1				
Goldeneye	26·0±7·6	7·7	21·4±10·0	8·8	10·8±10·4	5·6	20·7±10·3	7·1

Table 7. Average time (and S.D.) in seconds elapsed before successful ducklings commenced jumping and vocalizing (sample sizes as in Table 3)

Species	Day 1		Day 2		Day 3		Day 4	
	Call	Jump	Call	Jump	Call	Jump	Call	Jump
Wood Duck	46±41	73±46	27±17	49±39	7±4	8±5	9±7	19±10
Mandarin	16±9	30±21	40±54	60±49	20	21		
Hooded Merganser	10±9	28±18	4±2	14±9				
Goldeneye	48±53	55±48	15±18	23±18	16±20	54±39	5±3	59±24

the exception of the Mandarin, and leaving aside the Mallards, time before vocalizing of the remaining three species was shortest coincident with age at which they were most successful at climbing. One-day-old Wood Ducks, Goldeneyes and Hooded Mergansers took longer to utter first 'distress' calls than they did when 2 and 3 days old. Similarly, a longer interval preceded first attempts to climb in day-old ducklings than later when they were performing best.

Vocally and in attempting to jump out of the chimney, day-old Mallards responded with greater alacrity than any of the other species. Mallards were observed to be less well orientated in their efforts to escape, directing their jumps to all corners and sides of the chimney. The ducklings of the cavity-nesters all tended to orientate their jumps in direction of the overhead light. Data on this was gathered only for the Goldeneye: in day-old ducklings 70% of their jumps were directed at the light ($n=141$ jumps, ten test ducklings); at 2 days 80% ($n=312$ jumps, thirteen test ducklings); and at 4 days 97% ($n=123$ jumps, ten test ducklings).

Discussion

As mentioned, the samples were small and the experiments limited and relatively crude, and caution is required in interpreting the data and in reaching conclusions. Nevertheless, some of the results appear definite enough to justify discussion, including some speculation.

It is clear that the Wood Duck performed best—apparently due to its relatively superior initial response, climbing (motoric) ability and sustained effort. The Mandarin's poor showing is somewhat surprising in view of the species' supposedly close relationship to the Wood Duck. The Wood Duck's superior performance also is of interest in relation to the Goldeneye, and especially regarding a difference in nest-site ecology. Prince (1968) found in New Brunswick, Canada, that Wood Duck nest-cavities averaged deeper than those of Goldeneyes—61·0±61·0 cm (2–183 cm) for the Wood Duck, as against 46·2±19·6 cm (15–76 cm) for the Goldeneye.

Paucity of knowledge concerning the ecology and functional anatomy of the various ducklings considered here precludes discussion on climbing ability in relation to the advantages of particular anatomical arrangements; and Bock & Miller (1959) have pointed out that anatomical differences among species are not always explicable in terms of relative functional advantage. In the case of the Wood Duckling, however, it seems fair to state that the specialized caudal down represents an adaptation facilitating egress from relatively deep and vertically walled nest-cavities.

In relating the Wood Duck's apparent superior climbing ability to the natural situation, allowance must be made for factors such as specific auditory stimulation which would come from the maternal parent, and play an important part in facilitating egress of ducklings from the nest-cavity. In this context, ducklings of the other hole-nesters tested might have fared relatively better had they had the benefit of maternal calls to prompt their climbing. In other words, although female vocalizations promote a following-response in all the species, it is possible that auditory cues are of greater importance in some species than in others. Be that as it may, the fact that the experimental ducklings of all the hole-nesting species attempted to climb when first tested in isolation, and without previous experience, is in itself of interest. In nature, healthy Wood Ducklings accomplish the exodus from the nest well within 4 minutes from the time the parent begins calling from outside (Gottlieb, 1963). Later, Gottlieb (1968) concluded that the ducklings perceive and refine identification of maternal vocalizations during the 2 days or so before they leave (or attempt to leave) the nest, and that the initial jumping and climbing is a direct response to the call of the female. The current tests indicate that such activities can occur without auditory stimuli. Further, the tests suggest that motoric behaviour is most strongly developed and successful when the ducklings are 2–3 days old—the age at which they normally leave the nest in nature.

My observations, although mainly qualitative, indicated that Wood Ducklings, and the ducklings of the other cavity-nesters, tended to orientate their initial jumps towards light. In discussing the responses of Wood Ducklings to parental calls as well as visual stimuli, Klopfer (1959) postulated the existence of a releaser (for climbing activity) constituted by a light object in a darker field, which is the pattern presented by the nest entrance. However, according to Leopold (1951) female Wood Ducks often temporarily leave their newly hatched young in the cavity, returning later to brood. During the female's absence, the ducklings remain quiet and make no attempt to leave the nest. Therefore, in nature a round and bright nest entrance in itself is not enough to release climbing. Obviously the female's call is important in eliciting a following-reaction from the ducklings; and so promoting integrated departure, and guiding direction of the young from the nest. This need not, however, invalidate a suggestion that the female's call is a function of the 'instinctive' nature of the ducklings' motoric readiness. In short, it seems reasonable to believe that the female's call is not a releaser (strictly speaking) for climbing.

If the differences in response and ability to climb, as indicated among the hole-nesters tested here, are real, they must result from particular environments acting on the species. Clearly, more comparative studies and experimental analyses are needed to reach understanding of the processes and conditions under which parent and young have come to perceive selectively and to respond to particular stimuli.

Acknowledgments

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Summary

The tendency and ability of newly hatched ducklings to climb out of an experimental chimney were examined in the following species: American Wood Duck *Aix sponsa*, Mandarin *Aix galericulata*, American Goldeneye *Bucephala clangula*, Hooded Merganser *Mergus cucullatus* and Mallard *Anas platyrhynchos*. The Wood Duck performed consistently best. In climbing up a vertical surface, the Wood Duckling proceeds by a series of leaps and uses its tail as a brace, rather like a Woodpecker. The Wood Duckling has relatively short legs, strongly decurved toe-claws, and long and broad caudal down shafts. The importance of stimuli prompting the young of cavity-nesting waterfowl to leave the nest, is discussed.

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Foot adaptations in four species of Whistling Duck *Dendrocygna*

ERIC G. BOLEN AND M. KENT RYLANDER

Introduction

Adaptations in the foot structure of North American whistling ducks (=tree ducks) were examined using the comparative ratios of tarsus and mid-toe lengths as indicators of foot size (Rylander & Bolen, 1970). The results indicated that Fulvous Whistling Ducks *Dendrocygna bicolor* have proportionately larger feet than Black-bellied Whistling Ducks *D. autumnalis*. We believe this difference in foot size is correlated with the highly aquatic nesting and feeding habits of the Fulvous Whistling Duck.

A second pair of dendrocygnids, the Wandering *D. arcuata* and Plumed *D. eytoni* Whistling Ducks from Australia, were similarly examined to estimate divergence in foot structure. This paper reports these results, makes a brief ecological comparison between the Australian species, and discusses the evolutionary implications of these data with those obtained from the North American species.

Results

Mean lengths of the wings, tarsi, and mid-toes of the two Australian whistling ducks are presented together with measurements for the North American species in Table 1. Culmen length, while otherwise useful for size comparisons, was not used here because of the remarkably short bill length of *D. eytoni*; this feature remains singularly dissimilar from any of the other seven species of dendrocygnids. Hence, using the wing and tarsi data as indicators of overall body size, *D. eytoni* and *D. autumnalis* are shown as the larger birds of each geographical pair, respectively. Body weights also bear out the larger sizes of these species over their respective congeners discussed in this paper (see Bolen, 1964; Frith, 1967), but weight data are not useful for our present analysis.

Ratios comparing the relative wing and tarsal lengths (Table 2) show that the four species are proportionately rather similar (i.e. a wing/tarsus ratio of about 4 for two

Table 1. Comparison of wing, tarsal, and mid-toe lengths (mm) for four species of whistling duck *Dendrocygna*. Ranges shown in parentheses

Species	N	Wing	Tarsus	Mid-toe
D. arcuata	3	214* (196–230)	52·3 (51–55)	65·6 (64–68)
D. eytoni	6	232† (222–242)	59·6 (58–62)	55·8 (55–60)
D. bicolor	28‡	210 (196–225)	55·8 (52–60)	66·6 (64–70)
D. autumnalis	21‡	238 (229–248)	62·3 (58–66)	64·5 (61–68)

* Data from eighty-two males examined by Frith (1967 p. 65).
† Data from fifty-nine males examined by Frith (1967 p. 79).
‡ Data taken from earlier sources as cited in Rylander & Bolen (1970).

Table 2. Proportions among linear dimensions for four species of whistling ducks, *Dendrocygna*. Data calculated from means in Table 1

	Species			
Proportions	*D. arcuata*	*D. eytoni*	*D. bicolor*	*D. autumnalis*
Wing/tarsus	4·1	3·9	3·8	3·8
Wing/toe	3·3	4·2	3·2	3·7
Toe/tarsus	1·3	0·9	1·2	1·0

Table 3. Proportionate sizes for two pairs of sympatric whistling ducks, *Dendrocygna*, based on means and ranges for adult birds shown in Table 1

	Species (=sympatric pairs)	
Feature	*D. bicolor/D. autumnalis*	*D. arcuata/D. eytoni*
Wing	0·88 (0·86–0·91)	0·92 (0·88–0·95)
Tarus	0·89 (0·89–0·90)	0·88 (0·88–0·89)
Middle toe	1·03 (1·02–1·04)	1·18 (1·13–1·16)

Australian species and about 3·8 for the two others). However, when mid-toe lengths are introduced into the ratios, these similarities are no longer apparent and the ratios become distorted (e.g. a wing/toe ratio of 3·3 for *D. arcuata v.* 4·2 for *D. eytoni*). This discrepancy prompted still another comparison to determine the relative difference in size between each of the two species in each pair (Table 3). This revealed that *D. arcuata* is about nine-tenths the size of its sympatric congener, *D. eytoni*, and thus parallels the size relationship also occurring between *D. bicolor* and *D. autumnalis*.

In both geographical pairs, then, the smaller species—*D. arcuata* and *D. bicolor*—have proportionately larger feet as measured by mid-toe lengths. We believe these features are adaptations consistent with certain ecological distinctions that can now be briefly considered.

Comparative ecology

D. eytoni: Plumed Whistling Ducks (=Grass or Eyton's Whistling Duck) are found on tropical grasslands throughout much of Australia; no subspecies are recognized.

Nests are placed on the ground in the shelter of tall grass or a bush, and often at a mile or more from water. Lavery (1967) observed that the daily feeding routine started in the late afternoon when, at first, the birds walk or graze near roosting sites, then fly to feeding areas elsewhere. Plumed Whistling Ducks feed mainly on land, selecting foods heavily dominated by grasses. They will dive when wounded, but they do not otherwise exhibit this behaviour. Plumed Whistling Ducks perch rarely and awkwardly. Likewise, they are slow and awkward swimmers, whereas on land, the birds walk long distances gracefully (Frith, 1967 p. 80).

D. arcuata: there are three races of this species, differing in size, present in Australia, Indonesia, and the Philippines. The largest of these, *D. a. australis*, frequents the more permanent freshwater lagoons of tropical Australia.

The nest of the Wandering Whistling Duck (=Water Whistling Duck) is a sheltered, grass-lined depression on the ground often far from water; the species makes little or no use of tree perches. They feed entirely in water taking small amounts of animal matter in addition to various parts of aquatic plants; their foods are secured by expert and constant diving. Frith (1967 p. 66) once watched several thousand Wandering Whistling Ducks froth the water to a boil as they swam and dove for food. It is primarily in this respect—a utilization of aquatic foods in relatively deep water—that the Wandering Whistling Duck remains ecologically separated from the Plumed Whistling Duck throughout their sympatric ranges in Australia (Frith, 1967 p. 88). Wandering Whistling Ducks exhibit a nearly horizontal posture and thus are unlike the vertically oriented posture of Plumed Whistling Ducks (Rylander & Bolen, 1974a).

Evolutionary considerations

The foregoing comparisons show that *D. arcuata* possesses (a) a foot size disproportionately larger than its sympatric congener and (b) feeding behaviour that is distinctively aquatic and, as such, quite dissimilar from that of *D. eytoni*. Moreover, these same distinctions are also found in a pair of dendrocygnids *D. autumnalis* and *D. bicolor* sympatric in North America.

That such duplication in morphological and ecological features occurs in two geographical pairs of whistling ducks suggests an instance of parallel evolution. However, we believe this is best explained in the case of the two rather cursorial species of each pair, *D. autumnalis* and *D. eytoni*. The similarities between the highly aquatic species, *D. arcuata* and *D. bicolor*, more likely indicate a common and rather immediate genetic ancestry; they are perhaps best considered as super-species, as suggested by many additional similarities in their plumage

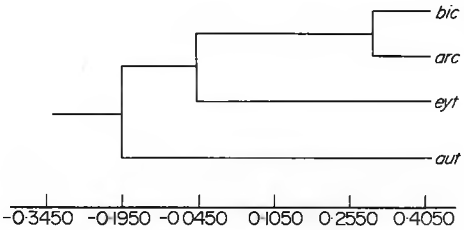

Figure 1. Correlation phenogram of four species of *Dendrocygna* based on NT–SYS computer analysis of thirty-five seemingly non-adaptive features (e.g. downy plumage pattern, threat displays, etc.). The computer program is adopted from the concept of numerical taxonomy as developed by Sokal & Sneath (1963). Note that *D. eytoni* is more nearly related in the correlation to *D. bicolor* and *D. arcuata* even though its foot adaptations and ecology closely resemble *D. autumnalis*. Scale shows units of correlation.

(*cf.* Delacour & Mayr, 1945) and their nearly contiguous distributions across southern Asia.

The case for parallel evolution gains strong support using numerical taxonomy, as developed by Sokal & Sneath (1963). Each of thirty-five presumably non-adaptive features for each species was coded for computer analysis using the standard NT-SYS program. The resulting phenogram, direct from the computer printout, shows that *D. eytoni*, the cursorial Australian species, is more closely related to the aquatic species, *D. bicolor* and *D. arcuata* than to the New World cursorial species, *D. autumnalis* (Figure 1). Hence, the cursorial habits and similarities of foot structure of *D. eytoni* and *D. autumnalis* may have evolved independently in each of two pairs of whistling ducks on opposite sides of the world. The associated similarities of gait and feeding adaptations are fully discussed elsewhere (Rylander & Bolen, 1974a, 1974b).

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Summary

A comparison of the mid-toe and tarsus proportions for two geographical pairs of whistling ducks *Dendrocygna* spp. shows that each pair contains one member with disproportionately larger feet. These species, *D. bicolor* and *D. arcuata*, have highly aquatic habits whereas the other members of each pair (*D. autumnalis* and *D. eytoni* respectively) are far less aquatic and exhibit cursorial habits. In the latter case, the similarities in foot sizes suggest an instance of parallel evolution that is strongly supported by phenetic analysis of other characteristics.

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The behaviour of wintering Smew in southern Sweden

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Introduction

The behaviour patterns of a large number of waterfowl species have been intensively studied and analysed (Johnsgard, 1965). Even so, some species, such as the Smew *Mergus albellus*, have been rather little studied in the field and published information is far from complete (Hollom, 1937; Hickling, 1957; Lebret, 1958; Richmond, 1939).

The behaviour of wintering Smew was studied in the Malmö area of the Öresund, south Sweden, in the winters 1968–1969 to 1971–1972. Displaying flocks were filmed and behaviour sequences were followed continually and registered on tape. Observations on Smew were also obtained during a general study on the winter ecology of diving ducks at the coasts of south Sweden, mainly in 1964–1965 to 1967–1968 (Nilsson, 1970a, 1972).

Study area

Malmö harbour is an important area for many waterfowl species (Nilsson, 1970b) and has the second largest concentration of wintering Smew in Sweden. Many temporary ponds and bays were formed during construction work in the harbour and they form excellent habitat for resting and wintering Smew. The water is shallow and there is a rich growth of *Zostera marina* on sandy parts and various green algae and *Fucus* on the dumped stones. The invertebrate fauna of the area is rich (Nilsson, 1972).

Habitat selection

Smew are scarce in Sweden during the winter. The total winter population in January 1971–1973 was between 300 and 500 individuals with about 90% concentrated to the two southernmost provinces (Nilsson, 1973). Here most Smew are found in two concentration areas: the Malmö harbour and the harbour of the small town Sölversborg on the south coast. Other similar areas in southernmost Sweden which freeze during hard winters are only used by small numbers of wintering Smew. Most other midwinter records are in river mouths or harbours.

Flocks of Smew arrive in south Sweden in late October and November (Nilsson, 1968) on various lakes or in sheltered bays in the archipelagos. They do not appear in the Malmö harbour before the inland lakes freeze. Similarly, the concentration at Sölvesborg is seen when the innermost bays in the nearby archipelagos freeze.

In spring, Smew leave the coastal areas with the first warm weather and are then seen on the first open water on inland lakes, staying for a short period before migrating northwards.

Sex-ratios

First-winter males of Smew are very similar to females and difficult to separate in the field under normal conditions. It is therefore more appropriate to discuss the proportion of adult males, which in south Sweden is about 50% (Table 1). Females and immatures arrive earlier than adult males. They also migrate further to the south than adult males, for Bezzel (1965) and Ehrlich (1963) found a predominance for females among wintering Smew in Germany.

In December, 54% of coastal Smew were adult males compared with 23% on inland waters but there were no differences in January to April. Food is probably more easily accessible in the shallow inland lakes and it may be an advantage for the smaller females and immatures to stay there as long as possible. In January to March, on the other hand, open water is much restricted in inland areas and the food situation similar to that on the coast.

In Goldeneye *Bucephala clangula*, differences between the sexes in local distribution and food-seeking activity indicate that the smaller females are in a more difficult situation in the winter than the males (Nilsson, 1970a, 1970c).

General activity

The daytime activity of the Smew was followed for a standard period and the activities of the birds classified into main types (Nilsson, 1970a). Observations were made on several evenings and mornings to study roosting behaviour.

Smew spend about half their day food-seeking (Table 2), the highest frequency of

Table 1. **Percentage of adult males among Smew in south Sweden 1961–1973. Total numbers counted in brackets**

Month	Wildfowl counts	Öresund	Lakes in Scania
Oct.	8·1(74)	–	–
Nov.	27·0(122)	–	16·2(74)
Dec.	40·3(124)	54·2(170)	22·7(119)
Jan.	55·4(670)	50·0(360)	51·4(72)
Feb.	50·0(130)	58·0(510)	47·8(44)
March	43·8(192)	50·4(514)	50·8(226)
April	49·5(133)	45·4(75)	48·0(171)

Table 2. **Daytime activity of Smew in the Malmö area 1965–1972 as per cent of standard observations (i.e. the bird was followed for a standard period of time and its main activity was noted)**

Month	Diving	Swimming	Flying	Preening	Sleeping	Displaying	No. of observations
Nov.–Dec.	62	11	11	12	4	–	218
Jan.	47	30	9	8	6	–	161
Feb.	49	32	5	6	8	–	210
March	45	21	3	5	18	8	428

diving being found in November to December. Red-breasted Mergansers *Mergus serrator* spend a similar amount of time food-seeking, whereas Goosanders *Mergus merganser* spend much less, and Goldeneye much more (Nilsson, 1970a).

Smew that are not food-seeking spend their time during the day in moving around, preening or, a few only, in sleeping. The same was true of the Red-breasted Merganser, whereas 50% or more of Goosanders sleep and rest for long periods.

During the day individual Smew feed actively for periods of about 20–30 minutes, then the intensity decreases. The birds make longer pauses between the dives and finally start preening. The bouts of preening generally last about 3–5 minutes, sometimes longer. They mostly preen on the water but in midwinter often do so sitting on the edge of the ice. After preening they rest for some time either swimming around quietly or sleeping on the water or ice before starting to dive again.

Smew often stay in loose groups during daytime feeding. When diving these groups often separate but as the birds stop to preen and rest the flock reassembles.

In midwinter little difference in activity could be found through the day. In late winter and early spring, on the other hand, Smew often feed less during the afternoon and stop entirely 1 hour or more before sunset.

In most winters the Smew spend the night in their daytime haunts roosting in small flocks on the water or ice edge. In March 1969, however, when the species was unusually common, they had a communal roost in a sheltered bay of the harbour. The roost was situated about 0·5–1 km from the main daytime areas. The Smew in general stopped feeding at least 1 hour before sunset and gathered into groups with much preening and intense display. At sunset small parties left and flew to the roost. There they stayed in a dense flock, still with much preening and display. As it grew darker the birds gradually adopted the sleeping position, but new arrivals caused sleeping birds to display again. Sometimes very intense display was seen till it was almost completely dark. The Smew left the roost before or at sunrise and dispersed over the feeding grounds in small groups or in pairs. This bay has for many years been a traditional roosting site for Goldeneye, which had the same time-schedule and behaviour as the Smew, but the Smew used a different part of the bay. The behaviour in the smaller flocks in other years was the same as in the communal roost.

Feeding

Smew obtained all their food by diving in shallow water, in depths of less than 2 m. The range in diving time of 114 dives was 8–31 seconds with a mean of 18·2±2·3 seconds. As in the Goldeneye (Nilsson, 1969) the dives of paired Smew were synchronized.

Co-operative feeding was not seen, probably because the flocks are small. In the Netherlands a large flock were seen feeding co-operatively in January 1968 (Källander *et al.*, 1970).

The actual food choice of Smew in the study areas could not be ascertained, though in some cases small fishes were brought to the surface. A female killed in a fishing net in an inland lake was filled with larvae of caddisflies *Trichoptera.*

Feeding Smew were regularly accompanied by gulls, mostly Black-headed Gulls *Larus ridibundus*, but also Herring Gulls *Larus argentatus*. Black-headed Gulls regularly followed a diving Smew, often waiting on the water nearby, but hovering above when it surfaced. In general they did not harrass the Smew but sometimes, when they tried to snatch food from a Smew, it would make a short rush to avoid the gull. In some cases, watching Black-headed Gulls picked food-items from the surface. Herring Gulls behaved in a similar way. Once a Herring Gull was seen pursuing a male Smew which flew for about 200 m. Then the Smew alighted, the gull attacked, and the Smew flew away followed by the gull. Red-breasted Mergansers and Goosanders were regularly harrassed by gulls when feeding (Nilsson, 1965, 1966).

Pair-formation

No pairs were seen before February (Table 3); by March and April about one third of the Smew were paired.

In Schleswig-Holstine, Sudhaus (1966) found few pairs in December and January, whereas pairs were common in February, the peak number being in March. In southern Germany, Bezzel (1965) saw almost no pairs in December and January, whereas about 30% of the females were paired in February and about 40% in March and April.

A male Smew and a female Goldeneye were once observed behaving as a pair on a small lake. Wild hybrids between the two species have occasionally been found (Angel & Neuendorf, 1963).

Antagonistic behaviour

Aggressive behaviour is mainly seen in courting parties, only rarely between single pairs or individuals. Fighting for food, common in the Goosander in the winter (Nilsson, 1966), was only seen once. A female came up after a dive with an eel in her bill. A nearby male attacked, the female flew about 100 m followed by the male. Then she managed to swallow the fish and the male left her alone.

Smew have two types of attack: swimming attack in which the bird rushes for up to 2–3 m against its antagonist with the head thrust forward, and diving attack in which it approaches under water. Diving attack was only seen on a few occasions and is not so common as in the Red-breasted Merganser or, especially, the Goldeneye. In the Red-breasted Merganser and Goosander a *wild chase* occurs in which the pursuer follows its antagonist on the surface, both rushing with the wings beating against the surface until they are quite exhausted (Nilsson, 1965, 1966). This was not seen in the Smew.

In the display parties Smew show much aggressiveness, jabbing at others with the bill. This is also the commonest form in the female which only rarely performs proper attacks.

Paired males often defend their females, making repeated swimming-attacks against intruding males, chasing them a few metres away and then rejoining the female. The intruder often returns, to be chased away again.

Communal courtship

The display postures have been detailed by Hollom (1937), Johnsgard (1965) and Lebret (1958), so the present treatment will be re-

Table 3. The percentage of paired males and females among Smews in the Malmö area 1965–1972

Month	Total numbers counted	Per cent ad. males	Per cent paired	
			Males	Females
Jan.	210	49	0	0
Feb.	218	54	7	8
March	449	48	28	26
April	112	47	36	32

stricted to some general observations of Smew courtship in the field.

Courtship was noted in flocks of from eight males and four females down to two males and one female. Usually two to seven males displayed around one or two females. Display in larger flocks generally divided into several groups centred around active females. The display parties rarely had the same number of birds for long, but an active nucleus remained.

The first communal courtship was seen in late January but intense display not until late February or early March. The intensity decreased as more birds paired and was rather low in April. Display was infrequent in the morning and rare at midday. In general it was most intense in the afternoon and when the birds gathered to roost.

Courtship display in Smew could be spontaneous but was generally initiated by: (1) a male or female flying to an inactive flock: (2) a male swimming to a flock; (3) two pairs or a pair and a single male meeting; (4) various external disturbances.

During the period of most intense display about three-quarters of all meetings as in (3) led to display. An intruding male was often met by the male of the pair with aggressive behaviour and display postures. The intruding male also performed some display. In many cases such meetings led to the formation of a display party of several males and one or a few females.

The intensity of the display varied with the circumstances and the time since the last bout. Sometimes only few postures will be shown, in other cases the display will last for many minutes. During the most intense period of display males in the flocks remain *intent* almost all the time, making some display movements during diving pauses. Only a slight stimulus will be needed to start intense display of long duration.

Displaying males will generally group around more or less active females, but sometimes during the height of display, they will pursue inactive females for a long time. Typically a female swims ahead of a group of up to four or five *intent* males that follow close behind her making repeated display movements. Suddenly a male in the rear takes to the wing and flies towards the female, who dives, as do one or more males. When the female returns to the surface, the males fly or rush towards her again, leading to a new escape dive of the female. This may be repeated many times until the female finally takes to the wing pursued by the males. She continually tries to avoid the males, but they follow her and suddenly the group settles on the water only to continue the pursuit there. Sometimes the female and one or two of the males dive direct from the wing and continue under water. Chases of this type will often continue, with short pauses, for up to half an hour. They were generally seen when many of the adult females were already paired.

Copulations were sometimes initiated in a pair that had just left a display party, in other cases when they had jut stopped diving. Once copulation started after an external disturbance. The first copulations were seen in the last days of February, i.e. when the main display period started. In other areas, however, copulations were seen from January onwards (Bauer & Glutz, 1969).

Summary

The general, feeding, agonistic and sexual behaviour of wintering Smew *Mergus albellus* in southern Sweden is described, together with related aspects of habitat selection and sex ratios.

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A male Smew *Mergus albellus* crest-raising. *Phillipa Scott*

The number of adult Eiders in the Baltic Sea

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The Eider *Somateria mollissima* is the most common breeding duck in the Baltic and also the most important game species in Swedish and Danish coastal areas. The size of the Baltic Eider population has varied drastically during the twentieth century, but since the 1940s it has increased and still no levelling out is noted. The Eider of the Baltic Sea is now studied from several aspects. The results of those studies may clarify the dynamics of the Eider in the Baltic, give a basis for management and provide information to marine biologists studying the Baltic ecosystem.

The aim of the present investigation was to census the numbers of adult Eiders in the Baltic. An additional purpose was to study the possibilities of monitoring the population trends. Earlier counts have been conducted in winter quarters and along migration routes but proved to be not very reliable. The method of examining premoulting gatherings of males was developed during introductory investigations in 1971 (Almkvist

Figure 1. The Baltic Sea. Areas where Eider males were censused on 29 May–5 June, 1973, are numbered 1–21 and shaded. Number of Eider males for each area is given in Table 1. A = Laholm, R = Laröd, M = Lomma, F = Falsterbo, O = Ottenby, K = Kalmarsund, H = Huvudskär.

& Andersson, 1972) and 1972. In Finland a pilot survey was conducted in 1972.

The study has been carried out as a joint project between scientists from Estonia, Finland and Sweden coordinated by Almkvist and Andersson.

Chronology

From the main wintering grounds in the Danish waters, the Eiders migrate to their breeding areas during April. They nest on islands, in all the archipelago zones of central Sweden and southwestern Finland (areas 4–9, 14–19 in Figure 1), but also on islands off straight coastlines.

Shortly after the females have started to incubate, the males gather in small flocks (less than ten birds) close to the breeding grounds. In the archipelago areas these small flocks move to the outermost islets and form larger flocks (100–1,000 birds). Finally, most of these gather in traditional sites and form large aggregations of several thousands.

The migration of males to moulting areas in Danish waters starts in the beginning of June, or end of May. This first contingent is small and consists mainly of males probably from the southernmost populations. From the large aggregations, birds leave in the middle of June to the beginning of July for moulting quarters in Denmark. Those males which have moulted in the Baltic migrate south during late summer and autumn to their winter quarters.

Method

The census was made when the postbreeding males were aggregated at traditional areas, but not yet migrated south. These easily detected flocks afford an ideal opportunity to count Eider populations from large areas.

The field-work was undertaken from light aeroplanes and from a helicopter (area 13, Figure 1) on 29 May–5 June 1973, during thirteen flights. The concentration of flights to this short period was to avoid double counting, or ignorance, of flocks eventually moving between different areas. The areas censused are shown in Figure 1. The larger flocks (usually more than 100 birds) were photographed and the Eiders counted on enlargements. Flight altitude was usually 100–150 m and flight speed about 150 km/h. The weather during the flight period was mostly ideal for censusing Eiders, sunny and calm but sometimes with a slight sea-breeze in the afternoon. In the Gulf of Finland part of the flight was made in light rain. Further discussions on the method is given by Almkvist & Andersson (1972).

The number of adult males

Table 1 summarizes the number of adult Eider males found in different regions marked on Figure 1.

Table 1. Number of Eider males counted on 29 May–5 June 1973 in different areas of the Baltic Sea (all figures to nearest hundred). Numbers 1–21 refer to areas on Figure 1

1	Åhus–Torhamn	300
2	Kalmarsund and Öland	2,100
3	Oskarshamn–Östergötland	2,800
4	Östergötland	14,600
5	Östergötland–Landsort	12,900
6	Gotland	10,900
7	Landsort–Sandhamn	24,100
8	Sandhamn–Björkö	29,500
9	Björkö–Gävle	400
10	Gävle–Söderhamn	200
11	Ångermanland	0
12	Valsörarna–Sideby	100
13	Merikarvia–Kustavi	3,200
14	Åland, Brändö–N. Geta	2,400
15	Åland, W. Geta–Mariehamn	7,800
16	Åland, Mariehamn–Kökar	47,300
17	Korpo–Hitis	108,800
18	Bengtskär–Helsinki	2,900
19	Helsinki–Haapasaari	100
20	Koipse	100
21	Ösel and Dagö	500
	Total	271,000

A total of 271,000 Eider males was counted. This number is, however, not equal to the number of males in the Baltic. Four main sources of error will be discussed below.

First, scattered males could still be left in breeding areas. Due to differences in breeding time between southern Sweden and Finland some males in the northern and eastern archipelagoes had not gathered in the outermost areas but were still on breeding areas in the inner archipelagoes which were not censused. These areas were visited just before and after the flights to estimate the number of males there. In area 4 (Figure 1) no such scattered males were present. In areas 7 and 8 about 3% of the total male population was still scattered and not seen during flights. This makes approximately 1,700 males. The Archipelagoe Sea in southwestern Finland was only censused in its outermost parts (areas 14–18, Figure 1) but several flights across the inner archipelago gave the approximate figure of 2,000 Eider males still there. Similarly about 300 males in the Gulf of Finland (area 19, Figure 1) were estimated to stay north of the censused area. This gives a total of approximately 4,000 males not seen during the flights.

Second, flocks could be in areas not visited. No Eider flocks are known to stay far from the coast since the birds usually sleep ashore. The Swedish Coast Guard visited some remote banks during the census period, but no Eider males were seen. The northern coast of Estonia was not surveyed, but concentrations of Eider males are not known from that area. On a visit by boat to a group of suitable small islands (area 20, Figure 1) only 100 males were seen. In the Bothnian Bay and along the Baltic coast south of Estonia not covered in this census few Eiders breed and flocks of males are not known to stay there.

Third, some males may have migrated out of the area before the census. Regularly there is a south migration in June (see Chronology). Observations at Kalmarsund and Ottenby (Figure 1) from 22 May to 4 June showed low migratory activity with a maximum of 500 Eider males per day. No more than 5,000 males could have passed south before the surveys. This figure corresponds well with results from the regular countings in Kalmarsund (Almkvist & Andersson, 1972). Southwestern Baltic (west of Kalmarsund) was censused at a time when the majority of males already had gone westwards, or was not at all covered by flights. In this area the approximate breeding population is about 3,400 pairs (= males, see below), made up of 1,700 in Denmark (Joensen, 1973), 500 pairs in Scania, Sweden (Andersson, Kristersson & Schönbeck, personal communication) and about 1,200 pairs in Blekinge, Sweden (Gerell & Swahn, personal communication). Of these 300 were seen during the census (area 1, Table 1). In the eastern Baltic we have the Estonian population consisting of 6,500 breeding pairs (= males), where only small postbreeding gatherings of males were found in 1973. It is more likely, however, that the Estonian males had entered concentrations in Finland or around Gotland than that they had migrated to moulting areas in Danish waters.

Fourth, males seen could have been incorrectly counted. The Eider male flock in Figure 2 shows how easily a flock is discovered and how difficult it is to estimate the number of birds in it. We are convinced that all flocks, perhaps except a few minor ones, in the censused areas have been discovered. The major problem is to count the numbers in the flocks. Earlier experiences have shown the importance of counting the birds on photographs. For detailed information see Almkvist & Andersson (1972). The diving activity of the males is generally low at the time of day when the census was made

Figure 2. A premoulting flock of Eider males in Östergötland, Sweden, 1 June 1971. The photo shows that the flock is easy to discover, but also the difficulty of estimating numbers. About 2,535 adult Eider males can be seen on this photo.

B. Almkvist

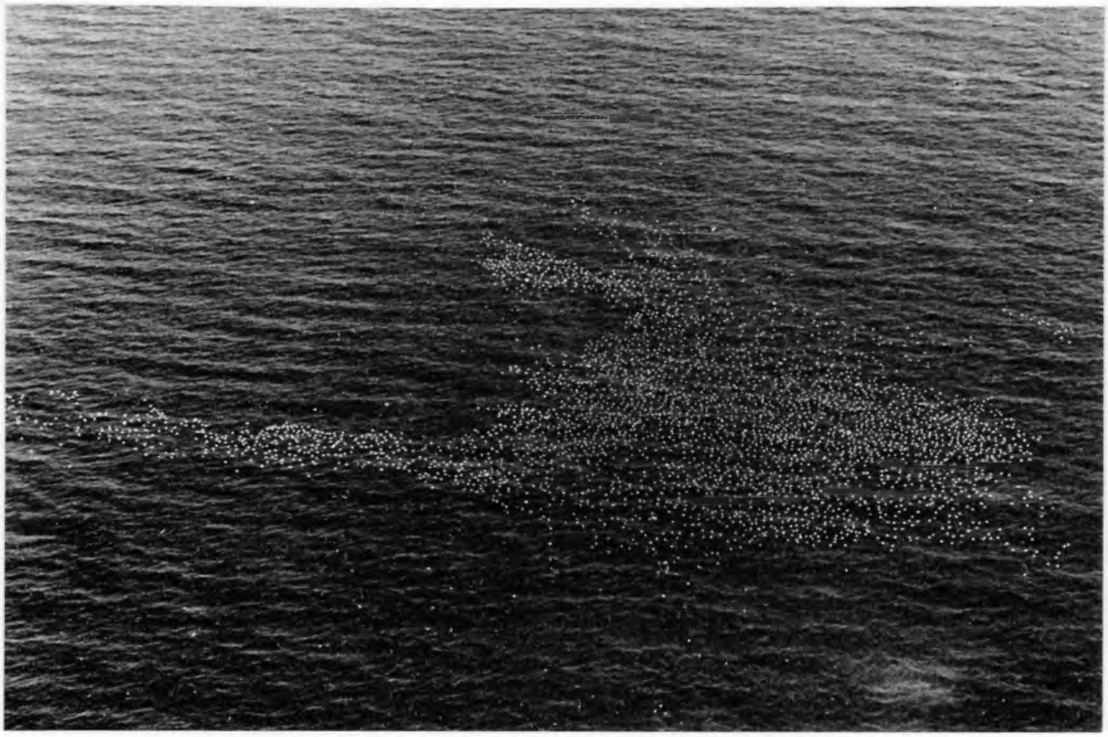

Table 2. **Sex ratio (♀:♂) from Eider counts in the Baltic in 1972 and 1973. Sites are given with numbers in accordance with areas in Figure 1**

Site	Date	Sample size	Sex ratio
On different breeding grounds	April 1973		
14 Archipelago sea	1	1475	1·00†
14 Archipelago sea	4–8	674	0·88†
19 Porvoo	13	217	1·13*
14 Archipelago Sea	15	1690	1·00*†
17 SW Archipelago	12	815	0·96*†
4 Östergötland	8	385	0·99
7 Stockholm arch	10	249	1·06*
On north migration	April 1972		
2 K Kalmarsund	5–18	1477	0·97
7 H Huvudskär	9–22	1813	0·97

* A few females had started laying and even incubating.
† Possibly influenced by spring shooting of males.

(09.00–16.00 hours) and since the normal reaction on the approaching aeroplane was to stay alert, ready to fly, no birds were seen diving. The error in counting the birds on photographs is difficult to estimate.

Some photographs were not good enough to count birds from and sometimes when several flocks were close together and several photos were taken it was difficult to cover all birds. Also sometimes the farthest parts of some large flocks was vague. We believe that we can have underestimated the number of males seen, 271,600, in this way by 5%.

In consideration of the errors discussed above, the 271,600 males seen should be corrected to approximately 297,000 adult Eider males in the Baltic population (including 4,000 left in breeding areas, 5,000 + 3,100 migrated south before census, 13,600 underestimation of flocks seen).

Sex ratio

Before the number of adult males can be used as a measure of the total adult population the sex ratio must be known. For this purpose, counts were carried out during spring migration and on breeding grounds.

Samples of migrating flocks were counted on two sites on the Swedish east coast during the peak and the terminating phases of the spring migration in 1972 (Table 2, Figure 1). Adult males, 1-year-old males and dark-coloured birds were separated. The sex ratio (adult males: all females) was 0·97. The deviation from 1: 1 is probably due to occurrence of 1-year-old females (compare frequence of 1-year-old males in Table 3).

The counts of Eiders on breeding grounds were made in 1973 by boat or aeroplane during the prebreeding time, and mainly included pairs more or less attached to breeding sites. The sex ratio varied between 0·88 and 1·13 with a sample average of 1·00. The relatively large variation presumably is caused by commencement of egg laying and possibly also by local influences of spring shooting of males, which is permitted from 1 April in Finland.

Even if the counts in 1972 did not cover the whole migration period and the figures

Table 3. **Percentage of 1-year-old Eider males in migrating flocks at different observation sites along the Swedish coast (Figure 1) in April 1972. Figures in brackets are numbers counted**

	Date			
Site	5–8	9–13	14–18	19–22
A Laholm	3·6 (1,377)	4·2 (1,511)	6·7 (640)	
R Laröd	2·9 (544)	5·1 (527)	15·7 (198)	
M Lomma	1·2 (607)	1·5 (342)		
F Falsterbo	0·4 (1,339)	1·6 (498)		
K Kalmarsund	0·4 (1,144)	0·0 (188)	3·8 (156)	
H Huvudskär		0·2 (1,185)	0·9 (463)	5·5 (181)

from the breeding grounds in 1973 are somewhat biased, we conclude that the number of females approximately equals the number of males.

The number of adult Eiders in the Baltic

From the results of the aerial census of the flocked males and the sex ratio we thus can calculate that within the Baltic the number of adult Eiders was about 594,000 specimens.

The size of the Baltic Eider population or countrywide parts of it has been estimated or at least elucidated with different techniques. The breeding population in Finland was estimated by Bergman to be 90,000 pairs (Alerstam, Bauer & Roos, 1974). The Estonian population was 6,500 pairs, and parts of the Swedish population (area 3–8 in Figure 1) to be 80,000 pairs (Almkvist & Andersson, 1972). This makes a minimum figure of 176,500 breeding pairs in the Baltic, but large areas were not surveyed.

In Danish waters, which are the main wintering area and where relatively few Eiders from other populations intermingle, Paludan (1962) on the basis of bag statistics, hunting pressure and Eider distribution, presupposed a minimum winter population of 600,000 Eiders, and extensive aerial censuses in January 1969–1971 revealed 450,000 individuals (Joensen, 1972). Because of incompleteness in cover the latter value has been presented as a minimum figure by the author himself. Of course the winter figures also include the yearlings.

The most serious attempt to calculate the size of the Eider population in the Baltic has been made by Alerstam *et al.* (1974). The result of their study was a spring population of 700,000–800,000 Eiders in the Baltic, or allowing for roughly 20% nonbreeders (= immature birds after Paludan, 1962), about 600,000 breeding adults. Their result can not, however, be directly compared with ours.

Alerstam *et al.* concludes that 20% of the birds passing Kalmarsund (K in area 2, Figure 1) are nonbreeders. From studies of the age composition of migrating flocks (Table 3) it is clear that 1-year-old males at Kalmarsund made up an insignificant fraction (0·0–0·4%) during the peak of the spring migration. But their frequency also increased as migration progressed. Young males were more frequent in southwest Sweden than further northeast. On the basis of the seasonal distribution of the migration (appendix 2 in Alerstam *et al.*) we conclude that 92% of the northward migration in Kalmarsund 1972 occurred during 20 March–15 April and 8% during 16 April–20 May. The frequency of 1-year-old females and 2-year-old males (usually considered nonbreeders) is not known. But if we assume that each constituted similar shares as 1-year-old males it is reasonable to believe that the frequency of juveniles/immatures during the whole spring migration at Kalmarsund is definitely less than 10%, probably not more than roughly 5%. In the calculations below the later figure is used.

A correct comparison with Alerstam *et al.* thus involves a reduction of their total of 700,000–800,000 Eiders with 5% immatures, to 660,000–765,000 adult Eiders or about 350,000 pairs, instead of 300,000 breeding pairs as they suggested. The discrepancy between the two investigations, approximately 50,000 pairs, is not great. Alerstam *et al.*, however, have to base their calculations on several assumptions and extrapolations, which are exemplarily described and explained. The main objection in our opinion is that they transfer the experiences from the size of the nocturnal migration over Scania, southern Sweden, to the situation in Kalmarsund, where the indications of such a large night migration are very small (see 'Diel periodicity' in Alerstam *et al.*). Also the large variation concerning the proportion of the migration falling during the standard hours of observation (see Alerstam *et al.*, appendix 2) may be an important source of error.

Monitoring of the Baltic Eider population

In wintering areas and on breeding grounds the Baltic Eiders are so dispersed that it is very laborious to count them and the figures received may also be inexact. The concentrations necessary for convenient and accurate censuses are provided on the spring migration along southeast Sweden and when the males gather in postbreeding flocks. Alerstam *et al.* (1974) demonstrated how traditional migration counts and radar observations can be combined and used also for estimations of population size. In our opinion the present investigation also turned out very successfully. Either of these two methods can be used for monitoring the Baltic Eiders. Beside economic advantages, the male counts offer the possibility of localizing parts of the population and following their changes. Since the Eider in many areas of the Baltic is still increasing it would be valuable to repeat the census after a few years and thus try to follow overall population trends in the Baltic simultaneously with counts on breeding grounds.

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We would like to thank Dr Thomas Alerstam for providing us with sex ratio and age composition data from spring migration in 1972, Mr Christian Hjort and Mr Robert Franzén who arranged counts of the south migration of males at Ottenby and Kalmarsund respectively, Professor Erik Kumari for organizing the flights in Estonia, and the Ornithological Club of Ångermanland for surveying area 11, Figure 1. The cooperation of Messrs J. Engdahl, Hj. Leijonmark, A. Selovuo, S. Suonperä, and H. Voutilainen of the Finnish Frontier Guard is acknowledged. Observations from boat in Sweden were reported by the Swedish Coast Guard.

Summary

An aerial census of adult male Eiders *Somateria mollissima* gathered in postbreeding flocks was made in the Baltic Sea on 29 May–5 June 1973. The dense flocks gather at traditional sites soon after the females start to incubate. 271,000 males were counted, mostly from photographs. This figure was corrected to approximately 297,000, including males still in the breeding areas, males migrating south out of the Baltic to Danish moulting areas and underestimations of numbers in flocks seen. The sex ratio was approximately 1:1, both in counts during spring-migration and on the breeding grounds. Thus the number of adult Eiders was about 594,000 specimens, or 297,000 pairs. This figure corresponds roughly with estimates from winter counts and radar studies of north-migration. The method of censusing Eider males in the Baltic, with male counts in postbreeding flocks, is suggested for monitoring purposes.

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Range expansion and population increase of the Gadwall in eastern North America

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In this era when papers discussing extinction rates and endangered species seem to be the norm, it is somewhat refreshing to report on a species that has extended its range and increased in numbers. Such is the case with the Gadwall *Anas strepera* in the north-eastern United States. This paper documents and discusses the range expansion of the Gadwall breeding population in the northern portion of the Atlantic Flyway (whose boundary is shown in Figure 1) and the resultant increase of Gadwall harvested by hunters.

Figure 1. Gadwall breeding sites in eastern North America. 1, Walpole Island; 2, Magee Marsh WMA; Luther Marsh WMA; 4, Presqu'ile Point; 5, Iroquios NWR; 6, Montezuma NWA; 7, Howlands Island, WMA; 8, Wilson Hill WMA; 9, Parker River NWR; 10, Great Meadows NWR; 11, Long Island; 12, Great Swamp NWR; 13, Brigantine NWR; 14, Bombay Hook NWR; 15, Egg Island WMA; 16, Little Creek WMA; 17, Blackwater NWR; 18, Prime Hook NWR; 19, Deal Island WMA; 20, Chincoteague NWR; 21, Martin NWR; 22, Wallop's Island NASA; 23, Fisherman's Island NWR; 24, Plum Tree Island NWR; 25, Back Bay NWR; 26, Bodie Island NS; 27, Pea Island NWR; 28, Swanquarter NWR; 29, Pamlico Point WMA; 30, Cape Romain NWR. ●—●, Flyway boundary.

Fifty years ago the Gadwall, as a breeding bird in North America, was restricted to the west and midwest. Phillips (1923) stated that the species did not nest east of Lake Michigan, although Bent (1923) added that it had formerly nested in Ohio and was a casual breeder on Anticosti Island, Gulf of St. Lawrence. However, Godfrey (1966) questions the validity of the latter record, which was based on a half-grown young.

Range expansion eastward was first recorded in 1939 (Grey, 1940), when a brood was seen at Pea Island National Wildlife Refuge (NWR) in North Carolina (see Figure 1 for locations). A brood was also seen in 1939 at Bombay Hook NWR in Delaware (Griffith, 1946). Sedwitz, Alperin & Jacobson (1948) reported the species first nesting on Long Island in 1947, and Springer & Stewart (1950) reported seven pairs nesting in Maryland in 1948. Bull (1962) indicated that sixty to eighty young had been produced on Long Island in 1947, 118 in 1950, and ninety-three in 1952. According to Parnell & Quay (1962) nesting had begun on Bodie Island (National Seashore), North Carolina, after 1954, and production at Pea Island National Wildlife Refuge had increased to an average of about 540 per year between 1950 and 1958. They also reported sixty-three pairs of Gadwall at Egg Island Wildlife Management Area (WMA), New Jersey, in 1959. By the 1960s the species was reported nesting at several other locations along the Atlantic coast, including Bull's Island (Cape Romain NWR), South Carolina (Chamberlain, 1960), and Pamlico Point WMA, North Carolina (Lewis, 1970).

Materials and methods

A high percentage of the Gadwall nesting records was from National Wildlife Refuges established in the Atlantic Flyway during the 1930s and 1940s or from more recent state-owned Wildlife Management Areas. Although Griffith (1946) discussed data from refuge narrative reports through the mid-1940s, information from refuges and WMAs

Table 1. Nesting Gadwall on National Wildlife Refuges in the Atlantic Flyway*

Year	Bombay Hook	Pea Island†	Montezuma	Blackwater	Chincoteague	Brigantine	Prime Hook	Great Meadows	Parker River	Great Swamp	Iroquois	Total
1972	300	217	300	10	89	190	55	2	32	10	14	1219
1971	300	363	500	0	283	270	50	0	24	5	6	2803
1970	200	293	280	0	400	600	25	2	20	6	0	1826
1969	200	137	510	0	400	400	25	4	10	0	0	1686
1968	100	97	520	0	100	50	20	4	4	0	0	895
1967	100	50	205	0	50	120	5	4	0	0	0	534
1966	50	53	185	5	50	150	12	0	0	0	0	505
1965	150	47	350	0	25	70	8	2	0	0	0	652
1964	50	83	300§	0	50	75	12	0	0	0	0	570
1963	25	97	250	0	15	2		0	0	0	0	389
1962	75	90	110	0	28	12		0	0	0	0	315
1961	70	170	130	0	30	6		0	0	0	0	406
1960	40	220	75	0	10	0		0	0		0	345
1959	10	170	60	0	20	0		0	0		0	260
1958	8	243	50	0	25	0		0	0		0	326
1957	15	180	150	0	12	0		0	0			357
1956	15	127	80	0	10	0		0	0			232
1955	10	310	20	4	2	0		0	0			346
1954	70	237	10	0	0	0		0	0			317
1953	130	293	12	0	4	0		0	0			439
1952	–‡	317	10	0	0	0		0	0			318**
1951	70	257	6	0	0	0		0	0			333
1950	–	203	10	0	0	0		0	0			213**
1949	–	147	0	0	0	0		0	0			147**
1948	–	30	0	0	0	0		0	0			30**
1947	–	100	0	0	0	0		0	0			100**
1946	–	70§	0	0	0	0		0	0			70**
1945	–	40	0	0	0	0		0	0			40**
1944	–	27	0	0	0	0			0			27**
1943	–	27	0	0	0	0			0			27**
1942	–	8	0	0		0			0			8**
1941	18	15	0	0		0						33
1940	2	23	0	0		0						25
1939	2	3	0	0								5
1938	0	0		0								0
1937	0			0								0
Year Established	1937	1938	1938	1931	1943	1939	1963	1944	1941	1960	1957	

*Data for earlier years at Back Bay NWR were not available; however, at least 8 pairs have nested on the refuge since 1969. Five pairs have nested at both Martin NWR, and Swanquarter NWR since 1969, and at least 1 pair at Cape Romain NWR in 1960.

†Index to breeding population was obtained by assuming that all broods were counted and that 60% of the breeding pairs produced broods.

‡(–) no data.

§Data not available (assumed average of 2 nearest years).

**May have been Gadwall nesting at Bombay Hook, but no counts were made.

has not been intensively reviewed during the last 25 years. We therefore examined refuge narrative reports and contacted state waterfowl biologists. The US Bureau of Sport Fisheries and Wildlife's Harvest Survey data for the Atlantic Flyway enabled us to obtain an estimate of the number of Gadwall harvested each year. Banding records from Manitoba and Minnesota allowed some insight into the contribution of birds produced in the Canadian prairies and the north central States to the harvest taken in the northern portion of the Atlantic Flyway.

Eastward range expansion

Gadwall have nested on fifteen National Wildlife Refuges in the Atlantic Flyway in recent years (Table 1), with the majority on five refuges: Montezuma NWR, New York; Bombay Hook NWR, Delaware; Pea Island NWR, North Carolina; Chincoteague NWR, Virginia; and Brigantine NWR, New Jersey.

The recent observance of large summer flocks of Gadwall at Bombay Hook NWR is indicative of further population growth. Peak August populations on a freshwater impoundment there have been 800, 700, and 1,200 in 1970, 1971 and 1972 respectively. These figures suggest that a considerable number of birds may also be nesting in the vicinity of refuges.

Range expansion and population growth in southern Virginia and northern North Carolina has also been apparent (*in litt.* O. Florschutz, Jr.). Since 1969 Florschutz has recorded a total of eight pairs at Back Bay NWR, five pairs at Martin NWR, and five pairs at Swanquarter NWR. During the last 2 years he also surveyed Wallops Island, Fisherman's Island, and Plum Tree Island, the latter two being satellites of Back Bay NWR. He recorded eight pairs, six pairs, and two pairs, respectively, on these areas.

Information obtained from state waterfowl biologists in Maryland, Delaware, New Jersey, and New York suggests that the breeding population on state wildlife areas is also increasing and expanding in range. At the Little Creek Wildlife Area in Delaware an estimated 173 young were produced in 1962, 272 in 1969, 307 in 1970, 648 in 1971 and 310 in 1972 (*in litt.* T. W. Whittendale, Jr.). V. D. Stotts (*in litt.*) indicated that aerial surveys of Maryland Wildlife Management Areas in late April during the period 1967–1972 gave estimated number of pairs for the respective years: twenty, thirty, forty-six, fifty-eight, forty-two and 132. The trend of singles and group birds recorded showed a similar pattern of increase. The majority of breeders in Maryland were reported from Deal Island WMA (an impounded area), although pairs were seen at Fishing Bay, Fairmont, Ellis Bay, Cedar Island, and Taylors Island Wildlife Management Areas. The Long Island breeding population spread to eight breeding locations by 1968 from Jamaica Bay to Gardiner's Island, about 130 miles ENE (*in litt.* S. Browne). In upstate New York, aside from the federal refuges, Browne indicated that an occasional brood was reported from Howlands Island WMA since the late 1960s and one from Wilson Hill WMA in 1970. Ferrigno (*in litt.*) established indexes for the major types of marshes in New Jersey and projected a total estimate of 3,000 Gadwall pairs. He indicated that 'the mixed *Spartina patens–Spartina alterniflora* marshes of Delaware Bay have always been ideal nesting areas for Gadwall. Gadwall are practically absent from the Atlantic coastal marshes except where impoundments were constructed: the Barnegat Bay Area and Hackensack Meadows.' Locations of all known Gadwall breeding records in the northeast are shown in Figure 1.

Boyer & Devitt (1961) reported Gadwall nesting on an impounded area in southern Ontario (Luther Marsh), and Bednarik (in Campbell, 1968), on another impounded area in Ohio (Magee Marsh). Godfrey (1966) states that the species also breeds very locally at Walpole Island in Lake St. Clair, Ontario. In 1971 and again in 1972, a Gadwall hen and brood of ducklings was seen by Charles Barwell (Ontario Ministry of Natural Resources) and Henny at Presqu'ile Point, Ontario. Further recent evidence of movement into eastern Canada is provided by band recoveries there of Gadwall produced in New York, New Jersey, Delaware, Maryland, and Massachusetts. These have been in southern Ontario (nine) and Quebec (six).

Transplant experiments

Borden & Hochbaum (1966) reported the first successful transplant experiment in the northern portion of the Atlantic Flyway. In late August and early September 1957, twenty-four Gadwall, hatched and captive-reared at Delta, Manitoba, were released at Great Meadows Ponds adjacent to the National Wildlife Refuge of that name in Massachusetts. A first brood was seen in 1961 and another in 1962, but no nests or broods in 1963. One nest, destroyed by a predator, was found in 1964. Another fifty-two Gadwall were released into the area in

April 1965. Twenty-one pairs were recorded in the area in 1965, as far as 5 miles from the release site.

No sightings of Gadwall at Great Swamp NWR, New Jersey, were reported prior to 1969. Fifty-five ducklings transplanted there in 1969 from Brigantine NWR, also in New Jersey, attained Class III size (see Gollop & Marshall, 1954). One hundred reached the same size from a transplant experiment in 1970. Breeding birds were seen on the refuge in 1970, 1971, and 1972, but no production was noted. Young produced in 1971 and 1972 on Iroquois NWR, in upstate New York, were the result of class II and class III ducklings captured at nearby Montezuma NWR and released at Iroquois, twelve in 1969, nine in 1970, and sixty-two in 1971. Table 1 indicates that these transplants have not yet led to an upsurge in local populations.

Harvest in northern portion of Atlantic Flyway

Gadwall were taken in all twelve states in the northern portion of the Atlantic Flyway (above Virginia) during the hunting seasons of 1961 through 1970. Most of the harvest occurred in Maryland (42%), New York (22%), New Jersey (14%), Pennsylvania (10%), and Delaware (8%). The remaining 4% was taken in the following states in descending order: Connecticut, West Virginia, Maine, Rhode Island, Massachusetts, Vermont, and New Hampshire.

Table 2. A comparison of the Gadwall breeding population on National Wildlife Refuges (from Table 1) with the numbers harvested in the northern portion of Atlantic Flyway. Data for 2-year periods are pooled together

Years	Breeding population	Harvest
1971–72	4,022	–*
1969–70	3,512	13,902
1967–68	1,429	10,817
1965–66	1,157	10,753
1963–64	959	4,087
1961–62	721	1,248
1959–60	605	–
1957–58	683	–
1955–56	578	–
1953–54	756	–
1951–52	651†	–
1949–50	360†	–
1947–48	130†	–
1945–46	110†	–
1943–44	54†	–
1941–42	41†	–
1939–40	30	–
1937–38	0	–

*(–) Not available.

†May have been nesting at Bombay Hook NWR, but no counts made.

The Gadwall harvest for 2-year periods is shown in Table 2 and compared with the size of the breeding populations on National Wildlife Refuges. It is readily apparent that the increase in harvest parallels the increase in the breeding population. However, the estimated harvest is much larger than the breeding population on the refuges could sustain. Therefore, a portion of the birds must be derived from other breeding sites. State Wildlife Management Areas within the flyway undoubtedly produce many birds, as do areas which are unsurveyed. Another source seems to be eastern Canada and adjacent states.

Our conclusion, that the breeding population of Gadwall in the Atlantic Flyway is larger than our observations can indicate, is borne out by the fact that birds banded in the eastern extreme of main breeding range are very seldom recovered in the portion of the Atlantic Flyway under study (Figure 2). Gadwall banded in Minnesota have yielded 135 recoveries, but only one in Maryland and one in New Jersey. Similarly, of 292 recoveries from Gadwall banded in Manitoba, only three were found in Maryland, one in New Jersey, one in New York, and one in Pennsylvania.

Discussion and conclusions

Phillips (1923) indicated that the Gadwall was extremely rare on the Atlantic coast from Chesapeake Bay north through New Jersey and all of New England. Furthermore, Stone's (1937) intensive observations yielded only five Gadwall in New Jersey during migration. In the next few years, however, band recoveries made it apparent that a few Gadwall from the main breeding range were in fact migrating into the northern portion of the Atlantic Flyway (Figure 2). The stock for the colonizing effort was believed to be a small percentage of birds from the 'prairie pothole' region of Canada and the United States.

Impounding of water on federal refuges and state Wildlife Management Areas seems to have provided a suitable nesting habitat for the species. Such impoundment has been a part of development plans in the east since 1935, and totalled approximately 2,000 acres by 1940, 4,000 acres by 1950, 7,000 acres by

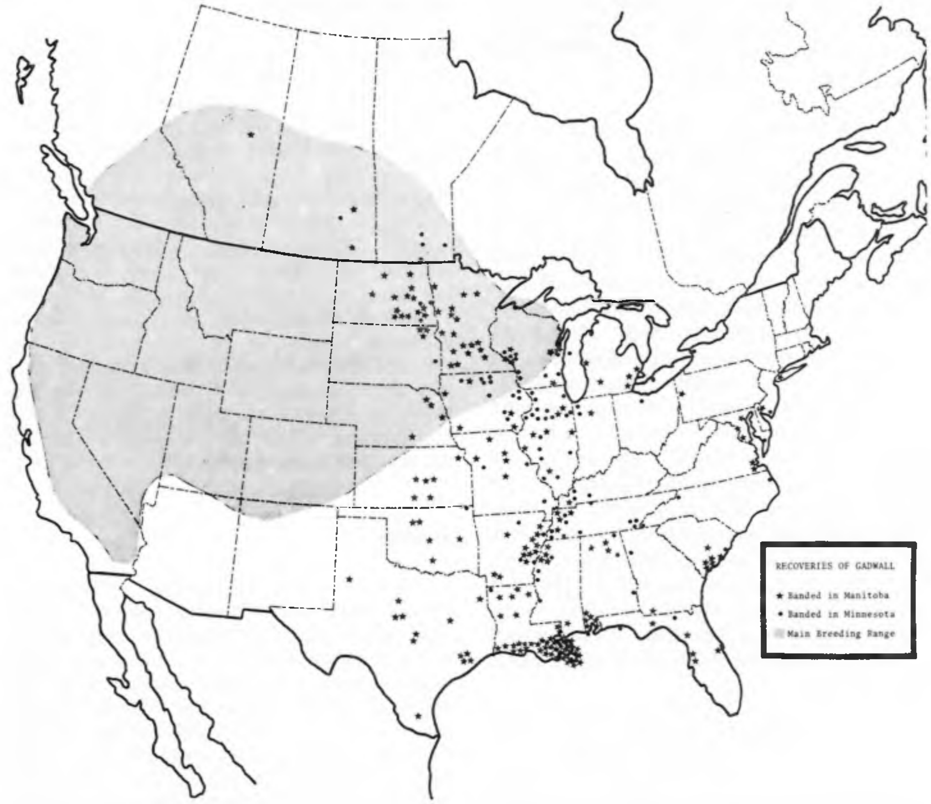

Figure 2. Main breeding range of Gadwall in North America (after Phillips, 1923), and the distribution of recoveries from bandings in Manitoba and Minnesota. Recoveries from within the State or Province where banded were omitted. Also, two recoveries in Mexico (Vera Cruz and Michoacan) were not plotted.

1960, and 12,000 acres by 1970. Colonization took place soon after the impoundments were completed and they act as focal points for nesting activities. Parnell & Quay (1962) indicated that at Egg Island, New Jersey, a definite preference for non-tidal ponds is exhibited by older broods, whereas at Pea Island the impoundments are used for the entire rearing period. Gadwall do not utilize wetlands with as much emergent vegetation cover as do other dabblers. They prefer deep open water, much like diving ducks, and the ducklings will escape by diving.

Stewart & Kantrud (1973) indicated that Gadwall in the 'prairie pothole' region of North Dakota were found in relatively greater numbers on semi-permanent ponds and lakes, reservoirs, and large impoundments. Duebbert (1966, p. 16) discussed a large impoundment island nesting situation in North Dakota and indicated that 'in late April and early May pairs frequented open shorelines... broken marsh and small water areas, but many pairs occupied open-water loafing sites... spent long periods of time (up to 3 to 4 hours) on open water...' Possible explanations for the correlation between impoundments and breeding Gadwall in eastern North America include: (1) the non-tidal water which is used for courtship activities, nesting and brood rearing; (2) the lower salinity which may be necessary for ducklings with poorly developed salt glands; (3) the food sources which are similar to those found in the main breeding range.

Water impoundments along the northern portion of the Atlantic coast produce dense stands of succulent submergent vegetation. Plant species found in abundance include Widgeongrass *Ruppia maritima*, Muskgrass *Chara* spp., Horned Pondweed *Zannichellia palustris*, Southern Naiad *Najas guadalupensis*, Redhead-Grass *Potamogeton perfoliatus* Var. *bupleuroides*. Adult Gadwall feed mainly on succulent vegetation rather than seeds (Martin, Zim & Nelson, 1951). However, recent work in North Dakota by Serie & Swanson (1972) reveals a markedly greater consumption of invertebrates for the species than previously described, particularly during the laying period. Invertebrate populations in coastal impoundments have not been studied.

Parnell & Quay (1962) compared the eastern coastal marshes with the inland western marshes. For example, Bear River Marsh, Utah, provides near-optimum breeding conditions for Gadwall, according to Williams & Marshall (1938). Parnell and Quay reported that the vegetation at Pea Island and Bear River was directly comparable in many instances. Sago Pondweed *Potamogeton pectinatus* was abundant in the ponds of both refuges. Large amounts of submergent plants, *Potamogeton* spp. primarily, were present in the non-tidal ponds at Bombay Hook, Egg Island, and Pea Island and these plants provided a food supply similar to that on western marshes. They concluded that controlled water levels and protection of nesting birds might allow substantial increases in nesting populations of Gadwall and other species of ducks on the eastern coastal marshes. Such a population increase of Gadwall has indeed taken place during the last decade.

The process may have been accelerated to some extent in recent years through transplant activities, both from within and without the Atlantic Flyway. Nevertheless, we believe that the inadvertent provision, by impoundments, of suitable production habitat for Gadwall is more important. The species responded immediately to the available habitat by extending its breeding range and increasing in numbers. The population is still increasing in the northeast, while the size of the population in the main breeding range has fluctuated since 1955 with no apparent trend.

Acknowledgments

The assistance of Howard D. Woon, and Otto Florschutz in providing Gadwall breeding information from the refuge narrative reports was most appreciated. The refuge managers and biologists in both Regions 4 and 5 during the last 35 years made this paper possible by recording the basic information. Discussions with Francis M. Uhler regarding Gadwall food habits and marsh vegetation along the Atlantic coast were most beneficial. Thanks are also given to Stephen Browne, Fred Ferrigno, Vernon D. Stotts, and Thomas W. Whittendale, Jr. for providing information from state Wildlife Management Areas. Harold F. Duebbert and Thomas J. Dwyer kindly reviewed the manuscript. Samuel M. Carney and Henry M. Reeves of the Office of Migratory Bird Management, Laurel, Md., provided the harvest statistics and banding data.

Summary

A disjunct breeding population of Gadwall in eastern North America was first recorded in 1939. This population has extended its range during recent years to the point where it is now found breeding in more than thirty locations (primarily National Wildlife Refuges and Wildlife Management Areas). These are 1,600–2,000 km (1,000–1,200 miles) from the main breeding range in the west and midwest. The number of breeding birds and the harvest have both increased during the last decade. Approximately 40,000 Gadwall were harvested in the northern portion of the Atlantic Flyway between 1961 and 1970. The impoundment of water seems to be responsible for the increase, providing focal points for nesting activities.

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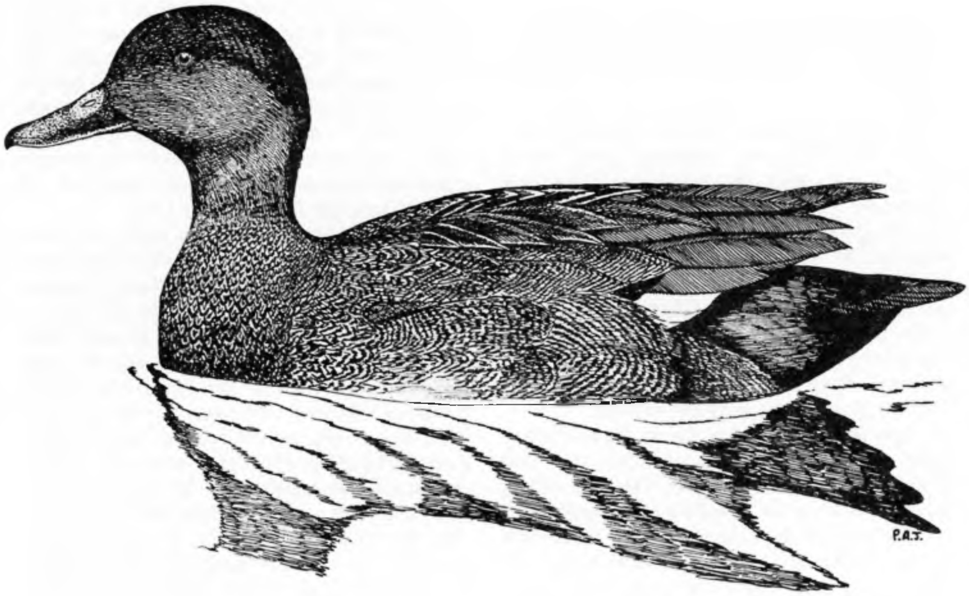


The Wildfowl Trust expedition to Spitsbergen, 1973

E. E. JACKSON, M. A. OGILVIE AND M. OWEN

Barnacle Geese *Branta leucopsis* winter in several places in the British Isles, principally on small islands off the west coast of Scotland and Ireland. Their main wintering haunt on the mainland is in the Solway Forth, on the borders of Scotland and England. Here the wintering flock, numbering two or three thousand before the last war, had been reduced to only a few hundreds after it. In 1954, the geese there were taken off the shooting list, and in 1957 a National Nature Reserve was created covering the merse and mudflats at Caerlaverock, Dumfries-shire. The birds responded well to this protection with an increase in numbers to around 4,000 by the mid-1960s. The history of the reserve and details of the numbers and habits of the geese has been given in a booklet edited by Harrison (1974).

Barnacle Geese breed in East Greenland, Spitsbergen, and on the coast and islands of western Siberia. Boyd (1961) suggested that the Solway wintering geese bred in Spitsbergen, while all the remaining birds wintering in the British Isles came from East Greenland. The Russian breeding geese were thought to winter in the Netherlands and Germany. His evidence came from a very few ringing recoveries plus counts of the proportion of young birds present in the flocks each winter. The adult/juvenile ratio in the Solway flock was often very different from those in other areas suggesting separate breeding grounds with differing summer conditions. Extensive marking subsequently proved Boyd to be entirely correct.

Two British expeditions to East Greenland, in 1955 and 1961, marked over 900 Barnacle Geese (Marris & Ogilvie, 1962), while a Norwegian expedition to Spitsbergen in 1962 caught and ringed nearly 700 (Larsen & Norderhaug, 1963). Simultaneously, the Dutch began to catch their wintering birds in clap nets. In February 1963 the Wildfowl Trust made a single catch with its rocket nets on Eastpark Farm, adjacent to the Caerlaverock Reserve. Of the 315 birds caught no less than ninety-four carried rings put on in Spitsbergen the previous summer but no Greenland- or Dutch-ringed bird was found (Boyd, 1964). In addition, the Greenland-marked birds, plus another 1,400 caught there in 1963, had been colour-marked, and these birds have since been sighted, as well as giving recoveries, at several of the Scottish and Irish island haunts. Only one has ever been seen at Caerlaverock—a wind-blown vagrant.

Further work was done in Spitsbergen in subsequent years to map the breeding distribution and to investigate the breeding ecology of the geese (Norderhaug, Ogilvie & Taylor, 1965; Norderhaug, 1970). The next major stimulus to further study came in 1970 when the Wildfowl Trust took on the lease of Eastpark Farm, which includes 95 ha of arable and pasture as well as the 240 ha of merse forming part of the Reserve. The Trust's main aims were to reduce disturbance to the geese, increase facilities for bird watchers coming to see the geese, and improve the feeding for the geese. An extensive system of screen banks and observation hides and towers was constructed, stock grazing in winter was reduced, and fields reseeded (Matthews & Campbell *in* Harrison, 1974). Last winter (1973–1974) this policy paid off with a great increase in the time spent by the geese on the farmland, where they are much more easily seen, as opposed to the merse where they can be up to 3 km from the nearest observation point. Additionally the flock increased to over 5,000 (see p. 170).

Having embarked upon a study of what the geese eat in winter, an investigation of their summer foods and conditions became desirable. In addition, if a worthwhile sample of geese could be caught and ringed, with plastic rings having engraved letters large enough to be read in the field, individuals could be followed over succeeding years and their behaviour and breeding performance noted. The effect of conditions at the wintering haunt on subsequent breeding success has received some attention in North America but hitherto very little in Europe. Here was a relatively small, discrete and protected population of geese, readily observable in the field, and ideal, in fact, for such a study.

Planning therefore started for a Wildfowl Trust expedition to Spitsbergen in 1973. Thanks to a generous grant from Macmillan Ltd., and to Anglia Television agreeing to pay for two film cameramen to accompany the expedition, it got off the ground. The personnel were as follows: Ted Jackson, Chief Education Officer of the Wildfowl Trust (and leader); Myrfyn Owen, ecologist at the Trust and responsible for the study being done at Caerlaverock; Malcolm Ogilvie, Ringing Officer of the Trust; Mike D'Oyly, Assistant Regional Officer for Gloucestershire of the Nature Conservancy Council; Chris Knights and Terry Andrewartha, freelance film cameramen working on this occasion for Anglia Television. The area of Spitsbergen selected was around the fjord of Hornsund, where the Norwegians had caught their geese in 1962 (Figure 1). The party left Slimbridge on 4 July arriving in Spitsbergen on the 11th. It was there a month and was back in England on 18 August.

The following narrative is based largely on the diary kept by one of us (M.A.O.). A summary of the results will be found at the end.

5–11 July. The Journey

In theory all the rush, panic and bother of an expedition come in the planning and preparation stages, allowing for relaxation once it is on its way to its destination. However, some further problems were reserved for us on our journey. One of the North Sea ferries, running from Newcastle to Bergen, ran aground a month before we were due to leave, and our baggage, nearly two tons of it, was rescheduled on an earlier boat. We were flown with other passengers on a charter flight to Bergen.

On arrival in Bergen we quickly located our baggage, fortunately intact, but also found to our astonishment not one, but both, of the 5-m fibre-glass boats that we were taking with us. One had come as arranged with the baggage from Newcastle, but the other had had to be sent on 3 weeks beforehand and was supposed to be awaiting collection at a radio station some 130 km north of our destinction in Spitsbergen. We had made elaborate plans for two of the party to collect it and come south to meet up with the rest of us. And now here was the boat still sitting in Bergen. It took a lot of hard work to arrange that both boats could accompany us, saving the time, trouble and petrol involved in the original plan. Out of some administrative muddle by the shipping agents, plus the luck of our spotting the boat on the dockside in Bergen, had come a positive gain to the expedition.

At last we were all on board the 1,600 ton 'Nordnorge', one of the fleet of passenger and cargo boats making the daily express run up the Norwegian coast. Once a week during the summer the ship leaves the northern tip of Norway and heads north the 700 km to Spitsbergen for a 5-day diversion, before returning to Bergen. Because we could only be landed if the weather conditions were good and there could be no hanging about waiting for an improvement, we remained in a mild state of tension throughout the otherwise delightful 4-day journey up the Norwegian coast. We lazed away our time on deck bird watching, as the ship cruised along narrow fjords and between innumerable islands. The 'best' bird we saw was undoubtedly the Sea Eagle of which we spotted five on the journey, one being dive-bombed by a Peregrine.

Leaving North Cape, the northern tip of mainland Europe, at midnight with the sun

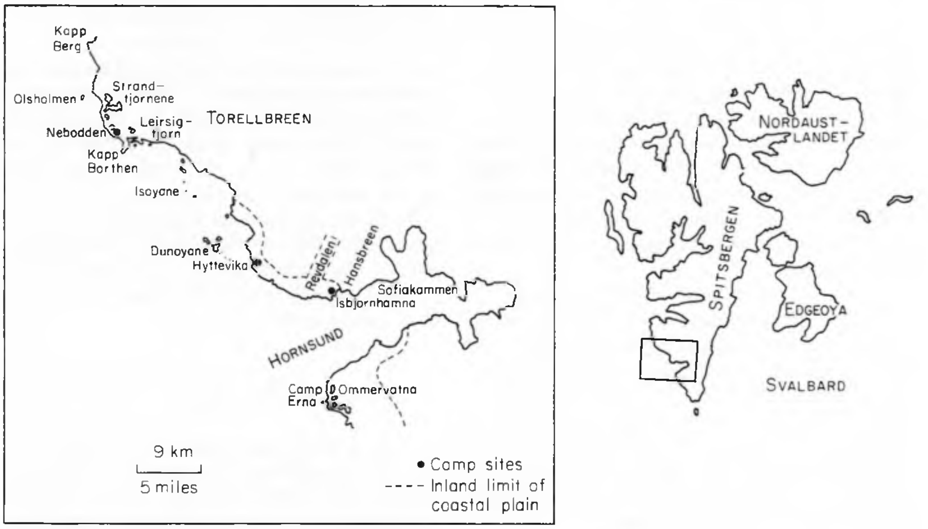


Figure 1. Map of Hornsund area of Spitsbergen, whole country in inset. Note that whole archipelago is now called Svalbard, while Spitsbergen remains the name of the main island.

well above the horizon, we next called in at Bear Island, roughly half-way to Spitsbergen. Here the ship steamed slowly past the towering bird cliffs of the south end of the island where countless auks and other seabirds breed in screaming confusion. A brief stop was made at the flatter north end of the island to drop supplies to the Meteorological Station there. And then north again to Spitsbergen.

12 July. Arrival

We were due to arrive at Hornsund, the 8-km wide fjord on the south-west corner of Spitsbergen, at about 05.00 hours. Some of us stayed up all night, taking advantage of the duty-free drinks, a party and the almost non-existent hours of closing of the ship's bars, others tried to sleep and couldn't, and one slept soundly despite it all. By 04.00 hours the ship was moving slowly into the mouth of the fjord, with little or no wind blowing, just a long lazy swell rolling her gently. The prospects for landing could hardly have been better.

We were all a little tense because we could muster very little experience of being dropped over the side of a large ship into very small boats and ferrying a lot of heavy baggage and equipment ashore on to an open beach. However, it all went fairly well, if rather slowly. The ship's crew left us to our own devices, just working the winch to get our boats from the deck down on to the water, and then lowering slings of rucksacks, food boxes and jerrycans down into them. Standing in a small boat, which was rising and falling on the swell, trying to prevent it banging too hard into the ship's side, and simultaneously attempting to receive cargo neatly into, but not through, the bottom of the boat without being knocked into the water, was an experience that one was glad not to have too often. However, no-one and nothing was dropped into the water and after 2 hours and five journeys all our things were ferried the 2 km to land.

The most prominent object, a couple of hundred metres back from the shelving shingle beach on which we had landed, was a large, yellow wooden hut. We had learnt on the ship that some Polish glaciologists and geologists were in residence and that the hut had been erected in 1957 when a party of Poles overwintered during the International Geophysical Year. Now it was only in casual use during the summer months.

We were warmly welcomed by Stanislav Baranowski, the leader of the ten-man Polish expedition, invited into the hut, sat down at a table and plied with coffee, porridge, bread and jam, and plum vodka. Baranowski spoke good English, while another Pole had spent 2 years in Canada and was quite fluent, and a third spoke excellent French, so conversation was not too difficult. They had heard of our impending arrival from the Governor of Svalbard who had been to visit them a couple of weeks before. We were offered the full run of the hut, including a large room cleared for sleeping, a kitchen complete with coal stove and cold running water, and tables and chairs. It all seemed luxurious in contrast to the tents and primus stoves that we had brought with us. For these and other kindnesses we are extremely grateful to the Polish expedition.

Our base was at a place called Isbjornhamna (Polar Bear Bay); the bears are only there in the winter. It lies on the north side of the 15-km long Hornsund, about 3 km inside its mouth. Here there is a narrow coastal plain, nowhere more than 2 km wide, consisting of bog, pools, rocky outcrops, and low gravel ridges. It rises gently inland to the foot of steep scree slopes that run up into a line of jagged peaks and ridges about 500–700 m in height—a mountain wall separating the coastal strip from the permanent ice inland. Where there is a gap the ice flows through as a glacier to debouch into the sea. Hansbreen, nearly 3 km across, did so just to the east of our landing bay (Figure 2), while beyond it more peaks rose, culminating in the 700-m sheer cliff of Sofiakammen, the site of an enormous seabird colony. Beyond that again, several more glaciers flowed into the fjord; the ice calving incessantly from them was to prove a hazard to some of our boat journeys. Across the fjord the scene was dominated by the peak of Hornsundtind, at 1,400 m the second highest mountain in the country. We never tired of watching and photographing it in the endless variety of light, cloud and mist (Figure 3).

We had scarcely arrived before Myrfyn headed for the nearest prominence with a pair of binoculars and came hurrying back to report the first sighting of Barnacle Geese by a pool not far away.

13–20 July. Reconnaissance

Our first week was spent in exploring the area, locating Barnacle Geese for subsequent capture, and making a start on the scientific programme. This included finding what the geese were eating and in what quantities, collecting lichens for the British Museum,

Figure 2. Hansbreen glacier. The ice-cliff is about 30 m high. *E. E. Jackson*

and identifying plants for a proposed atlas of European flora.

Exploratory trips were made first to the Dunoyane islands, lying about 25 km north up the coast, and about 4 km offshore. There are three flat islands about 40–100 ha in extent, each with one or more freshwater pools. It was on them that the Norwegians had caught their geese in 1962. That year had been a very cold one and hardly any geese had bred, but in the 2 following years plenty of breeding birds had been found. Our first visit produced something of a shock because the eighty or so breeding pairs had by no means all hatched their eggs, although we had expected hatching in the first week of July. The 350 non-breeding birds that were present were only just beginning their flightless period. We had tried to time our expedition so that we would arrive after the hatch and be able to start rounding up the flightless birds immediately without disturbing the breeding birds. However, Chris and Terry were able to get some unexpected film

Figure 3. Hornsundtind seen across Hornsund. A small freshwater pool lies on the near shore. *E. E. Jackson*

of the geese at the nest, and of the eggs hatching.

A second trip was south across Hornsund to the further shore and then on foot southwards for a considerable distance. Nearly 150 geese were located on large pools near the shore, including a few family parties, the first definite breeding record for that locality. On one of the pools was a wonderful flock of about 180 King Eiders.

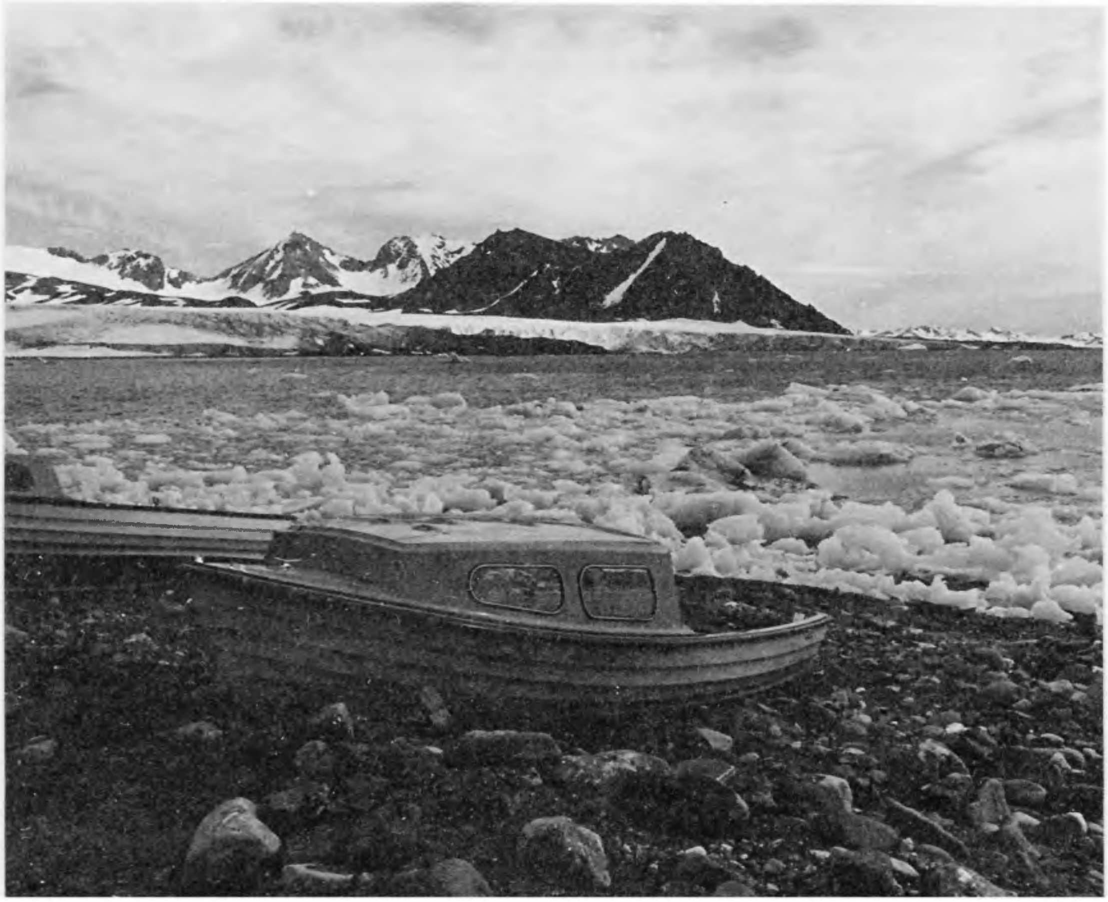
Close to our base a hide was erected beside a small pool, surrounded by a mossy bog. Here, five family parties of Barnacle Geese were living and Myrfyn spent hours checking on their feeding rates and collecting droppings for subsequent analysis. The rest of us spent some time in this hide because it not only gave close up views of the geese, but was less than 3 m from the nest of a Grey Phalarope.

The weather in this first week was mixed, fog interferring both with the filming and with some of our boat trips, and quite strong winds kept us confined to the land for 2 days. On one of these, the wind was from the east and it brought with it large quantities of ice, calved from the several glaciers. The bay where we kept our boats, hauled well up the beach, became choked, and even when the wind changed a belt of ice about 10 m wide was left stranded on the shore. The largest pieces were 2 or 3 metres across and 1 m thick, presenting quite an obstacle when we next wanted to launch our boats (Figure 4). To do so, we first had to cut a patch through with ice-axes and a borrowed crowbar. Larger icebergs fortunately never drifted into the bay; up to 60 m long and 20 m high, they made a steady procession out of the fjord, castles of ice, turrets gleaming in the sun, or ghostly aircraft-carriers, looming weirdly through the fog.

It was clear from these first trips that the Barnacle Geese were only breeding on offshore stacks and islets. Where these were large and vegetated, as were the Dunoyane group, the goslings would be reared there, but elsewhere the parents took the young in the first few days to the nearest suitable mainland. Much of the coastal plain was bare stones and rock, or covered with lichens and mosses. It was only around pools, along the banks of the small streams, and beneath the scree slopes that the vegetation became at all lush, and included grasses and flowering plants. The water that flowed down from

Figure 4. The expedition's boats blockaded by ice floes.

E. E. Jackson



the screes was greatly enriched by the droppings of the countless thousands of Little Auks breeding among the rocks. The lower slopes of the mountain wall, that ran for over 20 km from Isbjornhamna northwards to a point opposite the Dunoyane, was one continuous Little Auk colony. We tried making rough estimates of how many birds there were, and never got lower than 3 or 4 million. The air overhead was filled with wheeling flocks of thousands; their high-pitched laughing calls dinned into our ears. They feed on plankton, which abounds in the shallow arctic seas, and must bring in a very considerable weight of it during a breeding season. The waste and droppings are washed down by the melting snow, itself often stained red, into the many small streams and pools of the coastal plain. The bright green of the plants growing by the pools contrasted with the dull browns and greys of the stony and lichen-covered ground.

On such green patches we found most of the geese. The pools offered them some security, though when they saw us the birds would often run down to the sea, waiting there until we had passed. There were only a handful of family parties on the mainland between our base and the Dunoyane, none worth a catching attempt this early in the season, when the young were still too small to ring and the parents not yet all flightless. We therefore kept to our original schedule of catching the non-breeding birds on the Dunoyane first, though delayed by the lateness of the season.

21–24 July. Goose catching on the Dunoyane

After a false start on the 20th when the engine of one of the boats played up and then the sea became too rough to go, we finally left base camp late in the evening of the 21st for Hyttevika. This was a point on the mainland immediately opposite the Dunoyane islands, and almost the furthest point north on the coastal plain before the way was blocked by the huge Torell glacier. We took with us sufficient food and petrol to last a fortnight, as we hoped to go further north when we had finished catching on the Dunoyane. We had to give up the comfort of the large hut at Isbjornhamna for small three-man tents, and cooking on primuses.

This camp site was very close to a part of the continuous Little Auk colony. Here the coastal strip narrowed to a few hundred metres, and was partly taken up by a vast lateral moraine. In it the Little Auks were breeding in greater density than we had seen before. The only avian predator on Little Auks is the Glaucous Gull and a number of these were constantly patrolling along the boulder slopes. As each gull flew by, the auks sitting on the scree beneath would rise in a cloud and stream out, turning and flying back as the gull went past, their droppings adding a camouflage of whitewash to the previously pristine orange of our tents.

We made out first catching attempt on 22 July, and it was a complete failure. We copied the technique used by the Norwegians when they caught on the Dunoyane islands in 1962. The idea was to approach the chosen island without being detected by the geese, to land, and then spread out and creep along the shore below the storm beaches and low cliffs, hidden from the geese feeding on the flat top of the island. We therefore cut our engines when over a kilometre from the island, and rowed the remaining distance in boats that were very evidently not designed for rowing. However, we made it, landed quietly and crept along the beach. On rounding a corner, a sizeable flock of geese was seen swimming on the sea well offshore, and our simultaneous emergence over the brow of the storm beaches produced only six evenly spaced goose catchers with just two geese in the middle; both quickly demonstrated that they could fly.

Only slightly daunted by this fiasco we moved on to the next island but again the geese were not to be surprised. We therefore withdrew and laid our plans for the following day. We decided not to attempt to surround the geese but to move straight on to an island and while four of the team stayed out of sight around a convenient pool close to a good landing beach, the other two would use a boat to try to herd the geese, by then on the sea, back to land.

On 23 July this plan worked. The geese were comparatively easy to shepherd, with the boat, manned by Ted and Malcolm, manoeuvering slowly and quietly some distance from them, zig-zagging to and fro keeping the birds on the correct heading (Figure 5). The only problem encountered was that the sea close to the island was littered with rocks. Fortunately neither the fibre-glass of the boat, nor the propellor guard of the outboard suffered more than minor scratches.

This first drive was made more exciting by the presence in the flock of about 120 birds, of two white Barnacle Geese. They stuck very close together and we assumed that they were the two young birds, hatched in 1972, that had been at Caerlaverock all the previous winter. Soon the geese were landing on the right beach and hurrying up

E. E. Jackson

Figure 5. A flock of about 100 flightless Barnacle Geese being driven on the sea towards a landing beach on one of the Dunoyane islands.

the bank beyond. The boat landed hard on their heels and the two people manning it were just in time to plug the gap round the pool on to which the birds were running. The other four had risen to their feet as the geese came on to the water, and there the birds were, neatly surrounded.

A horse-shoe-shaped pen of 1·3-m high netting was erected at one end of the pool and two wings led out to guide the birds in. The pond was about 100 m long and 40 m wide, and up to 2 m deep. With two, one-man plastic dinghies in the water, paddled gingerly by Mike and Malcolm, and the rest walking up the banks we moved the flock slowly towards the pen. The drive went very well but the pressure of so many birds in the pen caused a side wall to collapse and we had the mortification of seeing nearly three-quarters of the geese stream out, including the two white ones. A quick rush, and the pen was secured but with only thirty-two inside. However, not all the rest were lost as twenty-nine went back on to the pond instead of choosing the obvious escape route to the sea. They were held by two of the party while the ringing, weighing and measuring of the captured birds went ahead. Two rings were put on each bird, a metal one on which was stamped a serial number and the address of the Stavanger Museum, from which the Norwegian ringing scheme is administered, and a yellow plastic one on which was engraved three black letters repeated three times round the ring. These letters can be read at up to 300 m with a telescope, enabling individual identification of the geese in the field.

A second drive of the pond caught the twenty-nine remaining birds. Of the total catch of sixty-one, three carried Norwegian rings put on at the same locality in the years 1962–1964.

On 24 July we repeated the catching operation, this time with complete success. The pen was reinforced and the poles more securely guyed. Our catch on this occasion totalled 159, including the two white ones (Figure 6), which proved to be brother and sister, sixteen repeats from the previous day's catch, seven with old Norwegian rings and five from the 1963 catch at Caerlaverock.

25 July–1 August. Goose catching north of Torellbreen

We had now made two good catches on the Dunoyane, totalling 220. We had agreed with the Norwegian Ministry of the Environment, who are responsible for some newly promulgated conservation laws for Spitsbergen, that we would minimize catching on the Dunoyane so as to reduce disturbance. We were permitted not more than one catch on each island during the first part of our stay followed by repeat catches towards the end.

We now wanted to move about 25 km to the north past the uncompromising 15-km face of Torellbreen. Beyond it the coastal plain began again, quite wide and with

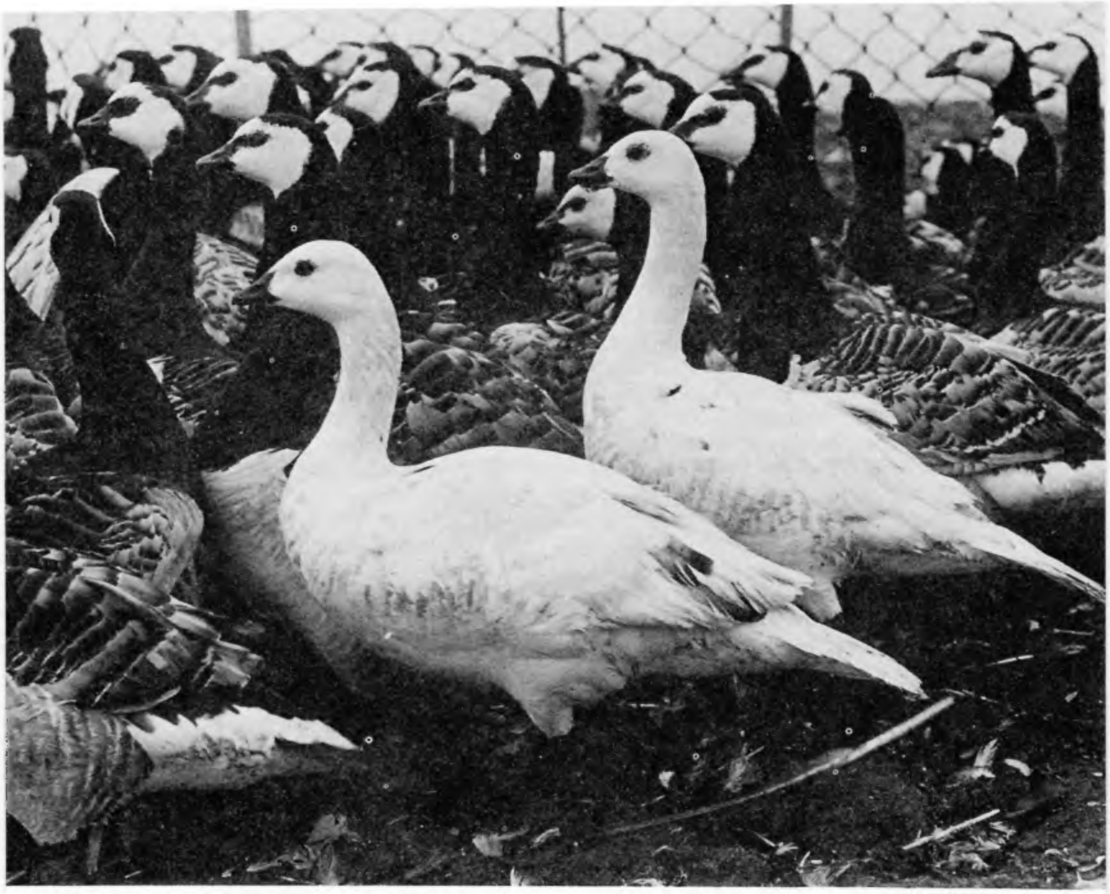


Figure 6. Two white Barnacle Geese rounded up with normal birds.

M. Owen

numerous large shallow pools. There had been several hundred geese there in 1964, the last time the area was surveyed in detail, probably breeding on some small offshore islets.

The expedition members became very used to making plans which had then to be changed. On 25 July we were ready to move north, but we awoke to find thick fog obscuring everything and visibility no more than 300 m, occasionally lifting to 2 or 3 km. This was not nearly good enough weather for our projected journey. We needed to keep sufficiently far away from the glacier and yet still be inside a group of small islands and rocks, and also avoid some complicated shallow areas near our intended landfall.

Figure 7. Inquisitive Little Auks.

July 26 was an equally wasted day. Visibility gradually improved but the wind rose to be a fairly steady force 3–4 from the west, the worst possible direction as we would be exposed to it almost throughout the journey. With heavily laden boats we were not in the mood for taking risks. At least there was a little sunshine in the afternoon and Terry and Christ got their cameras busy on the Little Auks (Figure 7).

On the 27th we made it. The wind dropped, the visibility was fair, though never good, and the sea was down to a long swell. We were off about 10.00 hours cramming everything into the two boats. We passed quite close by the Isoyane islands on the way, where breeding Barnacle Geese had been reported by the Norwegians 10 years previously. We saw adults with young on at least one of the islands. Most of the journey was steady chugging along at 7–8 knots with the two boats never far apart. Even with masses of clothing on, topped off by waterproofs and a life jacket, sitting still in a small boat is not a warm occupation and we were all of us relieved when, at about 12.30 hours, we landed at Kapp Borthen. Our intention was to round the point and find a camp site a few kilometres to the north, close to some of the pools. The charts suggested a clear channel 100 m or more in width between the point and a chain of offshore rocks. At close range there appeared to be broken water right across the channel, so we decided to land before the point.

From the land there seemed to be a tide race through the channel, so we waited about 2 hours until the steep confused seas had subsided somewhat. We eventually went through without any trouble but it was only too clear that the channel was nothing like as wide or free of rocks as the charts showed. We had been encouraged to see about 100 Barnacle Geese, including some goslings, close to the point.

A short, choppy boat ride took us another 3 km north of Kapp Borthen, to a sheltered shelving beach beside another small point, Nebodden. We quickly selected a camp site in a slight hollow between some rocky hummocks. We erected our conventional tents, and also made an interesting structure out of driftwood, which was very plentiful here. Over it we stretched a large polythene tarpaulin to make a cooking and general purpose shelter. All Terry's building skills were called into play to construct a robust framework out of pitprops, tree trunks and planks, held together with 6-inch nails that just happened to be part of the expedition equipment.

The evening allowed for short exploratory walks during one of which we found a whale's rib half buried in the sand of a storm ridge. On digging it out we found that it measured 6·1 m (19 feet). We also located some geese on two nearby ponds.

Our first catching attempt on 28 July was rapidly terminated when the geese, about thirty of them, spotted us and ran on to the sea. We therefore proceeded straight to the next pool, rather further inland where about fifty birds, adults and goslings, had been seen the night before. This time the surrounding of the pond went very well and the birds had no choice but to swim on to the water and stay there while the catching pen was erected. We lost five adults right at the last minute, all fliers, but several other full-winged birds entered the pen. Our catch consisted of twenty-three adults and twenty-three goslings, most of the latter about 2½ to 3 weeks old. Their legs were large enough to take the metal rings but not yet long enough for the tall plastic rings. There were two quite small goslings, only about a week old. They ran up and down the pen cheeping loudly, while one of the full-winged adults that had escaped at the last minute was honking on the pond equally loudly. We therefore caught up the goslings, and having marked them, released them on to the pond. They swam vigorously away and before they had gone 30 m the adult took off, and landed close alongside. As they continued to swim away a second adult flew in and landed with them to the accompaniment of much calling and greeting display.

The following day was wet and foggy. In the late evening the weather cleared enough for us to undertake a reconnaissance of some more pools about 5 km up the coast, where we located nearly 200 birds.

Terry and Malcolm walked north on the morning of the 30th and managed to persuade a flock of just over 100 geese to go on to a small pond. The boat was rather behind schedule in arriving and there were some fairly frantic moments during the wait when only Terry's fleetness of foot prevented the flock from getting away. Eventually the boat party arrived and soon four people were guarding the geese while the other two erected the pen. The drive through the pond, which was barely knee-deep, went very well and we were soon processing a catch of fifty-eight adults and forty-three goslings. There were two British- and four Norwegian-ringed geese in the catch, in an area where none had previously been caught. We left the nets in position and returned to our camp, intending to try again at the same place at least once more.

On the 31st we made two more catches at the same pool. With Chris and Ted in the boat and the other four walking, we arrived more or less together and then the boat party went looking for geese on the sea while the rest of us took up position round the pool. The drive went very smoothly, the geese landed in the right place, ran up the beach, across a wide stretch of tundra, and on to the pool. We wasted little time in moving the geese into the pen and found that we had caught thirty-nine new adults plus one repeat from the previous day.

As there were still unringed geese in the area the boat put to sea again and the whole operation was repeated. It did not go quite as smoothly as the time before because as the geese neared the entrance to the pen they became increasingly reluctant to go any further. However we pressed forward and although a number of birds broke back and escaped between us, thirty-six finally entered the pen of which twenty-six were new. We had caught a total of 166 birds at this one site.

On 1 August we attempted to make our way south, back to Hyttevika. But, as before, the weather dictated otherwise. It was a glorious sunny day but also quite windy and the sea was covered with white horses, too rough for well-laden boats. We therefore spent the day in a variety of ways. Ted and Myrfyn scaled the nearest scree slopes in search of seabirds, getting some spectacular views across Torellbreen in the process. Chris and Terry went filming Red-throated Divers on a nearby pool, while Mike and Malcolm walked south towards Kapp Borthen, botanizing, and watching the sea for signs of calming.

The next morning the wind had dropped and we set off. We had hoped to call in on the Isoyane islands but a heavy swell was running and with an east wind beginning to rise there was nowhere very sheltered to land, and driving birds off the sea would have been next to impossible. We arrived back at Hyttevika after a 3-hour trip and while Chris, Terry and Myrfyn stayed there, Ted, Mike and Malcolm continued on to base camp at Isbjornhamna.

2–10 August. Frustration

On the morning of 2 August, Ted, Mike and Malcolm returned to Hyttevika to join the others in further catching on the Dunoyane. It was, however, to be a week of increasing frustration. We thought that one if not two catches would be made on the islands without difficulty. As Ted and Malcolm went out in the boat to bring geese back to the island where the other four were waiting, the wind and sea got up until those in the boat were having to concentrate more on watching the waves than the geese, and the latter were obviously also beginning to find the conditions unpleasant. So we called off the drive and returned to Hyttevika, where we packed up the camp there. Then as conditions had not worsened any further and the wind would be behind us, we went back to base.

Figure 8. Arctic Fox. *E. E. Jackson*

The next morning we set out to catch the geese on the pools on the south side of Hornsund. Chris stayed at base to do some filming. We landed to the north of the pools and were diverted by a flock of geese sitting beside a marshy area quite close to us. At first we wondered why they did not start running away, as flightless geese usually did, but on closer approach they flew. Unfortunately the geese we had come to catch were mostly on a small offshore island and although we had crossed Hornsund without difficulty, the beach where we wanted to land the birds was exposed to the sea that was running and therefore driving the birds was not practical.

We tried again the next day, 5 August. The area of the base camp was comparatively calm with little wind. However, before we had gone very far across the fjord it was much windier and we were soon battling with a steep choppy sea. We therefore turned tail and came back to spend a day botanizing, filming, photographing and other activities.

All plans for the next day went out of the window when we woke to a strong easterly wind, increasing slowly during the day. Despite not being able to catch, the cameramen in particular had a good day, managing to get some footage of a flock of flying Barnacles around a small pool a few kilometres to the west. The geese briefly visited the pool near the base while Myrfyn was in the hide and he managed to read several rings on birds we had caught on the Dunoyane. That evening two Arctic Foxes came round the hut and Chris and Terry were soon out there with their cameras, providing a certain amount of entertainment for the rest of us. The foxes seemed particularly skilled at moving off just when the button was about to be pressed.

August 7 was even worse. Not only was it still very windy, but it rained heavily for most of the day. A rather late nest of Purple Sandpiper was found; almost the only bright spot of the day. The incubating bird allowed photography from within a few centimetres without concern. Another example of tameness was an Arctic Fox (Figure 8), well away from the hut, which accepted a piece of chocolate from Ted's fingers.

The wind dropped late in the evening but during the next morning it increased rapidly back to a full gale, gusting force 9, and goose catching never seemed more remote. Further rain fell, turning to snow by evening and lying almost down to sea-level. The summer seemed nearly over and winter pressing upon us. We managed some more filming and botanizing, but little else.

August 9 was much the same. By now we were less concerned with whether the wind would moderate sufficiently for goose catching and more with whether it would drop enough for us to be picked up on the 11th. If the ship could not get in, or we out to the ship, we were there for another week. On the 10th the wind dropped, though a heavy swell con- the wind dropped, though a heavy swell continued to run. We started to pack and organize our gear into boatloads.

11 August. Departure

The day was fine and sunny, with little or no wind. The visibility was perfect and the air positively warm. There was little doubt that we would be able to leave as scheduled, but how we wished we had had this sort of weather for the past week.

The ship was due in the late evening so we had plenty of time to get packed and down to the shore. Chris and Terry even managed to film a couple of family parties of geese swimming in sheltered water at the end of the bay. They were filmed standing on the rocks or feeding on the seaweed, backed by the swell crashing down in clouds of spray.

Just before midnight the ship was spotted heading into the fjord, and within half an hour she was close inshore. She came in much further than had the ship which brought us, making boarding much easier. The first boat pulled alongside the companion ladder and Ted went aboard to see the captain and tell him there were going to be three boatloads. The first was unloaded item by item into a door in the side of the ship and then the boat headed back to the shore for the remainder of the baggage. The second boat, fully laden, was tied into a sling let down on the derrick and then lifted bodily out of the water and on to the foredeck. The first boat was soon back, lifted out and placed gently alongside. It had all taken less than half an hour and contrasted strongly with the operation when we arrived a month before.

We repaired to the ship's cafeteria and sat far into the night talking and drinking and watching the receding coastline. There was a final moment of interest when Ted spotted two Storm Petrels fluttering over the sea when we were still only a few kilometres out of Hornsund. We think these are the first recorded in Spitsbergen.

The expedition was virtually over. The days south down the coast of Norway passed rather too slowly while we got used to more civilized living and hours of darkness, but Bergen was finally reached on a really scorching day. We transferred to the North Sea ferry to reach Newcastle on the 18th. We left Spitsbergen with its summer almost over and probably the highest temperature we had there was about 50°F. The day we returned the thermometer in London reached 90°F.

Results

We caught and ringed a total of 416 Barnacle Geese, including sixty-six goslings (Table 1). All the 350 adults were marked with the plastic rings with engraved letters, scaled down versions of those originally designed for swans (Ogilvie, 1973). Had it not been for the adverse weather in the last week we would certainly have ringed more. We weighed and measured virtually all the geese and collected data on the growth of the goslings (Tables 2 and 3). We had located, in all, just over 1,400 Barnacle Geese (details in bird list in the Appendix), and that in an area thought to be the headquarters of the population in Spitsbergen. This it was clearly not, at least in 1973, as subsequent counts at Caerlaverock showed the population to number 5,100.

The botanical studies had revealed a lot of new information about the food and feeding preferences of the geese in summer. A considerable list of flowering plants (forty-five species) and a collection of lichens (over eighty species including one new record for Spitsbergen) were compiled, and these have added considerably to the knowledge of this little-covered area.

The cameramen shot over 7,000 feet of film of Barnacle Geese and of other birds. Selections from this are to be combined with material from Caerlaverock to make a television film.

It was with considerable anticipation that we awaited the arrival back at Caerlaverock of the geese. They duly came in late September and Colin Campbell reported seeing many yellow rings. In early November,

Table 1. Catches of Barnacle Geese and brief details of recaptures

		New ringed		Recaptures			
Date	Locality	Adult	Pullus	Norwegian	British	Repeats	Total
23 July	Dunoyane islands	58	0	3	0	0	61
24 July	Dunoyane islands	131	0	8	4*	16	159
28 July	Leirsigtjorn	21	23	2	0	0	46
30 July	Strandtjornene	52	43	4	2	0	101
31 July	Strandtjornene	39	0	0	0	1	40
31 July	Strandtjornene	26	0	0	0	10	36
Totals		327	66	17	6	27	443
Total ringed 416.							

* One of these also carried a Norwegian ring

Details of recaptures:

Ringed Dunoyane 1962—caught Dunoyane 1973	8
Ringed Dunoyane 1962—caught Caerlaverock 1963—caught Dunoyane 1973	1
Ringed Dunoyane 1962—caught north of Torellbreen 1973	4
Ringed Caerlaverock 1963—caught Dunoyane 1973	4
Ringed Caerlaverock 1963—caught north of Torellbreen 1973	1
Ringed Dunoyane 1964—caught Dunoyane 1973	2
Ringed Dunoyane 1964—caught north of Torellbreen 1973	2
Ringed Caerlaverock 1966—caught north of Torellbreen 1973	1
	23

Figure 9. Barnacle Geese ringed in Spitsbergen photographed at Caerlaverock.

M. Owen

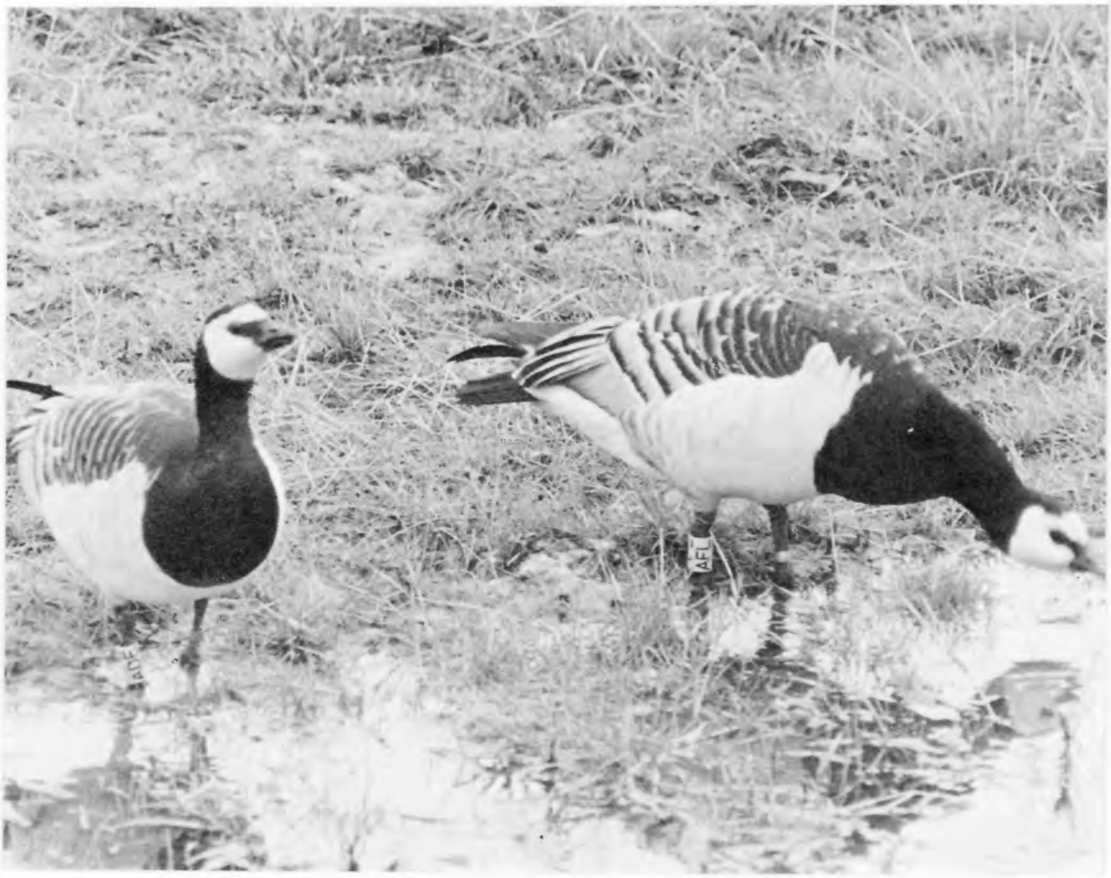


Table 2. Weights and measurements of adult Barnacle Geese

Sex	Total caught	Mean weight		Mean sternum length		Mean wing length	
		g	Sample	mm	Sample	mm	Sample
Male	176	1756	175	137·9	144	229	113
Female	174	1505	173	128·6	144	214	118

Wing length only gives an indication of the stage of moult. Non-breeders were further advanced than birds caught with goslings.
Weights are 75–80% of mean winter weights.

Table 3. Weights and measurements of gosling Barnacle Geese

Feathering		Number caught	Mean weight (g)	Mean wing length	
Class	Description			mm	sample
A	Downy	2	166	–	–
B	Tail feathers showing	1	(410)	–	–
C	Scapulars + tail feathers	2	470	–	–
D1	Primary quill stubs showing	23	637	80	12
D2	Primary feathers emerging	37	749	115	30
D3	Well-developed primaries	1	(710)	–	–

Sexes: twenty-eight male, thirty-six female, two undetermined.

Myrfyn went to Caerlaverock for a few days and the results began to flow in. In 4 days he read the letters of over 200 marked birds, discovering which was paired to which, how many goslings they had, who was unpaired, whether there had been any mixing between birds caught in different areas, the spread of ringed birds through the flock, and so on (Figure 9). He found that with a telescope and in good light it was possible to read the letters at distances of up to 300 m. So successful is the technique that by the end of March no less than 329 of the birds had been checked. We know that one of them is dead, picked up on the merse in the autumn, so about 94% of the rings put on in Spitsbergen have now been read. This particular technique of individual identification has thus been transferred from swans to geese with complete success. It should be possible to follow the fortunes of known pairs and families for years to come, checking on their annual breeding success, behaviour and other aspects whilst they go about their normal everyday routine.

Summary

An expedition to Spitsbergen in summer 1973 to study and ring Barnacle Geese *Branta leucopsis* is described. 416 geese were ringed, and weights and measurements taken. Other studies involved food and feeding behaviour of the geese, general botanical recording and filming. 94% of the 350 geese marked with large lettered plastic rings have been identified back on the wintering grounds in Scotland.

Appendix. List of birds seen and details of Barnacle Goose distribution

Red-throated Diver *Gavia stellata*. Found breeding on most larger pools.

Fulmar *Fulmarus glacialis*. Abundant on several seabird cliffs.

Storm Petrel *Hydrobates pelagicus*. Two seen from ship near mouth of Hornsund. Believed to be first record for Spitsbergen.

Pink-footed Goose *Anser brachyrhynchus*. Only small numbers seen and no goslings, though used nests found in Revdalen. Totals of twenty-seven south of Hornsund, thirty between Hornsund and Torellbreen, and twenty north of Torellbreen, all less than found in same areas in 1964 when they bred in all three (Norderhaug, Ogilvie & Taylor, 1965).

Barnacle Goose *Branta leucopsis*. The Table below gives the maximum number of geese seen at each site. Possible duplication because of movement by birds has been avoided where possible.

Area	Adults	Goslings	Total	% young
Camp Erna–Ommervatna	110	21	131	16·0
Isbjornhamna–Hyttevika	29	23	52	19·4
Dunoyane islands	480	100	580	
Isoyane islands	135+	some	135+	?
Kapp Borthen and islets	145	26	171	18·4
Kapp Borthen to Kapp Berg	315	73	388	
Totals	1214+	243+	1457+	18·4

The overall percentage young excludes Isoyane as those islands were only observed from the boats and the true total of goslings could not be determined. Barnacle Geese have not hitherto been recorded as breeding south of Hornsund (ponds near Camp Erna), a relatively little-surveyed area; indeed in 1964 none were seen there (Norderhaug, Ogilvie & Taylor, 1965). Other comparisons with the 1964 survey show an overall decrease in the number of geese in the whole area covered of about 100 despite an increase in the total population from about 4,000 to 5,100.

Brood size was recorded as follows: 5 goslings—1 brood; 4—11; 3—13; 2—19; 1—13; total 57, mean 2·4.

Light-bellied Brent Goose *Branta bernical hrota.* The only record is of three seen on the Dunoyane on 13 July. This contrasts with six used nests found and seventy birds seen on the islands in 1964.

Mallard *Anas platyrhynchos.* A female was seen on a small pond west of Isbjornhamna on 13 July. There are less than ten records for Spitsbergen.

Eider *Somateria mollissima.* Breeding plentifully on all the islands. Many young seen.

King Eider *Somateria spectabilis.* No breeding proved. Flock of 180 on pool, Camp Erna, 14 July. Flocks of up to twenty-five seen, Dunoyane and north of Torellbreen.

Long-tailed Duck *Clangula hyemalis.* No breeding proved. Flock of 100 moulting on pond on Nordre Dunoy island, 23 July. About 350 on sea off Nebodden, 27–31 July. Smaller numbers seen on other pools.

Ptarmigan *Lagopus mutus.* None seen but reported as present on nunataks in Hansbreen by Polish glaciologist.

Ringed Plover *Charadrius hiaticula.* One seen on Store Dunoy island, 22 July.

Purple Sandpiper *Calidris maritima* (Figure 10). Breeding in all areas, though not common. Flocks of up to 100 on Dunoyane, mid-July, and on shore north of Nebodden in late July.

Whimbrel *Numenius phaeopus.* Singles seen Dunoyane 13 and 22 July, near Camp Erna 15 July, Revdalen 15 July, four together Isbjornhamna 17 July. This is only a vagrant to Spitsbergen.

Turnstone *Arenaria interpres.* Two on Dunoyane 19 and 23 July, three on the 22nd. One Camp Erna 4 August.

Grey Phalarope *Phalaropus fulicarius.* Only one nest found, at Isbjornhamna. Seen in small numbers in other areas.

Pomarine Skua *Stercorarius pomarinus.* One near Isbjornhamna every day from 2 to 11 August. Three, Camp Erna, 4 August and apparently holding territory. Has not been proved to breed in Spitsbergen.

Arctic Skua *Stercorarius parasiticus.* Breeding widely in every area.

Long-tailed Skua *Stercorarius longicaudus.* One, Nebodden, 27 July.

Great Skua *Stercorarius skua.* Two, Hyttevika, 20 July. Six in Nebodden area, including at least one pair holding territory. One, Camp Erna, 4 August. Has not been proved to breed Spitsbergen, though has bred Bear Island since 1966.

Glaucous Gull *Larus hyperboreus.* Breeding commonly on all suitable islands and rocks.

Great Black-backed Gull *Larus marinus.* Four seen Dunoyane.

Kittiwake *Rissa tridactyla.* Abundant at seabird colonies.

Ivory Gull *Pagophila eburnea.* Singles seen Isbjornhamna, 17 and 19 July. Presumably on feeding flights from known colonies on nunataks north of Hornsund.

Arctic Tern *Sterna paradisaea.* Breeding singly and in small colonies in several localities.

Brunnich's Guillemot *Uria lomvia.* Abundant in seabird colonies.

Razorbill *Alca torda.* Small numbers seen among other seabirds at colonies and on feeding flights.

Black Guillemot *Cepphus grylle.* Widely distributed round coasts, with flocks up to fifty around Dunoyane.

Little Auk *Alle alle.* Bred in all available scree slopes.

Puffin *Fratercula arctica.* Very small numbers seen among other seabirds.

Wheatear *Oenanthe oenanthe.* Pair feeding three young in rock crevice, Hyttevika. Young ringed on 19 July. First breeding record away from Longyearbyen, 130 km north.

Snow Bunting *Plectrophenax nivalis.* Breeding commonly around Isbjornhamna; less frequently north of Torellbreen.

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Figure 10. Purple Sandpiper on its nest.

M. A. Ogilvie

Preliminary observations on waterfowl of Western Madagascar

DAFILA SCOTT AND JOANNA LUBBOCK

Introduction

In early July 1973 we left England for Madagascar, an island more than twice the size of Great Britain, 250 miles off the S.E. coast of Africa.

Our aims were to make a general study of the waterfowl of the western region and in particular to look for the rare Bernier's Teal *Anas bernieri*, a small rusty brown duck related to the Grey Teal *A. gibberifrons* of Australia and the East Indies. It was first described by Hartlaub in 1860, and has been seen infrequently since. According to Milne-Edwards and Grandidier (1879–1881) it is found either along the great water courses or in the marshes and small morasses, usually in small groups. Rand (1936) spent 2 years on the island in the 1930s and failed to see the bird at all. However, Salvan (1970) reported considerable numbers of Bernier's Teal in the area of two remote lakes Bemamba and Masama in western Madagascar in July 1970.

Itinerary

On arrival in Tananarive, the capital, on 14 July, we were met by scientists from the French organization ORSTOM (Organization pour la recherche scientifique et technologique outre mers) who assisted us with our plans throughout our stay and to whom we are most grateful.

On 27 July we flew west to Antsalova accompanied by Georges Randrianasolo, a zoologist from Orstom who acted as guide and interpreter. During a 4-day delay in Antsalova we found Pygmy Geese *Nettapus auritus* and White-faced Whistling Duck *Dendrocygna viduata* on a small lily pond.

Transport in this area was limited to ox-carts. Three days were spent at Ambondra, a marshy rice-growing area with lily ponds, 4 miles east of Lake Bemamba. The following 2 weeks were spent on the shores of the Lake itself. A shallow saline lake, it is situated 6 miles from the west coast of Madagascar and 12 miles S.E. of the Soahanina estuary. In July it was about 1½ miles long and ½ mile wide, interspersed with many clumps of tall reeds, but it is said to dry up during September and October prior to the rains which commence in November or December. To the south and west it is bordered by dry scrub, to the east by dry deciduous forest and to the north by the rice fields of Befaroratse.

August 16 and 17 were spent 6 miles to the S.E. at Ambereny, staying with a French wood merchant, who took us to Lake Masama, which lies on calcareous rock and is very different in nature from Lake Bemamba. It is deep and wide with much less fluctuation of the water level. Its relatively steep shores are bordered immediately by palm trees and deciduous forest. No anatidae were seen here and the only common water-birds were herons, taking advantage of the very abundant supply of *Tilapia*. We were also taken to Lake Andranolava, a lily covered lake ½ mile long just north of Masoarivo. Unfortunately it was not possible to visit the Soahanina estuary nor the marshy area described as Lake Soahanina on the map due to problems of transport and time.

Waterfowl sighted

Bernier's Teal *Anas bernieri*

Two pairs were sighted on a reconaissance trip to the eastern shores of Lake Bemamba. The following day we moved camp to this area and spent 4 days there. We saw not more than ten pairs of Bernier's Teal, usually rather isolated, both from other pairs of their own species and from other waterfowl. Moving camp to the western shores of the lake, we found larger numbers of Bernier's Teal. At one place it was common to see up to thirty or forty in quite close proximity. The majority were paired and in the early mornings we frequently observed intense courtship activity, during which individual pairs would often be split. There was much aggression and short chasing flights were common, either between males or between females and even some between males and females. The females performed inciting displays in the manner of Grey Teal (see Johnsgard, 1965) and in both sexes there was much head bobbing with a circular motion. The most commonly observed courtship posture of males was an upright one with neck elongated and wings and tail slightly raised. Owing to the difficulty of following particular individuals during these bouts of courtship activity and skirmishing and to the speed of the birds' movements no other displays were adequately described in the short time available.

It was on the western shores that we saw three instances of copulation, in the early morning when most of the birds were feeding. Two instances involved the same pair with an interval of half an hour. Precopulatory display was similar to that of the Chestnut Teal with the typical mutual head-bobbing. The female solicited copulation flattening herself on the water while the mate swam round head-bobbing with raised head, wings and tail. After treading the male performed a 'Bridling' display followed immediately by a 'Down-up' in which the breast went under water and the tail was lifted high. He then in each case chased the female for several yards after which both birds bathed and preened. These observations suggest that the birds might breed from the middle of September onwards. Information from local people differed, some stated that the teal breed in November, others in April. It is possible that they breed twice a year, before and after the rains. We also learnt that the local people hunt the duck with dogs and take eggs from nests. The teal apparently will not return if driven from the nest. Information on clutch size varied drastically, from two to four eggs in one instance to eight to ten in another.

The ducks chiefly fed in the early morning and evening, and the middle of the day was spent sleeping on mud banks. They always fed in shallow water or dabbled in the mud at the lake's edge. No upending or diving was observed. Nor were they observed to drink, and there was no evidence to suggest that they flew in search of fresh water during the night as do Australian Grey Teal living in saline habitats (Lavery, 1972). This suggests that they may have well-developed supraorbital nasal glands for maintaining ionic balance. The flight is swift and low and the characteristic white-bordered speculum is conspicuous. The call is similar to the Whistling Duck but di- rather than trisyllabic.

We spent one week on the western side of the lake and during this time saw a maximum of sixty-one Bernier's Teal along the shore. It seems probable that there were no more than 120 birds on the whole lake and possibly less.

The amount of movement to and from the lake during July and August is probably slight. However, later in the year when the lake dries up the birds are thought to disperse either to the Soahanina estuary to the north, or to the remaining small freshwater pools and lakes in the forest and rice fields. As there are no other large lakes in the vicinity except Masama, where no anatidae were seen, the population of Bernier's Teal at Lake Bemamba may be the largest for hundreds of miles.

Madagascar White-backed Duck *Thalassornis leuconotus insularis*

The Madagascar White-backed Duck is clearly different from the African White-backed Duck *T.l. leuconotus*, being smaller and darker than the latter. White-backed Duck were first sighted at Ambondra where we saw four on one pond and a family of five on another. We spent 3 days in this area and were able to watch the family. The young were accompanied by both parents at all times, and spent much of their time diving. One parent always kept watch on the surface. Occasionally the Whitebacks were displaced from their feeding area by a small group of Fulvous, but despite the difference in size the Whitebacks defended their young ferociously and succeeded in driving off the intruders. Typical aggressive postures of head lowering, stretching the neck along the surface, and making short rushes with open beak, were observed. When alarmed these ducks freeze and practically submerge making them very hard to detect. We estimated that the young could not have been more than 10 days old. There were no Whitebacks on Lake Bemamba, probably due to the absence of water lilies. We saw a large concentration of approximately eighty Whitebacks on Lake Andranolava, where we also saw three family groups of two, three and five young, during a short visit of 2 hours.

Observations on other waterfowl in the vicinity of Lake Bemamba

Pygmy Goose *Nettapus auritus*

This species is relatively common on lily-covered lakes. We estimated up to 300 to be present at Lake Andranolava. No courtship activity was observed at any time, and paired birds did not appear to be territorial. This was perhaps surprising in view of the possibility of them breeding prior to the rains, although a number of immatures were seen.

Fulvous Whistling Duck *Dendrocygna fulva*

White-faced Whistling Duck *Dendrocygna viduata*

Both Whistling Ducks were very abundant in most areas, especially on Lake Bemamba itself. A crude estimate of their numbers was 6,000 of each species. Courtship activity was not observed in either species although pairs of White-faced Whistling Duck were frequently seen mutually preening. A number of immatures were seen.

Red-billed Teal *Anas erythrorhyncha*

These were common in the area and we estimated 2,000 on Lake Bemamba. Courtship activity was observed on several occasions. We were shown a pair of hand-raised Redbills in Antsalova, which had apparently been caught as downy young in September/October 1972 at the beginning of the rainy season.

Hottentot Teal *Anas punctata*

These were much less common than the Redbills and we estimated there to be 500 on Lake Bemamba. Although no courtship activity was observed a large percentage of birds appeared to be paired. Except on Lake Bemamba they were seen infrequently.

Comb Duck *Sarkidiornis melanotus*

This species was quite common on Lake Bemamba and the numbers were estimated at 1,000. No courtship activity was observed, and the birds were never seen in large concentrations. In other areas they were seen in small numbers.

Greater Flamingo *Phoenicopterus ruber*

We estimated this species to number 1,500 on Lake Bemamba, but they were not seen elsewhere. No courtship activity was observed. At dawn they were observed flighting in from the north, possibly from the Soahanina estuary.

Lesser Flamingo *Phoeniconaias minor*

We estimated this species to number 1,500 on Lake Bemamba, but they were not seen elsewhere. Although juveniles were seen, we presumed them to be first-year birds. No courtship activity was observed.

Adaptation to captivity of the Madagascan White-backed Duck and the Pygmy Geese

During our final days in the west we stayed at the home of the French wood merchant at Ambereny. A local duck-catcher from Masoarivo brought four Pygmy Geese and two White-backed Duck, the latter having been conveyed on foot for 18 miles in a tiny basket. Unfortunately one male Pygmy Goose had died and the only female had a broken wing and was in very poor condition, and she died shortly after. We were therefore left with two male Pygmy Geese, one adult and one juvenile, and one pair of White-backed Duck.

We had not come prepared to keep birds in the bush. However, we were able to construct a small pen in the shower of our room, in which we placed stones and large water lily leaves, thus making a pond containing 4 inches of water. It was extremely hard to find food for the ducks as there were no lily lakes in the immediate vicinity, but eventually some seeding lily heads were found. These were cut up to release the seeds, and placed in the water. The following day the birds were put into a temporary travelling box and taken by lorry to Antsalova. The trip took us about 4 hours, and we were able to collect a fresh supply of lily heads en route, whilst the other occupants of the lorry shot a Comb Duck and a Fulvous Whistling Duck.

After spending the night in a small shed the birds were re-boxed and flown back to Tananarive. At the Orstom headquarters we were able to release the birds into a small aviary containing slow flowing shallow water. Here there was duck weed, lilies from the ornamental lakes, and commercial cage bird food was obtainable. We remained in Tananarive for 4 days and were worried about the sudden change in temperature from day temperatures of 90–100°F in the west, to 40–50°F in Tananarive. Although the birds spent much of their time huddled in the vegetation they adapted well. The White-backs seemed less shy than the Pygmy Geese and spent more time on the water. In fact considering the continual human proximity they settled quickly, despite the fact that they had to be caught up and boxed in order to be taken to obtain a veterinary certificate on one occasion.

A new travelling box was made and divided into two compartments, each containing food and water trays. The final stages of the journey involved the flight from Madagascar to Nairobi and from there direct to London, and on to Slimbridge; total time in transit was approximately 18 hours. The birds are now doing well, and two females have been acquired to join the two male Pygmy Geese, thus making two pairs.

It is possible that the duck catcher could have caught Bernier's Teal, so that a breeding stock could be started at Slimbridge. However, we were not prepared to risk losing these rare birds, due to inadequate facilities and equipment, when numbers are so low in the wild.

Conclusions

Hopefully, it will be possible to return to this area to reassess the Bernier's Teal and other waterfowl populations, and to visit other areas in the western region.

Reassessment is warranted in the near future due to the recent and rapid decline of waterfowl numbers on Lake Bemamba. In the 1940s we were informed that 70% more birds were present. The reason for the decline is not clear although it may be due to lower lake levels or possibly to encroachment of rice cultivation. Hunting pressure does not appear to be great, although three instances of shooting were witnessed at the beginning of the legal hunting season which runs from 1 August to 1 October.

From these preliminary observations it appears that Lake Bemamba may be extremely important for waterfowl especially Bernier's Teal, and it would therefore be beneficial if this area became a reserve. Bernier's Teal may not be in immediate danger of extinction but its status throughout the western region and the cause of its decline merits further study.

Acknowledgments

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Summary

A reconaissance was made to Madagascar to study waterfowl, particularly the rare Bernier's Teal *Anas bernieri* in the vicinity of the shallow saline Lake Bemamba. The habitat and behaviour of the teal and also of the Madagascar White-backed Duck *Thalassornis leuconotus insularis* are described. Estimates of numbers are given for other waterfowl, and a list of all birds seen. Two Madagascar White-backed Ducks and two Pygmy Geese *Nettapus auritus* were brought into captivity. Waterfowl in the area have declined in numbers and Bernier's Teal may perhaps be in danger of extinction. Lake Bemamba merits the formation of a reserve.

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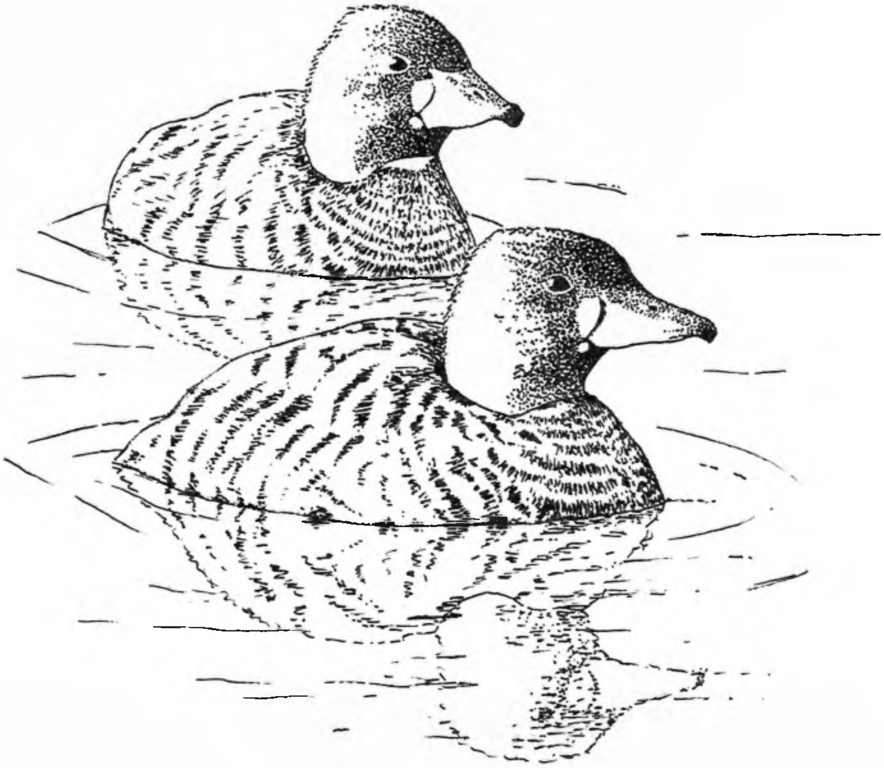

Philippa Scott

Above: Andaman Teal *Anas gibberifrons albogularis.* Three pairs arrived in 1973, a new form for Slimbridge. They are markedly different from other Grey Teal races.
Below. Young female Coscoroba Swan *Coscoroba coscoroba*, reared at Slimbridge in 1973, the first for nineteen years.

Philippa Scott

Etho-ecological studies of Teal wintering in the Camargue (Rhone Delta, France)

ALAIN TAMISIER

Through the numbers of its wintering ducks and their specific diversity, the Camargue is one of the most important wintering areas for West Palaearctic Anatidae. The population of Teal *Anas crecca* is particularly well represented there and was studied from 1964 to 1972. The results obtained have been published in detail (Tamisier, 1972b) and are presented in summary here. An ecological sketch of the Camargue (Hoffmann, 1958), a detailed phytosociological analysis (Molinier & Tallon, 1970) and a study of edaphic (soil) and climatic factors (Heurteaux, 1970) should be read usefully for a total understanding of the importance and uniqueness of the Camargue as a whole.

I. Analysis of the population

Origin

Teal are ringed intensively in the Camargue (Station Biologique de la Tour du Valat) and from 50,000 Teal caught (1952–1970), 10,000 recoveries have been obtained, 7,000 from hunters. These data give a good idea of the origin of the population.

Most of the Teal wintering in the Camargue come from an area covering Finland, the Baltic Republics, the Leningrad' and Novgorod's provinces and White Russia (Hoffmann, 1960; Wolff, 1966; Shevareva, 1970). The majority of Teal in this breeding area winter in the Camargue. The Camargue is the terminal stage of their migration, except for a few birds continuing towards W and SW. However, during cold spells, many Teal leave the Camargue and reach the French and Portuguese Atlantic coasts as well as some more inland areas.

Fluctuations

Variations in numbers are determined by the different migratory movements and by the effects of mortality. The former are the more striking. Teal arrive in the Camargue from July and their numbers increase progressively until November when numbers are maximum (mean 40,000; maximum 80,000 in 1972). The first departures occur in January and the last Teal leave the Camargue by April (Figure 1). These fluctuations of numbers are similar to those for the other species of ducks. The total number of Anatidae wintering there ranges from 120 to 150.000 birds.

The effects of mortality on the numbers are less spectacular. This mortality is mostly due to hunting which removes 20,000–25.000 Teal each shooting season (15 August–31 March) in the Camargue. The mortality rates evaluated by means of composite and dynamic life-tables (Hickey, 1952) are 65% for juveniles and 45% for adult Teal annually. These rates are always higher for females than for males. They have tended to increase since 1955 because of the increase in hunting pressure. This occurs mostly during the 2 first and 2 last months of the winter season. Natural mortality is very slight, masked by the major effects of hunting pressure (Tamisier, 1970a).

Structure of the population

Sex-ratio always favours males: 70% is the mean and by August it is 80–85% (earlier migration of males). These ratios from counts *in natura* are higher than those from ringing. The comparative values show that the traps are 1½ times more attractive for females. The higher proportion of males is usual in the other wintering areas and it is to be expected in the Camargue which is the terminal stage of this population. This weakens the hypothesis that females winter more to the south than males. If the sex-ratio is equal at hatching (which is probable, but not checked), one would think that females have a higher mortality rate (they are actually more vulnerable to all the mortality factors), and/or have a different range, being less attracted than males by the large wintering areas from where most of the data are obtained. In fact, they have distinct requirements and such differences can reduce intraspecific competition (Blondel, 1971).

Age-ratios obtained from ringing data indicate a proportion of 80% juveniles during the first months of wintering in the Camargue. Calculated from life-tables the percentage of juveniles decreases strongly, from 65 to 45%, between the beginning and the end of the annual cycle: the very narrow age-pyramid (Figure 2) indicates the heavy action of mortality factors (mostly hunting) during the first year. The mean life span of Teal

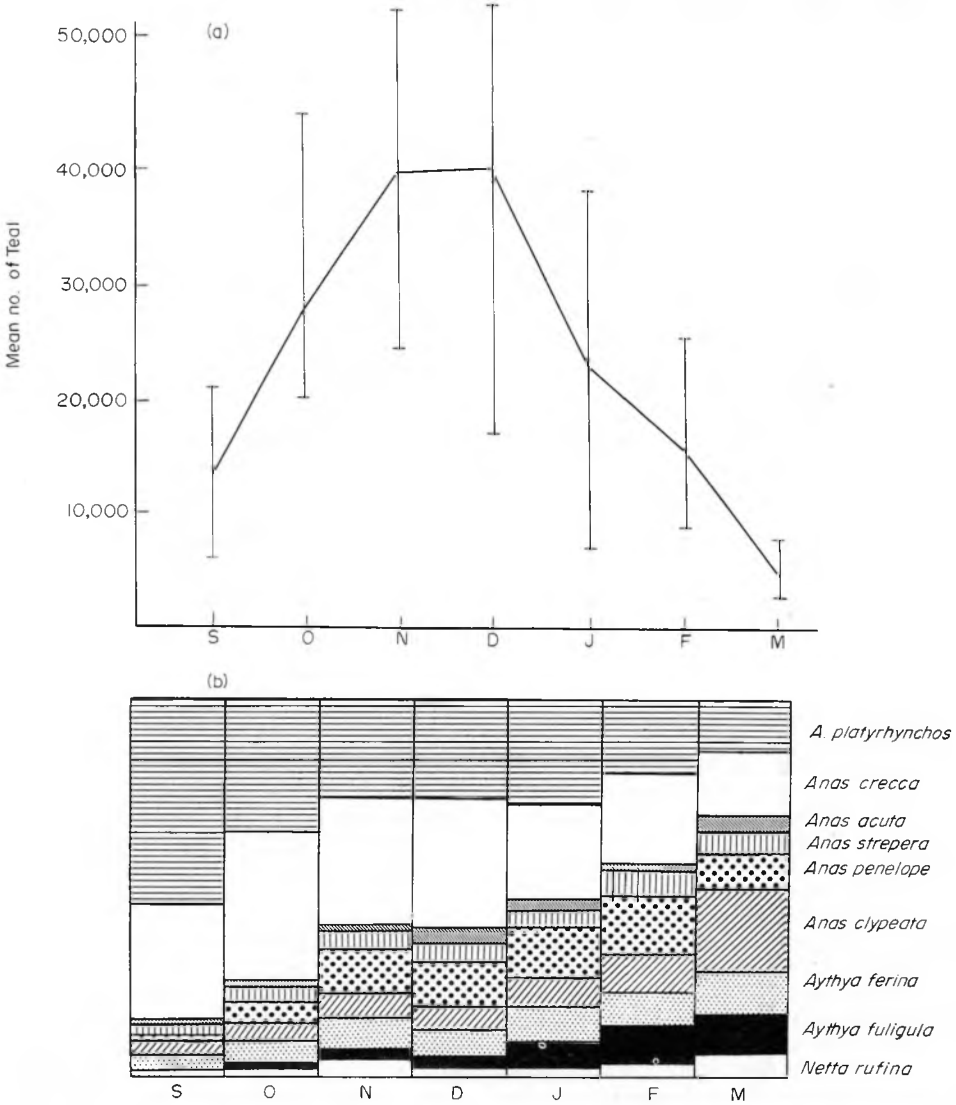

Figure 1. (a) Mean number of Teal in the Camargue (1964–1965 to 1971–1972). Vertical lines show the maximum deviations. (b) Relative abundance of the different species of ducks (total 120,000–150,000 birds). Surface feeding ducks are predominant and Teal the most abundant except in August and March. The monthly variations of total numbers parallels that of the Teal.

ranges from 1 to 2 years while their theoretical mean age is probably 9–10 years (Tamisier, 1970a) and their potential longevity is 17 or 18 years (Ryabov, 1960).

II. Daily rhythms

The two phases—diurnal and nocturnal—of the daily cycle have distinct behavioural aspects (Tamisier, 1972a). By day, wintering Teal are gregarious and concentrated on large open waters called 'remises' where they sleep, preen and rest. They feed very little. At night, they leave their resting places and scatter on nearby marshes for feeding (nocturnal observations have been made on moonlit nights and in darkness with an infrared telescope).

Analysis of the activities

Resting occurs on the water or on the shores

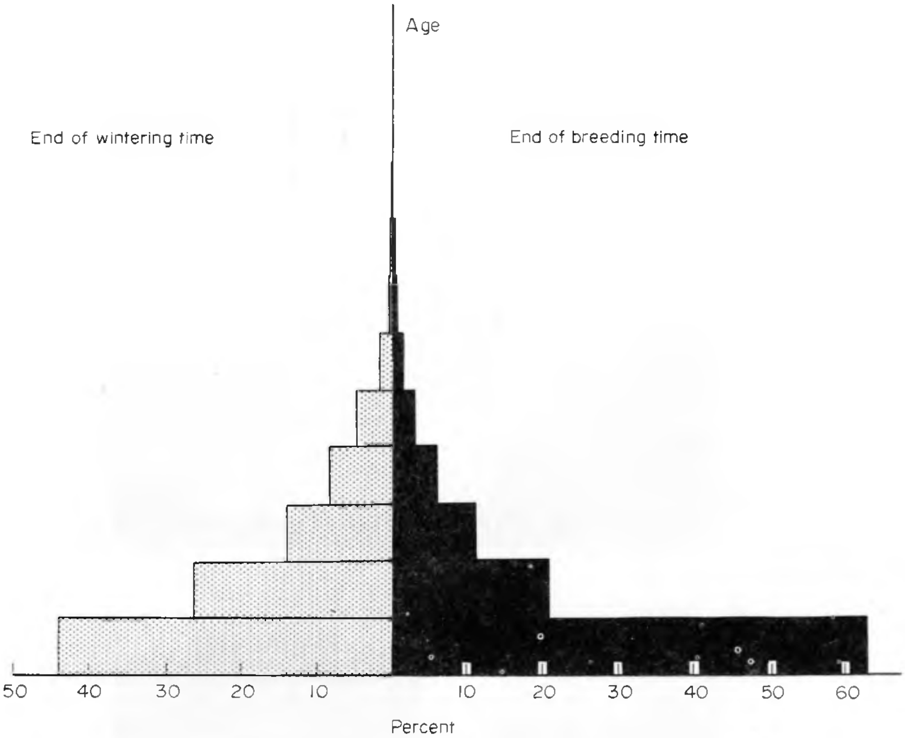

Figure 2. Age-pyramids of Teal. Hunting is the main mortality factor, particularly for juveniles (65% for first year Teal in the Camargue).

where Teal sleep while keeping frequent contact by sound and sight with other individuals. They often stand on the ground, roost on clumps of vegetation or perch in trees. They sleep for 6–10 hours per day.

Preening occurs mostly standing on the shore close to the water. It lasts at most 3 hours during the 3 first months of wintering (moulting period) and very little thereafter.

Swimming appears as a diversion activity allowing a constant adjustment of the distribution of the Teal on the remise, in reaction to environmental pressures (disturbances by predators, drift by wind, etc.). It involves both courtship activities and social displays. Its duration ranges from 0·1 to 6·5 hours per day.

Feeding occurs only on very shallow waters (less than a few centimetres) in which Teal walk slowly, filtering the mud with their bill. This behaviour is most effective: 80% of the time spent is used in filtering the mud, only 20% in walking. It occurs most frequently (70%) during nocturnal feeding and Teal appear well adapted to it. Other feeding behaviour (head under water, head and neck under water, up-ending) are less effective and occur mostly during diurnal feeding. Daily feeding time varies according to the month (8–13 hours per day). It is independent of the duration of darkness.

Schematically, diurnal rhythms show three successive phases.

(a) Pre-wintering (August–September). Teal, 80% being juveniles, arrive in the Camargue: their weights are low, their energy requirements are very high: the daily feeding duration is long (12·7 hours in August; 10·4 hours in September). The vital moult involves a daily preening time of 3 hours. All these physiological conditions require a long resting time (8·5–10 hours). The daily cycle is completely occupied with indispensable activities.

(b) Wintering (October–December). Teal are in a phase of physiological equilibrium with high weights and little or no moult. The climatic conditions are mild (except sometimes in December) and energy loss is slight. Swimming can occupy a long time (3–6 hours).

(c) Post-wintering (January–March). Low temperatures, sexual activities and preparations for spring migration result in a substantial increase in energy requirements (more than 12 hours feeding) and of sleeping

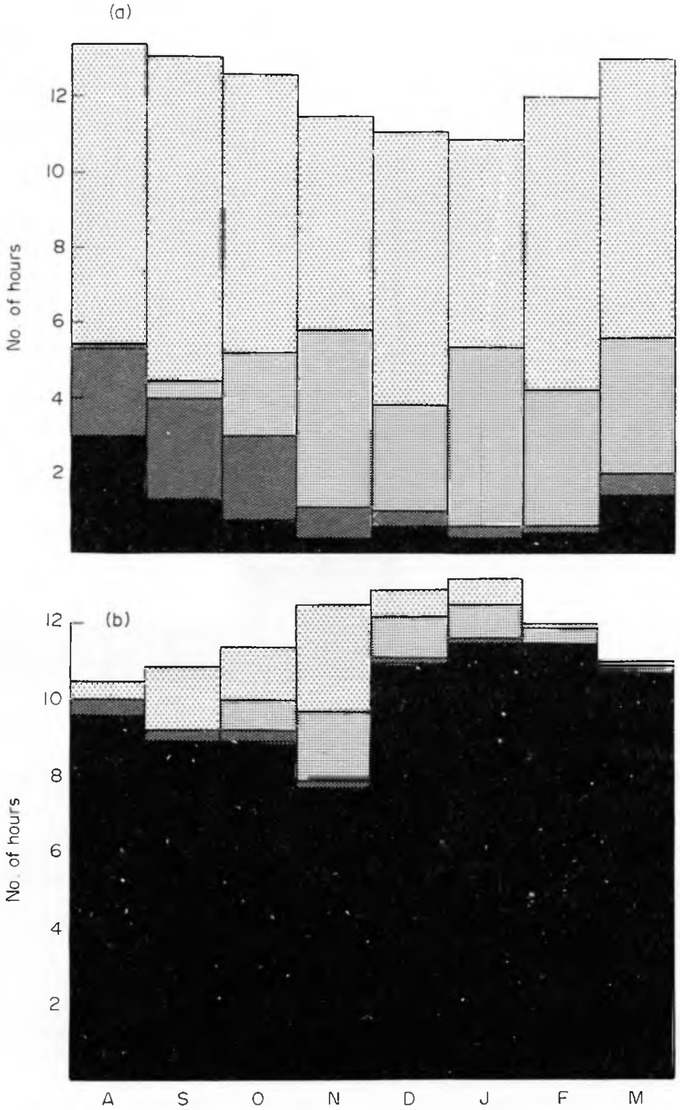

Figure 3. Periodicity of activities according to months. The time spent by day (a) on the remises and by night (b) on the feeding grounds varies as the daylength. Lightly stippled, sleeping; heavily stippled, swimming; cross-hatched, preening; solid, feeding. Feeding is mostly nocturnal and comfort activities are mostly diurnal. But in August, February and March, the daily feeding time is longer than the night length and Teal have to feed partly by day. (After Tamisier, 1972a.)

and courtship time. The daily cycle again is fully occupied with vital activities (Figure 3).

The total duration of diurnal activity is always shorter than the daylength. In contrast, feeding time exceeds the night length at the beginning and at the end of the wintering season; 30% of feeding then occurs by day, around margins of the remises. This is the one case where the duration of light impinges upon the periodicity of a behaviour pattern of Teal.

Lunar phases, by contrast, have no role in this periodicity in the Camargue. During the wintering phase they shift the time at which Teal flight from resting to feeding places by 10–20 minutes, without reducing the daily feeding time. On tidal wintering grounds, however, activity rhythms are determined by variation of water level and partly by moon phases (Lebret, 1970 and personal communication).

III. Winter habitat

The analysis of group behaviour allows us to define the ecological requirements of Teal. Just as for behavioural patterns, these requirements differ radically by day and by night.

(a) *Diurnal habitat*

Because of the predation pressure by avian predators, Teal are gregarious and require large marshes able to hold some thousands of individuals. Their mean density is two to three individuals per square metre and this can be doubled when a bird of prey is approaching which will put the whole group to flight. The open water allows a permanent visual contact between all the birds. On the edges of the marsh Teal preen and sleep, often standing. A slightly sloping shore (less than 1/1,000) is indispensable. Thus, whatever the water level, large and shallow surfaces are available for the ducks which prefer, moreover, those exposed to sun (best for preening and resting). There, densities can reach thirty to forty individuals per square metre and females are always more numerous than males having somewhat different requirements. But the birds are never in contact for Teal are 'distance-birds' (Hediger, 1950). The fringing vegetation (tamarisk *Tamarix gallica* and glasswort *Salicornia* sp.) is equally used for perching up to 2 m above the water. Finally, the fineness of the soil is required to allow feeding by the Teal.

Teal choose the resting place according to requirements which vary with the season. In the pre-wintering period, preen (relation to moult), sleeping and partly diurnal feeding being important, the remises should offer large, fine-particled beaches. In the wintering period, swimming and sleeping need large open waters. For the post-wintering period, for courtship and partly diurnal feeding, Teal seek around the remises enclosed fine-particled marshes with a well-vegetated border. This biotope looks something like the breeding habitat on which they have been 'imprinted' in the early days of their lives (Tamisier, 1970b).

During the whole wintering cycle, such successive requirements could mean that several localities would have to be used as remises. But as soon as they reach the Camargue, Teal select those remises which will remain favourable at best during all three phases of the wintering cycle. This selection implies a knowledge of the seasonal variation of the biotopes, and is acquired by tradition.

The 40,000 Teal which, on average, winter in the Camargue are mostly found on only four remises. The two most important places are Marais des Bruns, used by 20,000 birds with a maximum of 35,000, and Tour du Valat, holding 5,000–10,000.

(b) *Nocturnal habitat*

This is fundamentally defined by the feeding behaviour and by the nature of the diet.

Diet of Teal (*Figure* 4). From 300 analyses (Tamisier, 1971b) it appears that Teal are mostly seed-eaters, taking oospores of Musk-grasses Characeae, seeds of Bulrushes *Scirpus litoralis* and *lacustris*, of pondweed *Potamogeton pusillus*, of wigeon grass *Ruppia maritima*, of water milfoil *Myriophyllum spicatum*, of seablite Salsolaceae, besides agricultural

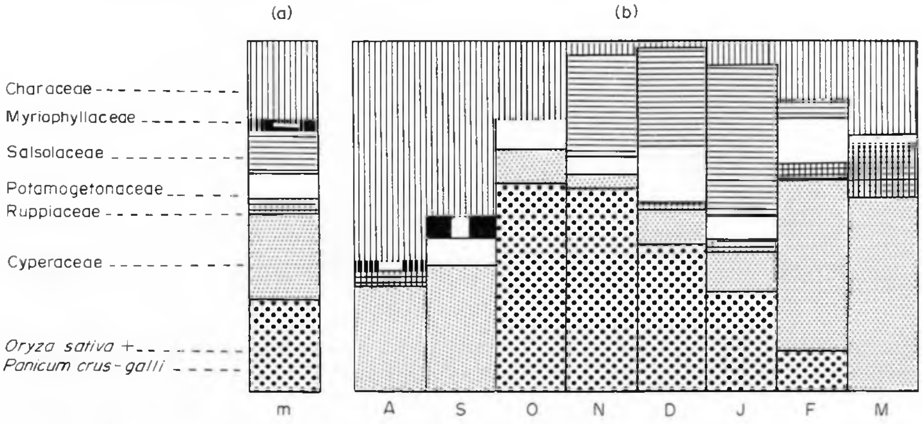

Figure 4. Diet of Teal. Winter mean (a) and monthly variation (b) by dry weight of seeds. (After Tamisier, 1971.)

grain such as rice *Oryza sativa* and cockspur *Panicum crus-galli*.

Such seeds are always present, whereas animal food occurs in only half the samples throughout all the wintering period. This is composed mostly of Molluscs (Hydrobiidae, Limnaeidae and Physidae). Chironimid larvae and Ostracods. Grit is always present: it enables the hardest seeds to be broken up and probably provides some essential mineral elements. Each individual carries seventy to eighty pieces of grit (0·5–3·0 mm) and some dozens or hundreds of smaller particles. But because of the scarcity of grit in the limonous soil of the Camargue, lead-shot lying in the depths of the marsh are used instead, giving rise to lead poisoning.

In the oesophagus, animal remains are twenty times more abundant than in the gizzard. Seeds of rice, panicum and musk-grasses also occur more frequently and in larger quantities. In these cases the Teal seem to have found very rich feeding places (mostly agricultural) and have temporarily stored their food in the oesophagus. By contrast, the seeds regularly taken in natural feeding places occur more frequently in the gizzard. Thus, seeds of *Scirpus litoralis* and *Potamogeton pusillus* occur respectively in 85 and 60% of the samples. They seem to be the typical food for which Teal are adapted: their sizes give the limits (1·2–2·6 mm) of the food particles on which Teal subsist (Figure 5). Identical results have been obtained by Olney (1963) for Teal in Britain. Smaller (muskgrasses) or larger (rice, *Panicum*) seeds are selected only when available in large numbers and then taken in enormous quantities. Animal prey are always larger, they involve a different feeding behaviour and bring some essential components of the diet, particularly proteins.

In summary, the feeding niche of the Teal is firmly defined by the physical conditions of the feeding grounds (fine mud under a few centimetres of water), by the nature of the food taken (Teal are the most specialized in seed-eating of the palaearctic ducks) and by the limitations on food particle size.

Biomasses of available food. All the feeding places have the same physical characteristics but differ in the nature and abundance of food. A total of 480 samplings were taken in the top 4 cm of mud (depth most exploited by Teal) in different biotopes and in different months of the winter. Their analysis showed that the biomass of seeds ranges from 3 to 50 g/m^2 (dry weight) (Figure 6). Most of the feeding places have biomass between 5 and 20 g/m^2. The most frequent seeds are those of Bulrush *Scirpus maritimus* and *lacustris* and *Eleocharis palustris* and oospores of Musk-grasses. Pondweeds are generally represented by *Potamogeton pectinatus* but seeds of this species are too large for Teal. In saline

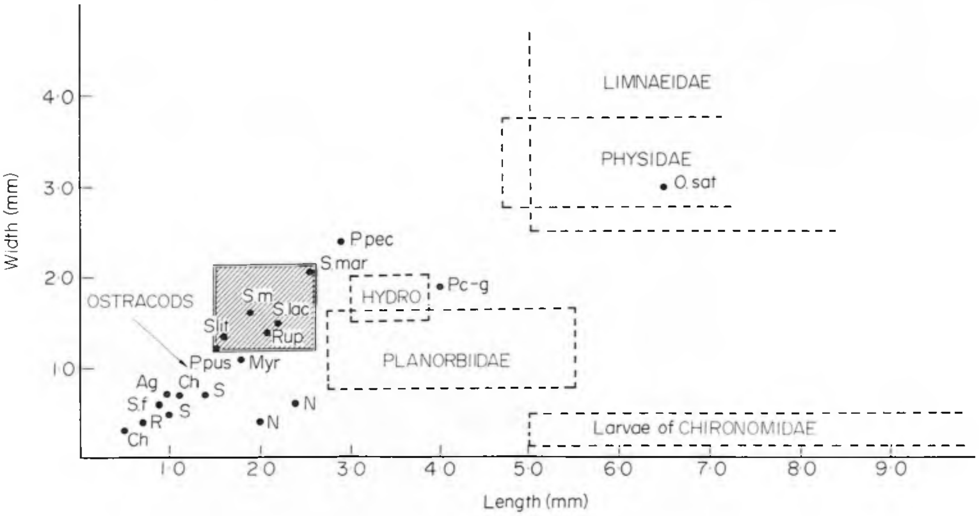

Figure 5. Limitations of food particle size of Teal defined by the size of the most frequently occurring seeds. Animal food as much as seeds of Characae, rice and *Panicum* have a marginal position. A.g.: *Arthrocnemum glaucum*; Ch.: Characeae; HYDRO: Hydrobiidae; Myr.: *Myriophyllum spicatum*; N.: *Naias* sp.; O.sat.: *Oryza sativa*; P.c-g.: *Panicum crus-galli*; P.pec.: *Potamogeton pectinatus*; P.pus.: *Potamogeton pusillus*; R.: *Ranunculus* sp.; Rup.: *Ruppia maritima*; S.: *Suaeda* sp.; S.lac.: *Scirpus lacustris*; Sc.lit.: *Scirpus litoralis*; S.mar.: *Scirpus maritimus*. (After Tamisier, 1972b.)

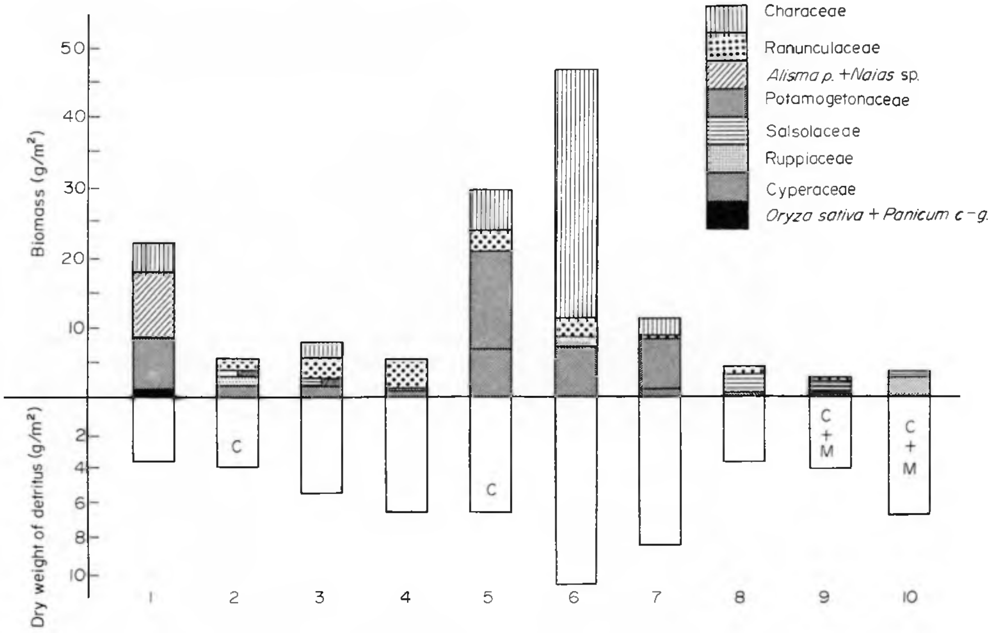

Figure 6. Biomass of seeds in the first 4 cm of mud in the feeding grounds of Teal. 1, Ricefields; 2, 3, 4, Bulrush marshes; 5, pondweed marshes; 6, Muskgrass marshes; 7, reeds; 8, 9, more or less flooded saline grounds; 10, saline marshes. Most detritus is vegetable, some are shelly (C) or mineral (M). Seeds are most available for Teal when detritus is less numerous. (After Tamisier, 1971a.)

biotopes, seeds of seablite and wigeon grass are the most abundant.

Animal food is mostly Molluscs (gastropods) and larvae of Chironomids. Saline swamps are the richest (holding on the average 20,000 *Hydrobia* sp./m^2). Fresh or brackish marshes support important concentrations of Chironomid larvae (2,000–20,000/m^2) and Physidae, Limnaeidae and Planorbiidae in lesser quantities.

Food in the soil is always mixed with vegetable detritus and sometimes shelly or mineral debris. These constituents vary in abundance and make filtration of mu ' by the ducks more difficult. Seeds are the less available the more the detritus, especially vegetable matter, is abundant.

There is little variation in the biomass present throughout the winter and the quantities available at the end of the season are everywhere generally high.

Method of exploitation of the habitat

Between the beginning and the end of the wintering season the variations of the water level are important, giving rise to large variations in flooded areas because of the flatness of the Camargue. In August and September, the water levels are low and few natural swamps are submerged. Teal at night are concentrated in a few feeding places, most hunting places artificially flooded with fresh water. This concentration (up to 100 birds/ha) results in a constant mutual disturbance of the feeding Teal. It would seem that before such artificial water surfaces were available, it was hard for Teal to feed at this period.

After the autumnal rains, the majority of the marshes are flooded and available for feeding ducks. Moreover, after the harvest (mid-October) many ricefields are ploughed and flooded with 10–20 cm of fresh water for 2 or 3 months. These numerous, rich places become very important feeding grounds.

At the end of the winter, all the marshes are filled up and Teal are markedly scattered over the feeding areas (only a few individuals/ha). Then, according to time and place, Teal exploit more or less abundant food resources. As seen earlier, the daily feeding time varies with the month as determined by the physiological condition of the birds and by climatic factors, but is completely independent of the biomass of available food. At any one time Teal using places containing a different biomass will take just as long to obtain their food (Figure 7). That

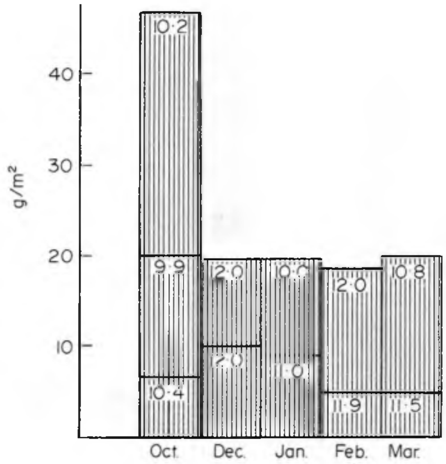

Figure 7. Independence of daily feeding time and value of feeding grounds. In any one month the daily feeding time is defined by the physiological state of the Teal and by climatic factors. It is independent of the biomass in feeding places. For instance in October, Teal feeding on three different areas (biomass: 7, 20 and 47 g/m²) have approximately the same feeding duration (respectively 10·4–9·9 and 10·2 hours/24 hours). (After Tamisier, 1972a.)

clearly means that the quantity of food available in the poorest biotope (5 g/m²) is sufficient for the normal feeding of Teal.

IV. Limiting factors

Three successive phases appear from the analysis of daily rhythms. During the first (pre-wintering) and the last phase (post-wintering) the daily cycles are completely occupied with essential activities and reveal the existence of pressures upon the Teal. Indeed, during the pre-wintering time, the high metabolism of ducks forces them to a long feeding period (12 hours). The nights are short and Teal must feed partly by day, around the remises and in marginal conditions. On the nocturnal feeding grounds they lose some time by mutual disturbance because of the small size of available marshes due to a low water level.

During the post-wintering time, the daily activity cycles again are completely occupied. Thanks to the high water levels, all the swamps are full and Teal have maximum space. But their nutritional needs are high, partly because of the low temperatures. In case of a cold spell, these needs increase and, as insufficient feeding time is then available, the Teal must leave the Camargue.

Under natural conditions, it appears that the limiting factors are successively low water levels and low temperatures (generally less than 0°C). Both these factors cause an increase of daily feeding time. But natural conditions do not prevail any longer, mainly for two reasons. Firstly, water-management on hunting places creates many good areas for the earliest ducks and increases the carrying capacity of the Camargue during the pre-wintering period. Secondly, hunting pressure, partly thanks to this water-management, has increased considerably, the Teal being drawn to the places where they are shot. And Teal are mostly killed during those months when, because of their high food needs and of the shortness of the nights, Teal must leave the remises before darkness and come back after dawn in order to increase the time spent on the nocturnal feeding grounds. Hence they are much more vulnerable to hunters. During these two periods, hunting pressure is superimposed on environmental pressures. But the hunting season has been closed only on 31 March (15 March from the season 1973–1974) and all the Teal killed at this time are potential breeders. Therefore, hunting pressure now regulates the population of Teal on their winter quarter, concealing the effects of the two natural limiting factors, water level and temperature.

Spatial organization and traditions

In the Camargue there are three or four main remises for Teal. Each diurnal remise has its own nocturnal feeding grounds which are only used by individuals of this remise. Twice a day at dawn and after sunset, Teal fly from one to the other (mean distance, 15 km). A remise and its feeding grounds constitute a functional unit which is exploited by an element of the population. Exchanges between two adjacent remises do occur, but for a few individuals only. From day to day the numbers present on each remise are nearly constant. The two main remises are far enough apart to avoid any overlapping. Their feeding grounds are located in opposite directions (Figure 8).

Teal are gregarious by day and scatter at night for feeding. This gregarious habit, characteristic of most wintering Anatidae, differs strongly from diurnal flocking for feeding (Lack, 1954) and nocturnal communal roosting (Crook, 1960; Morel, 1968; Siegfried, 1971). It should have a different significance. It may be understood as a response to human disturbance, particularly hunters. However,

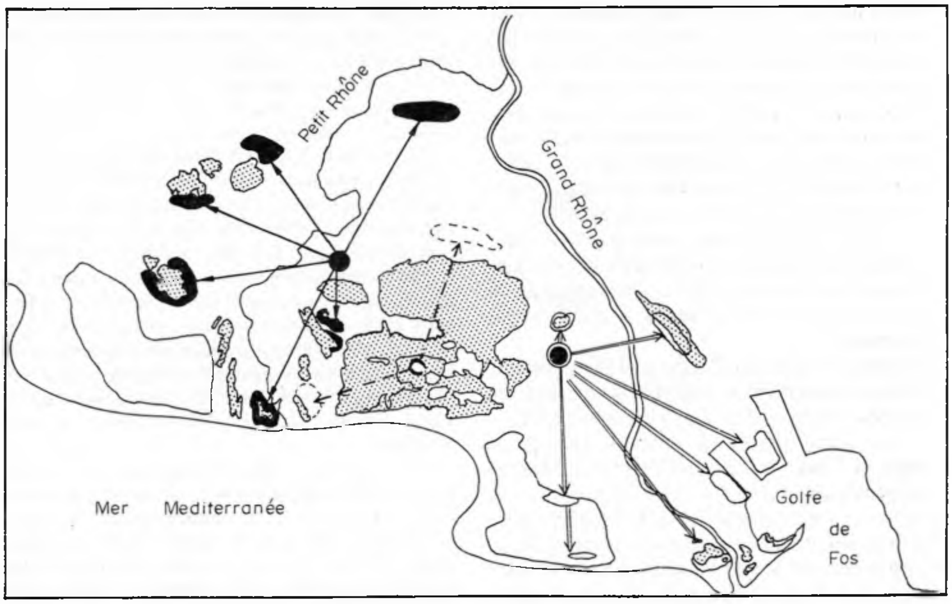

Figure 8. The 'functional units' of Teal in the Camargue. Each remise has its own feeding grounds (arrowed). The overlap between two 'units' is very slight. The mean distance between remise and feeding ground is *c.* 15 km.

the largest winter quarters suffer few (Turkey, Iran, Senegal) or no disturbance (Central delta of the Niger, Mali (F. Roux personal communication)). And there, as much as in Europe, the same alternation of diurnal and nocturnal activities occur. In effect, nocturnal feeding seems to be a direct consequence of the diurnal gregarious habit, which prevents densely grouped Teal from feeding. What, then, is the function of this gregarious habit? It appears (Tamisier, 1970b) to be an adaptation to predation pressure and is facilitated by some other factors.

Flocking of many individuals allows, by a 'multiplicity of eyes' (Miller, 1922), the best defence against predators (a Teal alone is much more vulnerable). The predators are mostly those more or less limited to wetlands (Spotted Eagle *Aquila clanga*, White-tailed Eagle *Haliaëtus albicilla*, Marsh Harrier *Circus aeruginosus*) or specializing on flocking birds (Peregrine *Falco peregrinus*). In the Camargue nowadays there is only the Marsh Harrier. But a new kind of predator, the Herring Gull *Larus argentatus*, has adapted to exploiting the niche newly left by the disappearance of the true birds of prey. The total frequency of disturbance by these two predators is high. The mean for the winter is seventy times/day, with a maximum in November of 160 times/day. Every time, 30–40% of present birds are disturbed. But the actual number of Teal caught is very slight. Predators seek among the ducks for those which cannot fly or are deficient in some way so as to make them more vulnerable. Inversely, the constant presence of predators close to the main winter quarters necessitates and favours the development of anti-predator adaptations by prey species (Murton, 1971; Zahavi, 1971).

Diurnal flocking allows the establishment of social communications, particularly expressed by the constant calls of males and females, giving each remise the function as an 'information centre' (Ward, 1965; Siegfried, 1971). This is particularly useful in the choice of feeding grounds: the best 'informed' birds lead the others to the most favourable feeding places. The communal flights of Teal on the remises could act as 'epideictic manifestations' helping this element of the population to keep in balance with the resources to be exploited (Wynne-Edwards, 1965). Facilitated by such large concentrations, traditions play a very important part in the Anatidae (Hochbaum, 1955) permitting each individual to return precisely to the same localities. Indeed the remises actually used in the Camargue are very constant from year to year. Wandering Teal in search of a suitable place are exceptional. As soon as they arrive in their wintering area, Teal seem able to go directly to their former remise. The same applies to the feeding grounds around the remise, to every species of duck in the Camargue, and also for the remises on the great African winter quarters which have not changed for years (F. Roux, personal communication). The establishment of such traditions depends on the experience of adult birds which lead juveniles to these 'functional units' they have used previously.

The gregarious habit during the winter months is probably facilitated by the physiological conditions of Teal, the absence of sexual activity often means a good social tolerance.

In aquatic birds, the keeping of the plumage in good condition is essential and the long periods of sun-bathing are indispensable.

To summarize, the diurnal gregarious habit of Teal, determined by the predation pressure and aided by other factors, has a survival value. It forces birds to feed by night. Human disturbance seems without any effect. It appears that a similar explanation can be given for most of the Anatidae in which a winter gregarious habit is characteristic.

Summary

The Camargue, with 120,000–150,000 wintering ducks, 40,000 of them Teal *Anas crecca*, is one of the most important winter quarters for Western Palaearctic Anatidae. The previously published results of a long term study (1964–1972) about Teal are outlined.

Ringing results have shown that this population's breeding area ranges from Finland to the Urals. Most of it winters in the Camargue. Only in a cold spell do they fly westwards to the Atlantic coasts. Data are given on variation of numbers, mortality rates, sex-ratio and age-ratio.

The different types of behaviour are analysed (sleeping, preening, swimming and feeding) and their diurnal duration measured. For each month (August–March) the exact composition of the daily cycle (diurnal and nocturnal activities) is known.

The wintering period is divided into three successive phases, varying in the composition of the daily cycle. Feeding behaviour, diet, and biomass of the available food are analysed. The daily feeding duration varies through the months with the physiological condition of the Teal and with climatic factors. There is always plenty of food available.

Under former natural conditions the limiting factors of the population were probably low water levels (beginning of the winter) and low temperatures (end of the winter). Their effects are today concealed by those of hunting mortality which very likely regulates the numbers of Teal wintering in the Camargue.

Wintering Teal are gregarious by day and scatter at night for feeding. Many feeding grounds are linked to each daytime haunt, constituting a 'functional unit' always exploited by the same birds. In the Camargue three or four such units show very little overlap.

The diurnal gregarious habit is shown as an adaptation to predation pressure, and not as a response to human disturbance. It enforces nocturnal feeding. This alternation is strengthened by some other secondary factors.

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An ecological outline of a moulting area of Teal, Vejlerne, Denmark*

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Introduction

This description of the moulting area of Teal *Anas crecca* in the marshland of Vejlerne, North-West Jutland, Denmark, is based on investigations by the Game Biology Station and was inspired by the Wetland Management Research Group of the International Waterfowl Research Bureau (IWRB).

As the literature gives extremely scanty information on the nature of moulting areas, the abiotic and biotic conditions in Vejlerne at the present time cannot be compared with the situation in other moulting areas for Teal. The Research Group therefore will consider it useful if the present description will stimulate to further research on moulting areas and on the ecology of dabbling ducks during the wingmoult period.

The marshland of Vejlerne (57°04′N, 09°00′E), which is privately owned, is a scientific reserve and Project MAR locality (Olney, 1965). It is administered by the owners in conjunction with the Nature Conservation Council (Naturfredningsrådet) of Denmark. The reserve covers an area of about 6,000 ha and includes shallow lakes, grazing meadows, and reed beds.

These coastal marshes were formed from shallow brackish inlets of the Limfiord during an unsuccessful attempt of drainage in the latter half of the last century. The reserve is now used for harvesting reeds, cattle grazing, fishing, supervised shooting and for scientific investigations. The marshland is mainly surrounded by agricultural land, and the moulting area comprises less than 1% of the total area of the reserve.

Data concerning the moulting area

The moulting area of approximately 50 ha occurs in the wide part of the south-western section of Selbjerg Vejle, a shallow lake of 900 ha (including reed beds (Figures 1, 2)). The immediately adjacent areas are refuges for pre- and post-moulting birds. The total number of moulting male Teal in the years 1966–1971 were 1,000–1,200, 1,000–2,000, 1,000–1,200, 800–1,000, 400–600, and 200–300 respectively. In addition, there were several hundred moulting male Mallard *A. platyrhynchos*, Shoveler *A. clypeata*, and Wigeon *A. penelope*.

The area has been by far the most important moulting area for Teal in the period of investigation and has probably long been used traditionally. In the other lakes of the reserve, where several important moulting areas for other species of dabbling ducks are found, occasionally a smaller number of groups of Teal (in all a maximum of 100 individuals in a year) moult, as for example in the north-western corner of Selbjerg Vejle, Glombak, Tömmerby Fiord, Veslös Vejle, and Hanvejle.

The moulting area in Selbjerg Vejle is probably the most important for Teal in all Denmark. According to the literature only one moulting area is known, viz. Nakskov Indrefiord, Lolland, South-East Denmark, where up to 1,000 birds have been observed (Bloch *et al.*, 1972).

Observations of smaller flocks of drakes (not moulting) in June–July in the eastern part of the country (Palm, 1950) indicate that birds on moult migration pass Denmark, or that the country holds several smaller moulting areas. On the basis of ringing recoveries Wolff (1966) has shown that moulting areas must exist in the north-western Europe.

In relation to the size of the breeding population in Vejlerne (presumed to be less than twenty pairs in the whole reserve), the number of moulting male Teal clearly indicates a moult migration into the area. The males arrive at the marshland of Vejlerne in late June–early July, and are found in shallow lakes and along lake shores in flocks of 50–300. During the wingmoult, flocks of ten to twenty birds are usually seen together, whereas post-moult flocks generally number several hundred and even up to about 1,000 birds. Immature birds, and possibly adult females, come to the area in the first half of August and can be observed together with the post-moult males.

The moulting period is mainly from 10 July to 10 August. Maximum numbers of flightless birds occur around 20 July.

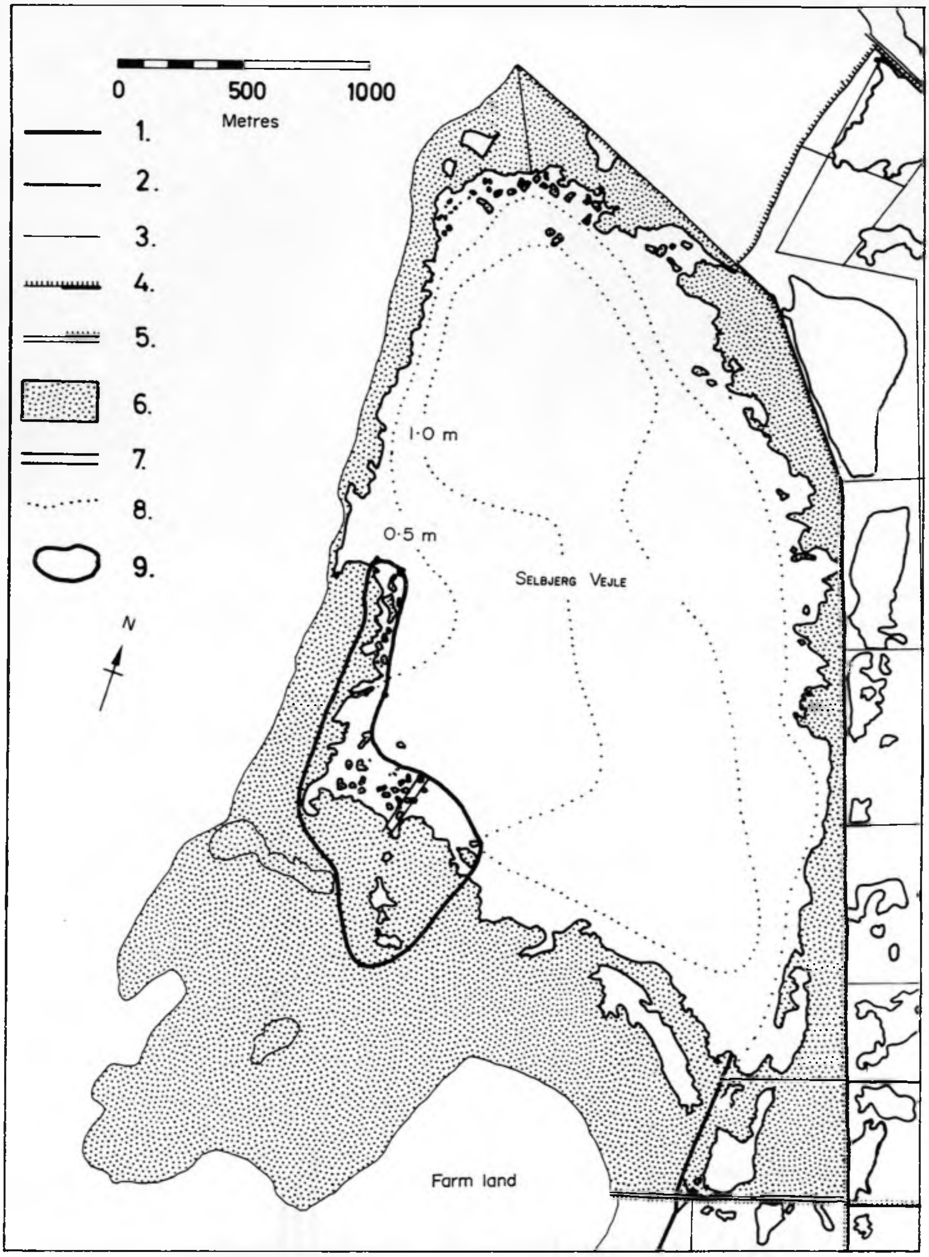

Figure 1. The moulting area and its surroundings in Selbjerg Vejle. 1, Main canal; 2, canal; 3, ditch; 4, dyke/dyke by canal; 5, road; 6, reed beds; 7, transect presented in Figure 4; 8, lines of depths; 9, moulting area.

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Figure 2. A view over the moulting area, where patches of reeds alternate (mix) with open water. In the background the vast reed beds of several hundreds of metres' width, which separate the moulting area from the neighbouring agricultural land.

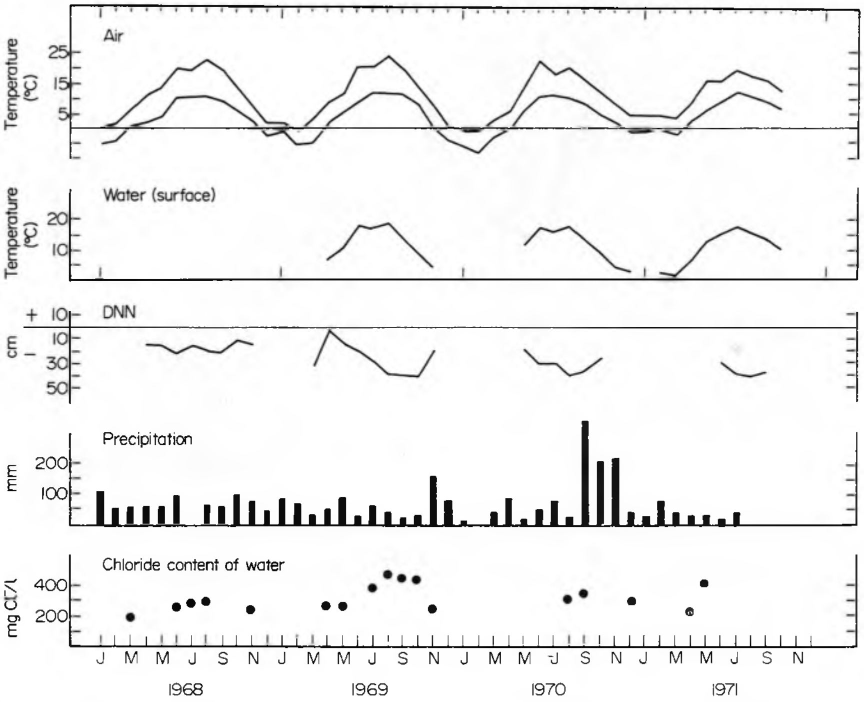


Figure 3. Average monthly values of meteorological observations and other physical factors. (DDN = Danish ordnance datum.)

The environment of the moulting Teal

The following are some of the physical, chemical and biological conditions, which are assumed to be of importance to the ducks in their choice of moulting area.

Climatic effects and other physical and chemical factors

The location of the moulting area in the south-western corner of Selbjerg Vejle is very much due to prevailing winds varying between south-west and north-west. A flourishing reed-marsh has developed at this, the leeward side of the lake. Consequently, much material is deposited in these sheltered surroundings. The birds prefer those parts of the reed-beds which are free from wind and waves.

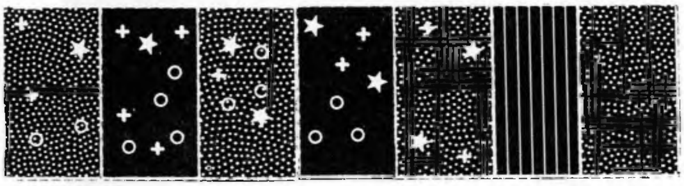
The water level (Figure 3) is generally at its lowest in August and September, by which time the summer evaporation has long been effective. The water level during the moulting period is determined partly by precipitation in the summer months and partly by that of the previous year. It appears that the water level is one of those factors which determine the distribution of the moulting ducks (Kortegaard, 1974).

The temperature of the water surface (Figure 3) generally follows that of the air. On average, the water temperature has been between 16 and 19°C during the moulting period, i.e. 2–4°C under the average monthly temperature of the air. Water temperature is important for the development of the plant and animal life on which the flightless birds are dependent for nutrition. Gavrin (1970) considered that water temperature was the factor which determined the time of moulting, whereas Hochbaum (1955) and Balat (1970) were of the opinion that the time of the wingmoult of dabbling ducks is determined by the time of breeding. In addition, different age-classes of males appear to have different moulting times, at least in a Mallard population (Boyd, 1961).

The chloride content of the water varies between 200 and 500 mg Cl^-/litre during the year, indicating that the water is slightly brackish (oligohaline, *sensu* Redeke, 1922). The concentration of chloride is apparently greatest in the summer months, when the water level is at its lowest (as seen in particular from the 1969 results). According to Schierup (1970), the bottom deposits of the

Table 1. A description of the plant community in the moulting area, south-west corner of Selbjerg Vejle. The occurrence of plants was determined by Hult-Sernanders method for analysis of the degree of cover.

Typical plant community (cf. Fig. 4)



Species							
Phragmites communis	5		5		5		5
Typha latifolia	1	5					
Scirpus tabernaemontani	1						
Scirpus maritimus	1						
Bidens tripartitus	1						
Sium latifolia	x						
Galinum palustre	1						
Potamogeton pectinatus				(1)	(1)	(2)	(1)
Potamogeton perfoliatus			(*)				
Myriophyllum spicatum			(1)	(2)	(2)	(1)	(2)
Lemna minor		1					
Calliergonella sp.					(x)		
Chara aspera			(1)	(3)	(2)	(4)	(3)
Chara polyacantha						(x)	(x)
Phragmites stems/m^2	>200	–	250	–	150	–	25

* Floating specimens.
x, Indicates that the species are observed.

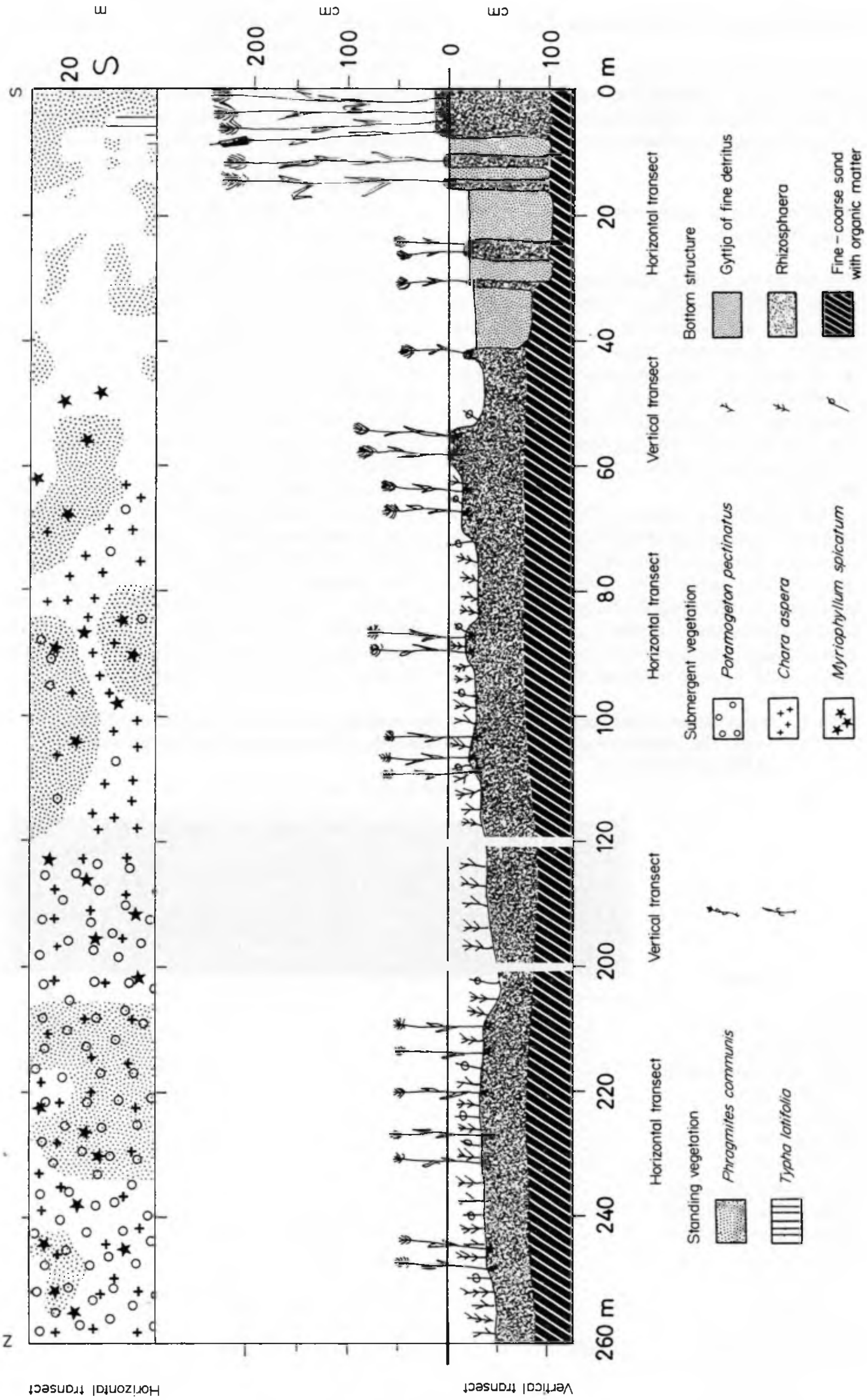


Figure 4. The botanical and topographical transect of the moulting area.

Vejlerne lakes contain residual salts from previous periods of salinity, which may explain the chloride values found. The present effect of the salt water of the Limfiord is presumed to be small, but it is possible that salt water may seep in from underground.

The water in Selbjerg Vejle is slightly polluted from neighbouring agricultural areas (grade II, i.e. β-mesosaprobic, *cf.* Liebmann, 1960–1962).

The botanical and topographical outline

The moulting area is a rather homogeneous biotope, so, although only one transect was investigated it is felt that it characterizes the environment satisfactorily. The transect (Figure 4) was made in a part of the moulting area in July 1968, in which the greatest number of flightless Teal were seen during the moulting period. It consisted of quadrats 20 × 20 m, started in the dry reed-beds nearest land and passing through the belt of vegetation to some way out into the open water, in all a distance of 260 m. The quadrats were laid in a straight line one after the other, and the corners marked with 2-m wooden posts.

The species composition of the plant community of each quadrat was determined, and the occurrence of each species recorded using Hult-Sernander's method for the analysis of degree of cover (Sernander, 1900; Du Rietz, 1921) using a scale of 0–5. In the present situation it was only possible to determine the occurrence of the standing vegetation in this way. The frequency of the submerged vegetation was determined by another comparative method, in which the bottom was scraped with a rake, and the amount of plant material collected was estimated on a scale of 0–4 (numbers in brackets in Table 1). This method was used because of the depth and poor light transmission of the water. In addition, the density of the reeds *Phragmites communis* was measured as the number of stems per square metre, and the height of the reeds (full grown) measured in each plant community; this is shown in the vertical transect of Figure 4.

At the corner of each quadrat and at one or more places within each single plant community, the depth of the water and of loose detritus (Gyttja, decaying organic matter) and the extent of the root- and rhizome-formations of mainly *Phragmites communis* (rhizosphaera-layer) were measured with a metre-stick. The water depth was taken to be the visible zone with clear water, and the depth of the detritus was taken as the depth through which the metre-stick passed before being stopped by a firmer layer. The rhizosphaera-layer was taken to be the distance through which the metre-stick passed before striking a hard layer.

In Figure 4, both horizontal and vertical transects through the moulting area are given, the symbols used representing the occurrence of the plants. Only the dominant species have been shown, the complete species list for the transect being given in Table 1. The following plants were also present in the moulting area: mare's tail *Hippuris vulgaris*, water crowfoot *Batrachium sp.*, purple loosestrife *Lythrum salicaria*, and lesser reedmace *Typha angustifolia*.

The occurrence of fungi and algae (except the Characeae) was not determined. On the extensive underwater rhizome systems of Selbjerg Vejle, the growths (especially of stonewort *Chara*) were amongst the most luxuriant in the area. In the inner zone of 0–60 m shown in Figure 4, larger aquatic plants are lacking and the water is poorly oxygenated. In addition, much marsh-gas is produced.

Small islands and clumps of reeds (probably formed by the stranding of floating masses of vegetation (Hürlimann, 1951)) contribute very much to the appearance of the area as a system of reeds and shallow water. Clumps and small islands serve as refuges and are of great importance, as dabbling ducks go on to land to preen (McKinney, 1965).

Human activity and the possible effect of predators

The area is almost unapproachable by terrestrial mammals (including man), and human activity has mainly been limited to visits in July and early in August, when flightless birds have been ringed by the Game Biology Station.

In the period of investigation 1965–1971 404 moulting Teal (practically all males) are ringed in Vejlerne, and of this all but two are ringed in the area mentioned here (the results of the ringing will be published in another paper from Game Biology Station). This involved the following actions, each of 3–5 hours' duration: two catches in the middle of July 1965; eleven catches from 7 to 29 July 1966; eight catches from 6 July to 3 August 1967; ten catches from 17 July to 7 August 1968; six catches from 21 to 31 July 1969; five catches from 15 to 28 July 1970; and six catches in the period 8 to 28 July 1971.

There has been a decline in the number of moulting birds in the period of investigation.

Whether this decline reflects the disturbance in connection with the ringing programme carried out is uncertain. It has been maintained by several workers that moulting dabbling ducks do not tolerate much human traffic in the moulting areas (Hochbaum, 1944; Szijj, 1965; Lebret, 1971). The pronounced shyness, present among ducks just before and during the flight-feather moulting and the remote location of the moulting areas (Oring, 1964; Kortegaard, in press) make this probable.

It is, however, difficult to estimate the importance of the disturbance, since a range of factors important to the habitat selection of the ducks, and of which disturbance is only one of them, are unknown or incompletely examined. Thus the number of other moulting dabbling duck species in Vejlerne have changed in the period of investigation both in and out of the areas, in which catches have been made. Previously Paludan (1965) has registered a decline in the number of moulting Greylag Goose (*Anser anser*) after some years of catches and ringing without known reason(s). However, contemporary with disappearance of the geese certain changes took place on the terrain. Thus a range of islands disappeared (probably because of raising of the water level). These had been important loafing places for the moulting geese. In addition, a strong overgrowing with *Phragmites* has taken place on the meadows in Bygholm Vejle, which was the most important foraging area before and after the wingmoult. All these conditions may have had an influence on the number of moulting geese, but here again it must be pointed out that our knowledge of the different factors of the habitat selection is insufficient.

Fox *Vulpes vulpes*, otter *Lutra lutra*, and more recently mink *Mustela vison* occur in the area, but it is presumed that the flightless birds are only in real danger from mink (cf. Oring, 1963).

On being disturbed, flightless birds swim away in the edge of the reed zone, often in the inner zone of 0–60 m (Figure 4). Flightless Teal are very timid, and the possibility of avoiding attention is almost certainly important in their habitat selection.

Description of the invertebrate fauna

In June, July, and August, samples of the invertebrate fauna were collected from such areas as the inner zone (0–60 m) and the outer zone (60–260 m) (Figure 4). A Birge-Ekmann bottom grab (Ekmann, 1911; Birge, 1922) and standardized net samples (mesh size 1 mm) were used. The outer zone comprised a rich variety of vegetation and many small invertebrates were found, the dominant forms being given in brackets in the list below: Oligochaeta (*Stylaria*), Hirudinea, Crustacea (*Gammarus*, Ostracoda), Ephemeroptera (*Cloëon* larvae), Odonata (*Coenagrion* larvae), Heteroptera (*Corixa*), Neuroptera (*Sialis* larvae), Trichoptera (Psycomyidae larvae and eruciform larvae), Lepidoptera (*Nymphula* larvae), Coleoptera, Diptera (Chironomidae larvae), Hydrachnidae (*Hydracarina*) and Gastropoda (*Planorbis*). In the inner oxygen-poor zone there was a less varied fauna (Hirudinea, Crustacea, Neuroptera, Trichoptera, Coleoptera and Diptera), and judging from the samples, the number of animals was only about one-tenth of that of the outer zone. In three bottom samples from the outer zone there were 2,500, 3,800, and 150 Chironomid larval tubes per m^2 respectively, whereas in three samples from the inner zone the numbers per square metre were 450, 720, and 415 respectively. It should be pointed out that collection of samples with a bottom-grab in the habitat described was rather difficult, and this may have effected the results obtained from the few samples collected.

Flightless Teal were observed several times to be feeding in the outer zone (Figure 4).

Food items

The food of flightless drakes was not clearly determined, as stomachs of eleven birds only were collected and examined. Of these, ten contained only small amounts of food, four contained duck down, and all contained gravel.

The birds were not collected immediately after feeding, nor was the digestive tract preserved immediately after death. Thus, according to Koersveld (1950), most of the soft parts will become unrecognizable in a short space of time due to the action of the digestive juices. Indeed, only the harder parts of animal material were found—statoblasts of Bryozoa, ephippia of Cladocera, the more heavily chitinized parts of Coleoptera, head capsules of Chironomidae and carapaces of Hydrachnidae. Animals lacking easily visible hard parts—Trichoptera, Oligochaeta (Chaetogaster, Stylaria), and Lepidoptera (*Nymphula*), all common on aquatic plants, were not observed. The collection of stomachs of flightless birds thus presents certain problems.

The majority of the stomachs examined contained soft plant remains, e.g. several fragments of *Chara* were found, which occurred as an interwoven mass in the stomach contents.

Seeds found included club rush *Scirpus sp.*, spiked watermil *Myriophyllum spicatum*, mare's tail *Hippuris vulgaris* and a few specimens of marsh cinquefoil *Comarum palustre* and sedge *Carex* sp. Flightless Teal, therefore, appear to exist on a mixed diet consisting of invertebrates, seeds, and fresh plant material.

The food of Teal during the moulting period has only been mentioned by Dement'ev *et al.* (1952) who reported that in different areas either plant or animal food was dominant in stomachs examined. This indicates that Teal are well able to adapt themselves to available food sources. Lebret (1971) has observed flightless Teals taking food on tidal mudflats.

A comparison with an important moulting area of Mallard

This moulting area for Teal in the south-western part of Selbjerg Vejle is quite different from the most important moulting area for Mallard, which is on the flooded overgrown meadows ('marshes') in the northern part of Bygholm Vejle. Here the water level is generally lower, and the open surfaces of water cover comparatively limited areas. We have never observed moulting Teal in this area.

Conclusion and summary

Some of the features which are typical of the moulting area can be summarized briefly as the topography, water level (20–60 cm), shelter from prevailing winds, water temperature (16–18°C), food (rich plant and animal life), clumps and small islands as refuges, and occasional patches of standing vegetation in water, which offer shelter and a means of escape. These factors are presumably important in the habitat selection by the birds ('proximate factors', cf. Hildén, 1965). In addition, the relationship to predators (including man), social factors, past tradition (moulting migration) and internal factors (timidity and physiological stress) apparently also play a part in the habitat selection, but these factors have not been investigated.

From the experience gained in this study, a description of a moulting area of dabbling ducks should cover the following points. (a) Latitude and longitude; country; surface area; legal status; numbers and species of duck concerned; period of moulting. (b) Measurements of water level, air and water temperature, chloride content and other water qualities. (c) Description of the topography and vegetation of the moulting area, including species composition and relative occurrence of species. (d) Collection of invertebrate samples from typical plant communities during the moulting period. (e) Collection of duck stomach contents for comparison with points (c) and (d). These should be obtained immediately after the ducks have fed, and be preserved at once in 4% formalin (Harrison, 1960). (f) Description of other conditions which affect the flightless birds or their habitat.

It is hoped that this article will stimulate the investigation of moulting areas of Teal and other dabbling ducks in other localities. In this way, a fair impression can be gained of the general and specific requirements of these birds for their moulting areas. Such knowledge is necessary for the conservation and management of the moulting areas of duck.

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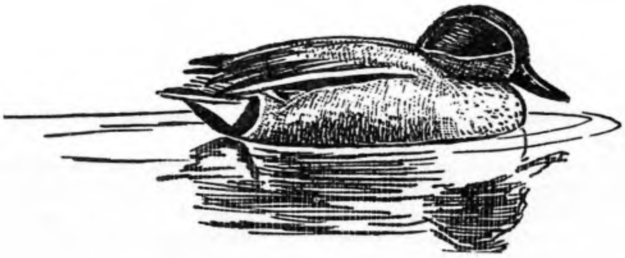

The ecology of the invertebrate community of Borough Fen Decoy pond

MARGARET PALMER

Introduction

Borough Fen is the oldest surviving Duck Decoy in Britain. It was constructed 4 miles north of Peterborough about 1640 for commercial duck-catching and continued in that use until the Wildfowl Trust converted it to a ringing station (Cook, 1960). The 2½-acre pond and the 14½ acres of mixed woodland in which it lies have thus formed an isolated, managed ecological unit for well over three centuries. With the drainage of the Fens it was one of the few permanent bodies of water remaining, until the relatively recent excavation of ballast and gravel pits. Woods are unusual in the Fen country too, often marking the sites of disused decoys.

The pond water is replenished in the summer, and other times of shortage, through a drain connecting it with the River Welland. Indeed the first written record of the Decoy's existence is an application made by the Earl of Lincoln to the Bedford Level Commissioners, in 1670, for permission to pierce the embankment of that river. In 1972 such topping-up took place on 5 days—28, 29 June, 24 August and 28, 29 September.

The water in the pond and its eight curved 'pipes' is clear and shallow. Nowhere is it more than 2 ft deep, in most places only a few inches. The bottom of fine gravel is overlaid by a thick layer of black mud. In 1947 it was cleaned out by dragline, and each year a different area is pumped clear of mud.

There are patches of algae on the mud, but apart from an island of reeds there are no rooted plants of duckweeds growing in the central part of the pond. Around the margins *Carex acuta*, *Glyceria maxima* and *Phragmites communis* flourish, and the encroaching vegetation is periodically dug out, as are the edges of the reed island. Aquatic plants grow readily in the pipes, which have to be cleared annually (Figure 1). This vegetation consists of *Glyceria maxima*, *Lemna minor*, *Callitriche stagnalis*, *Rorippa nasturtium-aquaticum* and filamentous algae including *Spirogyra*.

The pond often has a roosting population of up to 1,500 duck during the autumn, the birds flighting out in the evening to feed in

Figure 1. Borough Fen Decoy. The mouth of the North Pipe; a general impression of the vegetation round the pond.

the surrounding arable land, sometimes as far as the coast 20 miles away. In the winter the roosting population falls to 400–500. Few of the duck stay to nest. In 1972 one pair of Mute Swans, about ten pairs of Mallard and several pairs of Moorhen nested around the pond.

Water analysis

A water sample taken in June had approximately 90 parts per million (ppm) of calcium.

Two samples of water were taken on a sunny afternoon in July from the central area of the pond, where the water was 4 in deep, over 10 in of mud, with a water temperature of 21°C. Oxygen saturation was 135%/122% and the pH 7·98/8·02. The compounds in solution were, in ppm: oxygen 11·7/10·6; ammonia (as nitrogen) 9·2/10·2; nitrate (as nitrogen) 1·2/1·2; nitrite not detectable; phosphate (as PO_4) 2·1/2·1; total hardness (as $CaCO_3$) 250/250.

Animal survey

This was carried out between March and July 1972. Both *Pygosteus pungitius* (ten-spined stickleback) and *Gasterosteus aculeatus* (three-spined stickleback) were present in the pond. *Rana temporaria* (common frog) returned in 1972, after some years' absence from Borough Fen, but no tadpoles were seen. Some fifty species of invertebrates were found, half of them insects (Table 1).

Table 1. Invertebrates found in Borough Fen Decoy pond

Tricladida	
Dendrocoelum lacteum (Müller)	***
Polycelis nigra (Müller)	.
Nematoda	
Mermithidae	.
Annelida	
Oligochaeta	
Tubificadae	***
Nais sp.	**
Hirudinea	.
Erpobdella testacea (Savigny)	
Helobdella stagnalis (L.)	***
Mollusca	
Gastropoda	
Lymnaea peregra (Müller)	**
Lymnaea stagnalis (L.)	**
Planorbis planorbis (L.)	.
Planorbis contortus (L.)	.
Lamellibranchiata	
Anodonta cygnea	*
Crustacea	
Cladocera	
Simnocephalus vetulus (Müller)	
Daphnia pulex (De Geer)	****
Daphnia obtusa (Kurs.)	*
Daphnia magna (Straus)	*****
Scapholeberis aurita (Fischer)	*
Leydigia leydigi (Schodler)	***
Copepoda	
Cyclops agilis (Koch. Sars)	****
Cyclops vicinus (*uljanna*)	***
Isopoda	
Asellus meridianus (Racovitza)	.
Amphipoda	
Crangonyx pseudogracilis (Bousfield)	***
Insecta	
Hemiptera	
Gerris lacustris (L.)	.
Notonecta glauca (L.)	**
Callicorixa praeusta (Fieber)	.
Corixa punctata (Illiger)	*
Hesperocorixa sahlbergi (Fieber)	.
Sigara dorsalis (Leach)	*
Sigara falleni (Fieber)	.
Sigara lateralis (Leach)	****
Trichoptera	
Limnephilidae	.
Coleoptera	
Haliplus lineatocollis (Marsham)	*
Haliplus ruficollis (Degeer)	*
Hygrotus inaequalis (Fab.)	.
Ostracoda	****
Hydroporus granularis (L.)	.
Hydroporus palustris (L.)	.
Hydroporus pubescens (Gyllenhal.)	.
Diptera	
Ptychoptera contaminata (L.)	.
Ptychoptera minuta (Tonnoir)	.
Anopheles maculipennis (Meigen)	*
Paradixa aestivalis (Mg.)	.
Chironomidae	****
Ceratopogonidae	**
Pericoma sp.	.
Acarina	*

.. Scarce; *, fairly frequent; **, frequent; ***, very frequent; ****, abundant; *****, very abundant.

Notes on the ecology of the invertebrates

Tricladida

Dendrocoelum lacteum is a flatworm, found in productive waters where the calcium content is at least 10 ppm (Reynoldson, 1967). It feeds on arthropods, and its distribution is closely linked with that of *Asellus*, one item of its diet. *Polycellis nigra* is a widespread species, which feeds on oligochaetes and arthropods.

Nematoda

Mermithidae (rainworms) are relatively large roundworms, several centimetres in length, parasitic in their early stages in insect larvae.

Hirudinea

Helobdella stagnalis is a very common leech, typical of still waters rich in calcium. *Erpobdella testacea*, a less common species, is found in emergent vegetation, eutrophic ponds and organically polluted waters. Both species feed on invertebrates such as chironomid larvae and oligochaete worms, and *Erpobdella testacea* also takes water fleas.

Mollusca

Lymnaea peregra is the most widespread and abundant British freshwater snail. *L. stagnalis* is common in hard-water ponds. Similarly, *Planorbis contortus* is a widespread ramshorn snail, whereas *P. planorbis* is restricted to hard water. Shells of *Anodonta cygnea* found at Borough Fen measured up to 5½ in. in length. Sticklebacks here would be the hosts for the parasitic larvae of the swan mussel.

Crustacea

The pond teems with Cladocera. *Daphnia pulex* is typical of polluted ponds, as it feeds on unicellular algae with hard cuticles, which abound in these conditions. It can tolerate low oxygen concentrations, and its feeding limbs are not clogged by bacteria. *Daphnia obtusa* is associated with 'duck ponds'. *D. magna* is rather rare, occurring in hard waters in south and east England. *Simnocephalus vetulus*, which flourishes in hard, weedy waters, was restricted to the thick vegetation in the pipe ends. *Scapholeberis aurita*, a rare species, crawls on the underside of the surface film of the water. Before this survey it had only been recorded from Norfolk and Hampton Court (Scourfield & Harding, 1967). *Leydigia leydigi*, a widespread species, lives on the surface of the mud.

The Copepoda found at Borough Fen are common species. *Cyclops vicinus* is usually associated in ponds with *Daphnia pulex*.

Asellus meridianus was not as plentiful in this pond as might have been expected, as it is an abundant water skater in the Peterborough district, and can stand fairly low oxygen concentrations. *Crangonyx pseudogracilis* is a freshwater shrimp which was introduced from North America in the 1930s and is now fairly widespread. It appears to be able to stand pollution better than the common freshwater shrimp, *Gammarus pulex*, which was not found at Borough Fen.

Hemiptera

Gerris lacustris is probably the commonest species of pond skater in the Peterborough district, and *Notonecta glauca* is by far the commonest of the back-swimming water boatmen.

Macan (1954, 1963, 1965) has shown that each species of corixid has precise requirements, including the calcium content of the water and the amount of organic matter on the bottom. Of the six species of corixid found at Borough Fen, the only numerous one was *Sigara lateralis*. This water boatman is often abundant in ponds fouled by animals (in this case the waterfowl). *Callicorixa praeusta* is common in rich waters, often where there is some degree of organic pollution. *Sigara falleni* and *Corixa punctata* are common in calcium-rich waters. *Hesperocorixa sahlbergi* is typical of ponds with black mud on the bottom, where the water is not base-deficient. *Sigara dorsalis* is typical of waters with less organic matter than is present at Borough Fen.

Trichoptera

The two limnephilid caddis larvae found amongst *Carex* stems had constructed their cases from plant material.

Coleoptera

All the beetles found at Borough Fen are very common pond species.

Diptera

Anopheles maculipennis is a very common mosquito, and *Paradixa aestivalis* is a very widespread midge. The grub-like larvae of the Ptychopteridae (phantom craneflies) live in mud beneath shallow water, and breathe air at the surface by means of a long abdominal respiratory process. *Ptychoptera contaminata* is a common species, frequenting especially woodland pools. *P. minuta* is local in distribution, and has not previously been recorded from this vice-country (Stubbs, 1972).

Acarina

Parasitic mite larvae were found attached to the cuticle of *Callicorixa praeusta*.

Discussion

Apart from Cladocera, Copepoda and Ostracoda, only a very few species of animal were at all numerous in the areas of the pond free of rooted vegetation. These were *Dendrocoelum lacteum*, *Helobdella stagnalis*, *Crangonyx pseudogracilis*, *Sigara lateralis*, oligochaete worms, and ceratopogonid and chironomid midge larvae. In addition, the small, temporary areas of aquatic vegetation in the pipes accommodated numbers of *Lymnaea peregra*, *Lymnaea stagnalis*, *Notonecta glauca*, haliplid beetles and mites.

Three important factors influencing the composition of the invertebrate fauna of Borough Fen Decoy Pond are: (a) the high concentration of organic material; (b) the high calcium concentration; (c) the absence from most of the pond of aquatic plants other than algae.

(a) The concentration of ammonia was very high, about double the average for the effluent from Peterborough Sewage Works. The source of most of this ammonia is undoubtedly the excreta of the very large wildfowl population harboured by the pond from August to March. Leaves drifting in from surrounding trees augment this supply of organic material. The high calcium concentration of the water encourages rapid decomposition, resulting in the formation of the thick layer of black mud.

Water samples collected on a sunny summer day contained abundant oxygen. Most of this must have been derived from the photosynthetic activity of unicellular and filamentous algae. Under these conditions, oxygen production was outstripping the consumption of dissolved oxygen by the plants and animals in the pond, notably the bacteria and other micro-organisms breaking down organic compounds. The presence of nitrate indicates activity by aerobic bacteria utilizing ammonia. However, at night, especially when the temperature remains high, the water must rapidly become deoxygenated, and anaerobic breakdown processes must dominate. The aquatic animals must therefore be adapted to cope with wildly fluctuating oxygen levels, unless they breathe air at the surface.

The Trent River Board has worked out a classification of freshwater, using invertebrate organisms as indicators of the degree of organic pollution. The oxygen requirement of the members of the invertebrate community is one of the principal criteria upon which this Biotic Index is ultimately based. The Biotic Index ranges from 0 for foully polluted to 10 for thoroughly clean. The rating for Borough Fen Decoy Pond works out at approximately 6. Many species in the pond are typical of mildly polluted water, in particular *Erpobdella testacea*, *Daphnis pulex*, *Asellus meridianus*, *Sigara lateralis*, and *Callicorixa praeusta*. Tubificid worms and red chironomid larvae are extremely tolerant of pollution, but their presence does not necessarily indicate gross pollution unless all other species requiring dissolved oxygen are absent. Plecoptera (stoneflies), Ephemeroptera (mayflies) and most species of Trichoptera have aquatic stages unable to stand pollution, and, as would be expected, are absent from the pond.

Adult Coleoptera and Hemiptera, and the larvae of some Coleoptera and Diptera (including *Anopheles*, *Paradixa* and *Ptychoptera*) obtain gaseous oxygen at the surface, and so are independent of dissolved oxygen. Snails like *Lymnaea* use dissolved oxygen unless the concentration is low, when they come to the surface and breathe by means of a lung. Some adaptations to low oxygen concentrations of those aquatic invertebrates dependent upon dissolved oxygen are obvious. One such is the presence of haemoglobin in the mud-dwelling chironomid larvae and tubificid worms. The possession of haemoglobin makes possible the uptake of oxygen at very low concentrations. Some chironomid larvae produce it only in situations where oxygen is scarce. Chironomid larvae are able to respire anaerobically if necessary. Both chironomids and tubificids make respiratory movements. Chironomids build U-shaped tubes of salivary secretion in the mud, and undulate their abdomens to create a current through the tubes. Tubificids protrude their tails from the mud and undulate them. The scarcer the oxygen, the greater the length of tail which is protruded.

Other adaptations are less obvious. For instance, in dragonflies, the bottom-dwelling species of nymph appear to have lower metabolic rates, lower growth rates, and to move more slowly than those which live among water plants near the surface, where oxygen concentration, temperature and light intensity are higher (Corbett, Longfield &

Moore, 1960). Amongst the leeches, *Erpobdella octoculata* is widespread, but is replaced by the less common *E. testacea* in anaerobic situations such as emergent vegetation or waters otherwise rich in organic material. Mann (1965) has carried out experiments on the oxygen consumption of these and other leeches, and has shown that *E. testacea* is physiologically better adapted to life in low oxygen concentrations than is *E. octoculata.* The oxygen consumption of *E. octoculata* is dependent upon the concentration of dissolved oxygen, whereas, at low levels, the oxygen consumption of *E. testacea* is independent of oxygen concentration. Mann (1961) also points out that whereas *E. octoculata* breed in summer and lives for 2 years, *E. testacea* dies after breeding early in the year, so that in the warmest months, when oxygen is likely to be scarcest, it is small or in the egg stage. It is significant that *E. testacea* is present at Borough Fen, but *E. octoculata* was not found.

(b) Amongst freshwater invertebrates there are some groups in which the presence of calcium appears to favour all the species, and with decreasing amounts of calcium below a certain level the number of species decreases. For instance Boycott (1936) has shown that some species of Mollusca (e.g. *Lymnaea peregra* and *Planorbis contortus*) can live in hard and soft waters, whereas other species (e.g. *Lymnaea stagnalis* and *Planorbis planorbis*) are only present where there is at least 20 ppm of calcium. One reason for this may be that, as calcium encourages decomposition of organic material, hard waters are more productive than calcium-deficient ones.

In other groups, for instance the Corixidae, some species are characteristic of hard waters, while others are confined to soft waters (Macan, 1954, 1963, 1965). By invertebrate standards the water at Borough Fen is extremely rich in calcium. *Dendrocoelum lacteum, Helobdella stagnalis, Lynmaea stagnalis, Planorbis planorbis, Simnocephalus vetulus, Corixa punctata, Callicorixa praeusta. Sigara falleni, S. lateralis* and *Hesperocorixa sahlbergi* are all species confined to or favoured by hard water, and present at Borough Fen.

(c) The scarcity of vegetation in the pond limits the number of animals, especially snails and insects. Gastropods, Coleoptera and some Hemiptera (e.g. *Notonecta*) were nearly all confined to the temporarily uncleared ends of the pipes. The notable absence of dragonflies is due at least in part to this factor, as many species lay their eggs in aquatic plants, and most nymphs are weed-dwellers. The thick, soft mud does not provide a suitable substrate for some plants, but conditions are favourable for duckweed. This is eaten by the ducks as quickly as it grows. If left undisturbed, the pond would support a greater variety of invertebrates, but obviously plants would quickly engulf the pond if vegetation was left uncleared.

Lack of food probably contributes to the high mortality rate amongst the young of the resident wildfowl population of Borough Fen. In 1972 only three Mallard ducklings survived, and all the cygnets died. Olney (1967) has found in the stomachs of adult Mallard, seeds, aquatic plants, and many of the invertebrate species present in the Decoy pond. An examination was made of the stomacn contents of three Mallard killed at Borough Fen in October 1972 as a contribution to another programme of research. These birds may not have been feeding exclusively at Borough Fen, but the food items found were all present in the pond. Much of the food consisted of 'seeds', predominantly grain scattered on the pond to attract the ducks. However, one stomach contained only about sixty 'seeds' and a large number of insects. These were one land beetle, one larva of *Pericoma*, four larvae of *Ptychoptera*, ten chironomid pupae, and about 300 chironomid larvae.

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I am grateful to the Wildfowl Trust for allowing me to carry out this investigation, and I would like to thank the Decoyman, Mr W. A. Cook, for his help and encouragement.

I am obliged to Dr J. P. Harding for confirming my identification of *Scapholeberis aurita.*

Summary

The invertebrate fauna of the pond, which has existed for over 300 years, is listed. The ecological requirements of the different species are described, and the ways in which they are adapted to the particular conditions of Borough Fen discussed.

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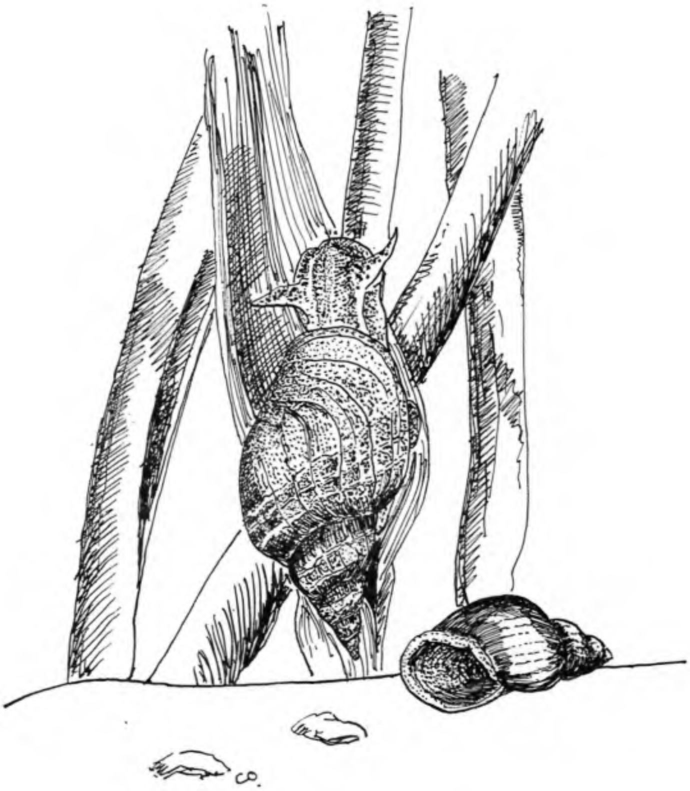

Ten years of intensive late-winter surveys for waterfowl corpses on the north-west shore of the Wash, England

R. E. M. PILCHER, J. V. BEER AND W. A. COOK

Introduction

The exceptional severity of the weather in western Europe during early 1963 lead to many studies of its effect on waterfowl populations. One contribution (Pilcher, 1964) was based on a survey of waterfowl corpses at the end of that cold spell. It was clear that the Shelduck and Redshank* had suffered severe losses, but detailed analysis was not possible because of lack of data on the numbers of waterfowl then frequenting the Wash—a notoriously difficult area to 'count' thoroughly.

Nowadays we have the Birds of Estuaries Survey, jointly organized by the Royal Society for the Protection of Birds, the British Trust for Ornithology and the Wildfowl Trust (see e.g. Prater, 1973) and a much clearer picture is emerging of present populations. The Wash is being especially thoroughly surveyed in connection with proposals for bunded water storage reservoirs along its coast. The effects of a future severe cold spell will therefore be relatively easy to assess. However, data on present-day populations can give but little indication of those passing through or staying in the Wash area during the winter of 1962–1963.

It was therefore decided to repeat the corpse count over the same stretch of coast for 9 more years, until 1972. This 10-year run of data would include the period in which populations severely affected by the cold-induced mortality should recover to normal levels. It would also be long enough to see how other factors such as wind and tides would vary the number of corpses beached in winters of comparable severity.

Since 1969 the Royal Society for the Protection of Birds has been organizing a much more extensive, indeed international, Beached Birds Survey (see e.g. Bibby & Bourne, 1974). However, it was felt desirable to publish our results since, although smaller in scope, our survey was always carried out over exactly the same stretch of coast and by the same personnel. Our findings could therefore have inferences applicable to the wider study, as well as providing connecting data through the period of overlap.

A secondary aim of our study was to collect a sample of corpses fresh enough to allow meaningful post-mortem examinations. From these it was hoped to throw some light on the natural incidence of waterfowl diseases, to compare with that in the captive flocks of the Wildfowl Trust.

Methods

The survey was carried out each year in late February or early March on the first suitable day following the highest tide at that season. The area covered extended from 52°58′N/00°04′E to 53°03′N/00°14′E along the north-west side of the Wash. The search fell into three natural sections: (a) east from Freiston shore to Glebe Farm, Benington (4·0 km); (b) north-east to Sailors' Home, Wrangle (4·8 km); and, in the same direction, (c) to Friskney flats (6·4 km), making a total of 15·2 km of tidal wrack examined.

This wrack consists of vegetable debris such as the heads and stems of grasses, mainly *Agropyron pungens*, sea purslane *Halimione portulacoides*, seaweed *Fucus* spp., and of man-made litter such as plastic containers, bottles, broken netting, packing cases and timber. Sometimes there may be a belt 2 m wide and ½ m deep. Many small birds could have been overlooked in such a mass, but passerines are not dealt with in this report, nor are the homing pigeons *Columba livia*, three Pheasants *Phasianus colchicus* and three Red-legged Partridges *Alectoris rufa* found, since these certainly are not waterfowl.

It was arbitrarily decided that a major portion of a carcase with appendages conconstituted a body, whereas one or both detached wings did not (even when the species was identifiable). Only birds that had died within the past 4 months were included in the body-count, though again some arbitrary decisions were needed.

It was obvious from local knowledge that the tides would carry corpses to the seawall during calm periods or with winds from NNE round to SW; other winds would tend to blow them away. However, the efficiency of the spring tides as transporters of corpses was tested by marking twelve dead birds and

*Scientific names of these and other species dealt with in this paper will be found in Table 2.

dropping three on the exposed mudflats; three on the *Salicornia* fringe; three on the short grass area; and three in the high marsh amongst sea purslane and tall grasses. Three days later after five high tides and north-easterly winds the area was revisited and the high-water wrack searched. None of those from the mud-flats was found, presumably having been eaten by scavenging gulls and crows. But two out of three corpses from each of the other three sites were found again. The figures are small but did indicate that a seawall search would recover a good proportion of the birds dying on the outmarsh.

General deposition of corpses

Over the 10 years a total of 1,443 waterfowl corpses of forty-six species were found along this stretch of coast (Table 1). The yearly totals showed considerable variations, reflecting the different tide and wind conditions. There is, however, some trend for the totals to rise as if the populations were indeed being restored to former levels after the 1963 catastrophe. However, even the highest total, 184 in 1972, was less than a third of the cold year. The very low figure in 1965 was explained by the virtual absence of tidal wrack over long stretches of the seawall. Similar conditions prevailed in 1967, but not in 1968 when there was plenty of wrack but rather few bodies.

Table 1. The incidence of corpses on the survey stretch of coast

Year	Total corpses	Total species	Corpses per km
1963	601	34	39·5
1964	86	21	5·7
1965	27	16	1·8
1966	114	24	7·5
1967	55	16	3·6
1968	52	17	3·4
1969	91	22	6·0
1970	128	24	8·4
1971	105	24	6·9
1972	184	31	12·1
Total	1,443	46	–

In the last 7 years, note was made of which of the three sections contained the most corpses. Section (a) was the most prolific, having 47%, as against 22% in (b) and 31% in (c). Expressed in corpses per kilometre, the respective mean annual values were 12·6, 4·8 and 4·9. Undoubtedly section (a) was so favoured because the saltings are wide (up to 2·5 km) at this southern end, being built up by the turbulence of the converging channels of the rivers Witham and Welland.

Variation between species

The forty-six species found in the course of the 10 years are set out in Table 2. As the numbers of any one species found per year are often small, they have been grouped, after 1963, into two runs, the first of 4 years, 1964–1967, the second run of 5 years, 1968–1972. The year 1963 was clearly exceptional and could not be included with the first run. If there were re-building of populations to be done, this would probably occur within the following 4 years (or even more quickly). The second 5 years should therefore give a long enough run under 'normal' conditions to iron out chance fluctuations and give a reliable base-line for comparison both with 1963 and with any future winter of severity. No such weather occurred during the 10 years of our observations; indeed the period has been characterized by the mildness of the winters.

Clearly, for many species the numbers of corpses found were still too small for any meaningful analysis. Further analysis has therefore been concentrated on the eighteen species for which more than twenty corpses were found in the 10-year period. These are marked with an asterisk in Table 2.

The numbers of corpses of each species found in 1963 may be compared with their mean annual totals for the 5 years 1968–1972 when the populations could be considered to be of 'normal' size. This is done in ratio form in the first column of Table 3. In all but three species the corpse-counts in 1963 were at a considerably higher level than they were in the last 5 years of the study. Because the data are somewhat crude, not too much emphasis should be placed on species in which the 1963 corpse count was two to four times the 'normal', but any species for which it was five times or more was certainly suffering an unusual mortality in the area that year. This, quite conservative, statement holds for half the species so examined.

The species are listed in descending order of magnitude of this 'mortality ratio'. While not too much emphasis should be laid on relative positions within the order, some species were predictably hit (or not hit) by the cold conditions. Thus the Dunlin, at the top of the table, Knot and Redshank are all feeders in the intertidal mudflats which were frozen over during the worst of the cold

Table 2. The species composition, and variation with period, of the corpses found

	Total 1963	Total 1964–1967	Total 1968–1972	Total 1963–1972
*Red-throated Diver *Gavia arctica*	12	8	7	27
*Black-throated Diver *Gavia stellata*	12	4	5	21
Great Crested Grebe *Podiceps cristatus*	9	0	2	11
Red-necked Grebe *Podiceps grisegena*	2	0	0	2
Slavonian Grebe *Podiceps auritus*	0	0	1	1
Fulmar *Fulmarus glacialis*	1	5	8	14
Gannet *Sula bassana*	1	2	2	5
Cormorant *Phalacrocorax carbo*	0	0	3	3
Shag *Phalacrocorax aristotelis*	0	1	1	2
Heron *Ardea cinerea*	2	0	1	3
Mute Swan *Cygnus olor*	1	0	2	3
Pink-footed Goose *Anser brachyrhynchus*	2	3	7	12
Canada Goose *Branta canadensis*	0	0	1	1
*Brent Goose *Branta bernicla*	12	12	21	45
*Shelduck *Tadorna tadorna*	58	7	38	103
*Mallard *Anas platyrhynchos*	7	5	15	27
Teal *Anas crecca*	1	0	3	4
*Wigeon *Anas penelope*	35	8	21	64
Tufted Duck *Aythya fuligula*	2	0	0	2
Scaup *Aythya marila*	0	1	1	2
Eider *Somateria mollissima*	0	2	2	4
Common Scoter *Melanitta nigra*	10	1	7	18
Goldeneye *Bucephala clangula*	0	0	2	2
Red-breasted Merganser *Mergus serrator*	1	1	0	2
Water Rail *Rallus aquaticus*	1	0	0	1
Moorhen *Gallinula chloropus*	2	0	0	2
Coot *Fulica atra*	0	1	0	1
*Oystercatcher *Haematopus ostralegus*	1	5	29	35
Golden Plover *Pluvialis apricaria*	0	4	3	7
Grey Plover *Pluvialis squatarola*	7	2	0	9
Lapwing *Vanellus vanellus*	2	7	4	13
*Knot *Calidris canutus*	104	34	53	191
*Dunlin *Calidris alpina*	33	23	13	69
Bar-tailed Godwit *Limosa lapponica*	2	5	8	15
*Curlew *Numenius arquata*	15	15	18	48
*Redshank *Tringa totanus*	144	9	113	266
Turnstone *Arenaria interpres*	0	2	3	5
*Black-headed Gull *Larus ridibundus*	26	40	41	107
*Common Gull *Larus canus*	51	34	60	145
*Herring Gull *Larus argentatus*	8	12	17	37
*Great Black-backed Gull *Larus marinus*	6	11	11	28
*Kittiwake *Rissa tridactyla*	9	9	9	27
*Guillemot *Uria aalge*	19	3	9	31
*Razorbill *Alca torda*	3	5	15	23
Little Auk *Alle alle*	0	0	1	1
Puffin *Fratercula arctica*	0	1	3	4
Totals	601	282	560	1,443

period. So too are Shelduck. However, the Oystercatchers were unaffected and the Brent Geese much less than expected in view of their rigid intertidal feeding habits. Wigeon, on the other hand, suffered severely even though they quite usually will move inland to graze winter cereals or grass fields when intertidal plants, *Zostera* and *Enteromorpha*, are not available. Again, several off-shore feeders, whose food supply should not have been rendered inaccessible or otherwise affected, apparently had high mortalities, namely Black-throated Divers, Guillemot and Red-throated Divers. Thus other factors must have been affecting the level of the kill than simple food deprivation on a relatively local basis.

Table 3. Comparison between the incidence of corpses when populations were 'normal' (1968–1972) with that in 1963 and in the 4 succeeding years (1964–1967)

Species	Ratio 1963 to mean 1968–1972	Ratio mean 1964–1967 to mean 1968–1972
Dunlin	12·7	0·5
Black-throated Diver	12·0	1·0
Guillemot	10·5	2·6
Knot	9·8	1·3
Red-throated Diver	8·5	0·7
Wigeon	8·3	2·2
Shelduck	7·6	4·2
Redshank	6·3	10·3
Kittiwake	5·0	0·8
Common Gull	4·2	1·4
Curlew	4·2	1·0
Black-headed Gull	3·2	0·8
Brent Goose	2·8	1·4
Great Black-backed Gull	2·7	0·6
Herring Gull	2·3	1·1
Mallard	1·4	4·2
Razorbill	1·0	2·5
Oystercatcher	0·2	4·6

Effect on the total population

A large number of corpses in the Wash area might simply reflect unusually large numbers of immigrants there, driven (and presumably already weakened) by harsh conditions further to the north and east. Similarly the virtual absence of Oystercatcher corpses might mean that the bulk of these birds had moved on further south and west, escaping the vicious conditions in East Anglia. By the same token, the birds actually dying on the Wash coast might not have been ones which normally would have wintered there. However, none of the corpses found had rings on their legs to indicate their geographical origins. Nor, as we indicated earlier, have we any idea of the size of populations from which the birds were drawn, and hence of the significance of the undoubtedly increased mortality in 1963.

We can make a stab at assessing the significance by comparing the level of corpse-incidence if the years immediately following the hard winter (1964–1967) with that in the years when the populations may be considered to have recovered to a 'normal' level, i.e. 1968–1972. This is done in the second column of Table 3. Of course, we have to discount any factors that may have *raised* the 1968–1972 populations (and corpse-counts) to an unusually high level and so made the 1964–1967 counts appear abnormally low. But in the absence of evidence to this effect the argument can be used as it stands.

If the ratio 1964–1967:1968–1972 was close to 1·0, then one can argue that the population level following the hard winter was little different from normal, i.e. natural replacements had rapidly offset the casualties and hard-weather mortality had been of little significance. If the ratio was considerably above 1·0 then the casualties had a more severe and lasting effect. Again, because of the crudity of the data, and because natural populations fluctuate quite widely in any case, only substantial values should be stressed. Thus the heavy mortality suffered by Redshank would appear to have given their population(s) a severe set-back. But the only others affected for a long time would seem to be the Oystercatchers, Mallard and the Shelduck; the first two thus did not escape the consequences by leaving the area. The Guillemot, Razorbill and Wigeon also have been affected to a lesser extent.

In summary, our data indicate that only the Shelduck and the Redshank suffered *both* abnormally high mortality in 1963 *and* a depression in their populations which extended over several years. In the case of the former we have the supporting data of the National Wildfowl Counts, organized since 1954 by G. L. Atkinson-Willes of the Wildfowl Trust. The circulated reports of the monthly winter counts on priority sites indicate that February 1963 had a United Kingdom population index for Shelduck of 148 (based on 1959 = 100), but in February 1964 it had fallen back to 98. It was not until 1967 that it was back to 140 and it maintained a mean of 150 over 1968 to 1972. This result, incidentally, is also justification for our division of data into two groups of years, the recovery period and the period of 'normal' population, used in the earlier analysis.

Comparison with data of the Beached Bird Survey

In the 5 years 1968–1969 to 1972–1973 a much more extensive survey has been made, organized by the RSPB. Thus in NW Europe in 1973 a total of 3,317 km were searched, producing 3,651 corpses (Bibby & Bourne, 1974). For East Anglia, which gives the most meaningful comparison for our data, the length of coast searched varied from 131 km (1969) to 296 km (1972) and the corpses found from seventy-nine (1973) to 162 (1971). This was for the same late winter periods of high tides towards the end of February or early in March. When the corpses/kilometre figures (Table 4) are compared with the same index for our survey (Table 1), it is apparent that the latter were very much higher; seven, twelve, ten and twenty-four in the 4 years of overlapping data.

Table 4. Data from the RSPB Beached Bird Survey: East Anglia only

Year	Corpses/km	Percentage oiled
1969	0·9	95
1970	0·7	73
1971	0·7	30
1972	0·5	69
1973	0·3	53

Such large differences cannot result from different assessments as to what constitutes a corpse. There may well have been differences in the degree of thoroughness of search. But probably our section of coast is particularly favoured by wind, tide and topography. Similar densities of corpses in the Beached Bird Survey were reported from, for example, SW Denmark. It would seem to emphasize that, as in many other biological surveys, if long term information is required, then it is best to concentrate intensive effort within circumscribed, favoured areas that produce a reasonable supply of data for effort expended. This is not to say that extensive surveys are not justified every so often, both to pinpoint the favoured areas initially and to check that they are continuing to provide data representative of the whole.

Aside from the immense difference in concentration of corpses, the two surveys agree that the level of mortality was similar in 1969, 1970 and 1971. Only in 1972 was there a radical difference, our data indicating a sharp up-turn, the Beached Bird Survey a decrease. There appears no obvious reason for this discrepancy.

The extent of oil pollution

One of the main aims of the Beached Bird Survey was to provide an indicator of the extent to which oil-pollution was still a factor of seabird mortality, despite restrictive measures imposed by various international conventions. Table 4 therefore includes data on the percentage of birds found oiled, around two-thirds. Of course this may well be an underestimate, since many species are not particularly at risk to oil pollution, or may be polluted subsequent to death from other causes. We preferred to concentrate on the species which, by feeding in the open sea, are especially prone to direct, mortal pollution by oil patches. These were, in Table 1, Black-throated Diver, Red-throated Diver, Common Scoter, Common Eider, Razorbill and Guillemot. Over the 10-year period these gave 124 corpses, but in thirty cases decomposition was too far advanced for a positive opinion to be expressed as to whether oil pollution had been sufficiently extensive to contribute to death.

In the 4 overlapping years, 1969–1972, 69% of twenty-six corpses were definitely oil-polluted. In the previous 5 years 82% or twenty-two. This may give some hope of a reduction of pollution in recent years, but certainly the data are too slender to rest much of a case on them. More interestingly, in the year of the big kill, 1963, the oiling incidence was slightly lower, 76% of forty-six. Thus, oiling mortality can at least be said not to have had an unusual incidence because of the cold-weakened condition of the birds. Oiling is generally sufficiently destructive in its own right, without help from nature.

Other causes of mortality

It proved possible to find only 115 bodies on which post-mortem examinations could reasonably be carried out. No diagnosis was possible in twelve cases. Twenty-four of the remaining 103 had been killed by gun-shot wounds, nine others died of injuries not attributable to shooting, and two were drowned.

In the remaining sixty-eight the pathological conditions found (sometimes more than one in the same bird) were, in descending order of importance: pneumonia (37), nephritis (11), pulmonary congestion (9), enteritis and tuberculosis (7 of each), internal parasites (6), hepatitis (4), aspergillosis (3), pericarditis, atherosclerosis, peritonitis, visceral gout, and lead poisoning (2 of each), and single cases of anaemia, splenomegaly, and bacterial infection.

Clearly pneumonia, brought on by the extreme cold conditions, was of the greatest importance. But it may often have precipitated death in an already sick bird.

Avian tuberculosis was found in one Oystercatcher (of five examined), in four Knot (of nineteen), in one Lesser Black-backed Gull (of three) and in one Dark-bellied Brent Goose (of seven). Aspergillosis was found in one Common Gull (of nine), one Red-throated Diver (of ten) and in one Dark-bellied Brent Goose.

While these findings are of some interest, it must be admitted that the pathological aspects of the survey were disappointing. This was largely because scavengers had all too frequently been at the corpses before they were found, leaving little but skin, feathers and bone.

Acknowledgment

We wish to record our gratitude to Professor G. V. T. Matthews whose advice has been of the greatest assistance in the construction of this paper.

Summary

A stretch of coast was searched for corpses late in the winter of 10 years. The results enable an assessment of the significance of waterfowl mortality in the extremely hard winter of 1962–1963. Only Shelduck *Tadorna tadorna* and Redshank *Tringa totanus* suffered mortality high enough markedly to depress their populations over several years. Comparisons are made with the results of other similar corpse surveys. The extent of oil pollution was measured and some information on the incidence of pathological conditions obtained.

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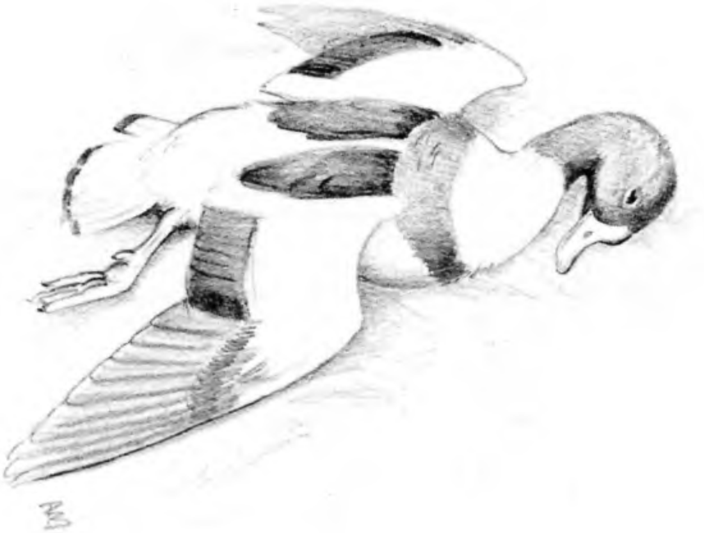

The taxonomy and relationships of the northern swans

PAUL A. JOHNSGARD

The recent (1972) publication of the Wildfowl Trust's book *The Swans* has brought together an unprecedented array of information on all of the swans of the world, and makes it desirable to raise once again the question: how many species of northern swans are there, and what are their evolutionary relationships to one another? Delacour (1954) suggested the comprehensive vernacular name 'northern swans' to distinguish 'the various knobless white swans which breed in or near the Arctic parts of the northern hemisphere' from the Mute Swan (*Cygnus olor*) and the three southern hemisphere swans. The northern swans have generally (e.g. Stejneger, 1882; Wetmore, 1951; Vaurie, 1965) been regarded as constituting four separate species, although as early as 1832 Yarrell questioned whether the smaller North American (Whistling) swan should be regarded as specifically distinct from the comparable Eurasian (Bewick's) swan. Yarrell's observations on the Trumpeter Swan's tracheal anatomy did convince him that it should be regarded as a species distinct from both the Whooper Swan and from the two smaller northern swans. Later investigators who argued for the merger of the Whistling and Bewick's Swan, as well as for conspecificity of the Trumpeter and Whooper Swan, include Hartert (1920), Delacour & Mayr (1954), and Mayr & Short (1970). Thus, two different taxonomic approaches to the group have gradually emerged as shown in Table 1.

A fifth described form, *jankowskii*, is now believed to be invalid (Vaurie, 1965), as is a supposed Islandic race (*islandicus*) of the Whooper Swan.

Two major taxonomic questions are present. First, how many species of northern swans should be recognized in order best to illustrate their probable degree of phyletic distinction, and second, if fewer than four are to be recognized, what forms should be merged with what other forms?

The general criterion of species distinction in higher animals is that of reproductive isolation under natural conditions—i.e., failure to hybridize in nature. This criterion may be readily applied when the populations concerned have sympatric breeding areas, but becomes hypothetical when their breeding areas are allopatric. Contact in wintering areas may be insignificant if pairs are formed during migration or on breeding grounds and, once formed, are permanent.

Obviously the two North American populations are geographically isolated from the Eurasian ones, but what if any breeding sympatry occurs between the larger and smaller forms found on each continent? In North America, sympatry between the Whistling Swan and Trumpeter Swan is essentially absent, with one possible exception. Hansen *et al.* (1971) state that the breeding range of the Trumpeter Swan in western Alaska extends out into the tundra, which represents the typical breeding habitat of the Whistling Swan. However, the breeding contact between these two forms must at most be marginal, as indicated by King (1973). The wintering areas of the two North American populations are likewise almost wholly separate, with the only area of probable contact being the coastal region of British Columbia and Washington (cf. *The Swans*, pp. 42 and 46).

In Eurasia the situation is similar. The breeding ranges of the Bewick's Swan and Whooper Swan are almost entirely complementary (cf. *The Swans*, pp. 43 and 48; Dementiev & Gladkov, 1967). In a manner comparable to the situation in North America, the Bewick's Swan is limited to Arctic tundra breeding habitat, while the Whooper Swan occurs to the south in the forested zone, extending only locally into

Table 1. Two taxonomic approaches

	'Splitter' approach	*'Lumper' approach*
Whooper Swan	*Cygnus cygnus*	*Cygnus c. cygnus*
Trumpeter Swan	*Cygnus buccinator*	*Cygnus c. buccinator*
Whistling Swan	*Cygnus columbianus*	*Cygnus columbianus columbianus*
Bewick's Swan	*Cygnus bewickii*	*Cygnus columbianus bewickii*

tundra (Dementiev & Gladkov, 1967) or into willow scrub (Vaurie, 1965). Vaurie suggests that the ranges of the two may be in limited contact along river valleys south of the tundra limits, as for example the Yenisei at about 68° Latitude. The wintering ranges of the Bewick's and Whooper Swans overlap to a much greater degree than do those of the Trumpeter and Whistling Swans.

Thus, in general the breeding ranges of these forms show the complementary pattern typical of ecological races adapted to different habitats. Wild hybrids are not known, but overlapping mensural characters for nearly all traits would make such hybrids virtually impossible to recognize. In captivity no fewer than four of the six possible hybrid combinations among the four forms have been reported; at least one of these combinations (Whistling x Whooper) was 'probably fertile' (Gray, 1958).

Since the lack of definite breeding ground sympatry fails to provide an answer relative to reproductive isolation, one must look to specific anatomical or behavioural traits that might indicate levels of distinctness. These can be considered sequentially under the general headings of mensural characteristics (weights and measurements), colouration of bill and soft parts, voice and tracheal characteristics, and behavioural traits.

The four northern swans form a progressive series from small to large in the sequence Bewick's–Whistling–Whooper–Trumpeter. This series is contrary to Bergmann's rule and, like various populations of *Branta* and *Anser*, is evidently related to decreasing size (and associated decreasing periods of fledging) as an adaptation to arctic breeding. This association between breeding latitude and times to fledging has already been mentioned by Janet Kear (in *The Swans*, pp. 117–118).

Weights of adults generally exhibit some overlap in sample extremes, although average weights show a progressive series in each sex. A comparison of average adult weights (data from *The Swans*, p. 198) and average wing chord measurements (pp. 199–200) indicates that the Bewick's and Whistling Swans are very similar, as are the Whooper and Trumpeter Swans (Figure 1). According to Banko (1960, p. 64), there is a 2–3 lb overlap in minimum Trumpeter Swan and maximum Whistling Swan weights among females, while those of immature and adult males apparently to not overlap. Weight data in *The Swans* also indicate weight overlaps for Whistling and Trumpeter Swans but not for Whooper and Bewick's Swans.

Most authorities (e.g., Stejneger, 1882; Banko, 1960; Hansen *et al.*, 1971) suggest that the bill length, and especially the relative position of the nostrils, is the most useful criterion for separating the larger pair of swan taxa from their smaller counterparts. The smaller swans not only have shorter and slightly more concave culmens, but also their nostrils are located relatively closer to the tip of the bill. This relationship may be seen in a diagram (Figure 2) that plots the distance from the bill-tip to the anterior edge of the nostril, relative to the distance from the tip of the bill to the anterior edge of the eye (data from Stejneger, 1882). These plotted points also indicate a progressive variation, with most of the forms exhibiting consider-

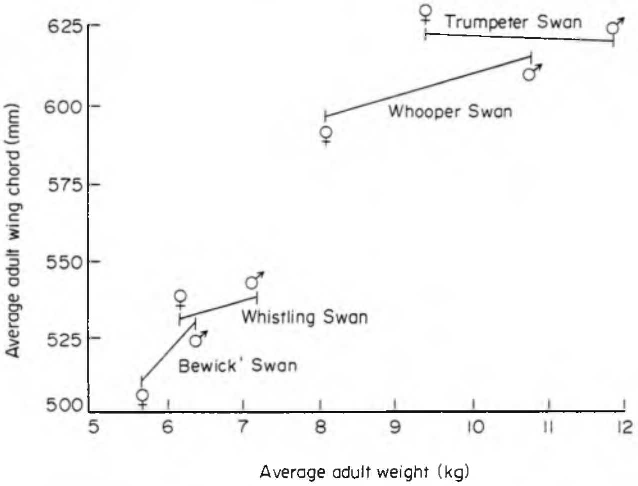

Figure 1. The relation between the average adult weight and average adult wing chord length in the four northern swans, as reported in *The Swans.*

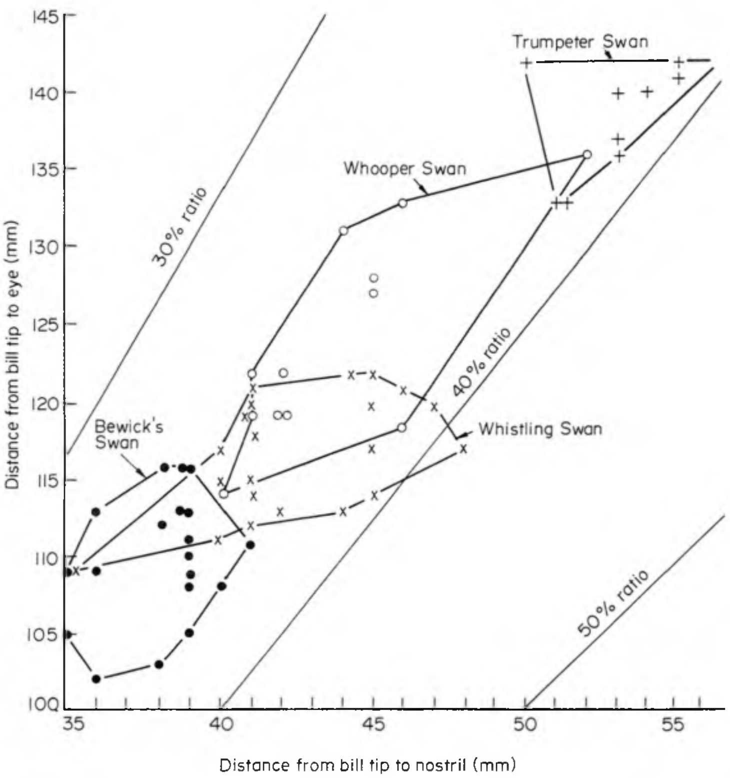

Figure 2. The relation between the distance from the bill-tip to the eye and the relative position of the nostril in adults (both sexes) of the four northern swans. Data from Stejneger (1882).

able overlap in this pair of measurements. It may be seen that, with increasing overall bill size, the distal part of the bill beyond the nostrils tends to become relatively longer than the proximal part. Hansen *et al.* (1971) observed that this same general relationship (body weight *v.* nostril-to-nail length) held for their sample of male Trumpeter Swans, but not for females. A similar progression of bill length relative to body size can be seen in these swans (Figure 3) and in various races of geese (e.g. *Anser fabalis, Branta canadensis,* etc.), and is clearly the result of allometric growth effects rather than the result of qualitative differences among the populations. Likewise, Boyd's comment (p. 22 of *The Swans*) that the most effective means of distinguishing Bewick's from Whooper Swans or Whistling from Trumpeter Swans is in their actual and relative neck lengths doubtless has the same explanation.

The colouration of the bill and soft parts is also deserving of mention. The standard 'field-guide' difference between Whistling and Trumpeter Swans is the presence of a yellow loreal mark on the former and its absence on the latter. The low reliability of this feature has been mentioned by Banko (1960) and by Hansen *et al.* (1971). Banko also noted that the presence of a reddish 'grinning streak' on the lower mandible is not limited to Trumpeter Swans. Tate (1966) reported that 30% of fifty-five adult-plumaged Whistling Swans she examined in California lacked the loreal mark, and that a pinkish or reddish colour was present on the lower mandible of all the Whistling Swans she examined. In the Bewick's and Whooper Swans the variable extension of yellow (below and beyond the nostrils in the Whooper) has been recognized as a useful fieldmark ever since Stejneger mentioned it in 1882. The enormous individual variation in this patterning among Bewick's Swans is now evident on the basis of the Wildfowl Trust's observations, but it does appear to provide a functional fieldmark separation of the two Old World forms. Yet few, if any, taxonomists would argue that it constitutes a species character, since logic would dictate that the two forms in greatest contact with one another should be the most dissimilar in their bill colouration, when the reverse is actually true. Lastly it might be mentioned

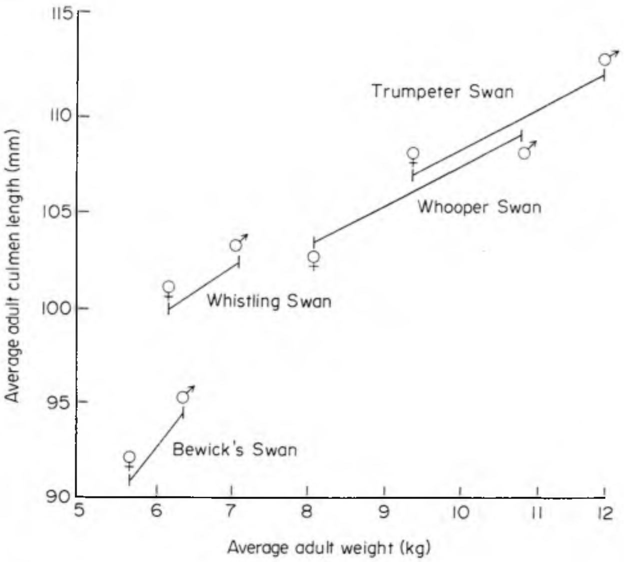

Figure 3. The relation between the average adult weight and the average adult culmen length for the four northern swans, as reported in *The Swans*.

that, contrary to Kortright (1943), the bill and foot colours of downy young and juvenile swans are virtually identical among the four forms (cf. p. 23 of *The Swans* and plate III of Delacour, 1954). Feathering on the foreheads of the downy young of the smaller swans is less extensive than in the larger ones, and as the birds mature the feather line on the forehead variably retracts. Stejneger (1882) mentioned that the Whistling Swan usually develops a pointed forehead line, while the Trumpeter Swan tends toward a rounded one, although he admitted seeing exceptions. Tate (1966) suggested that Whistling Swans might be recognized by their sparsely feathered brow-line, as opposed to the more continuously feathered brow of Trumpeter Swans. I have observed numerous exceptions to this, and believe that individual differences in exposure to abrasion probably account for these variations. Likewise, the number of tail feathers has long been recognized (Stejneger, 1882) as an unreliable and individually variable trait.

The voice and associated tracheal differences in these swans cannot be denied, and indeed is the basis for the vernacular name of three of the four populations. Yarrell (1832) initially recognized that the adult Trumpeter Swan has a unique dorsal protrusion of the sternum associated with a tracheal loop, and this feature has subsequently become the standard criterion for this form's identification. The other three swans also have extensive tracheal penetration of the sternum in a manner that is evidently progressive with age, and thus there is much individual variation in this trait (Schiøler, 1925; Tate, 1968). The dorsal projection of the Trumpeter Swan's trachea does appear to be constant, but Richard Banks (*in litt.*, 5 March, 1974) reported seeing two National Museum specimens of the Whistling Swan that show a slight dorsal bend in the trachea, forming a *buccinator*-like loop. He did not rule out the possibility that this was an artifact of drying. The possible resonating or other functions of the tracheal elongation achieved by sternal penetration are still being debated, but it is clear that the vocalizations of the four populations are qualitatively very similar, differing only in their fundamental frequencies and relative harmonic development (Johnsgard, 1972). As shown in Figure 4, the fundamental frequency differences show a progressive relation to body size and presumably also to tracheal length, although data are not yet available to test the predicted relationship between tracheal length and possible frequency modulation.

In terms of social behaviour patterns and displays, the four populations are extremely similar. All utilize a wing-waving triumph ceremony that is quite distinct from that of the Mute Swan, and all have virtually identical precopulatory and postcopulatory displays (Johnsgard, 1965; Kear, p. 83, in *The Swans*). Again, one might argue that on the basis of needs for reproductive isolation some differences in these patterns might have

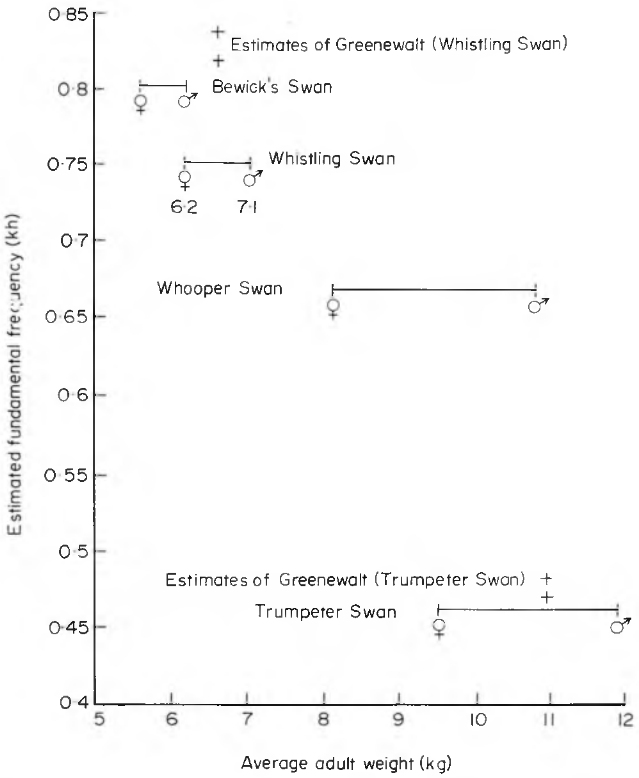

Figure 4. The relation between the average adult weight (as reported in *The Swans*) and the fundamental frequency of adult calls (sex unknown) for the four northern swans, as estimated by Johnsgard (1971) and Greenewalt (1968).

evolved if speciation between the geographically interacting populations had been completed.

In summary, the various anatomical and behavioural traits of these four populations tend to differ only in predictable quantitative ways that are associated with overall size differences, and these in turn are probably the result of ecological adaptation to differing habitats and breeding phenologies. Some of the criteria described above favour association of the two larger forms and the two smaller ones (e.g. wing chord and body weights), while others (such as degree of bill pigmentation) suggest affiliation between the two North American forms and the Eurasian ones. Yet others suggest a graded series without definite breaks. None, however, can be used to argue strongly that any single form is specifically distinct from any of the others. How then is the phylogeny of the members of this group to be explained and what is the most practical way of dealing with their taxonomy?

To account for the evolution of these four extant populations, one must accept one or the other of two general hypotheses. The first of these is to assume that a single ancestral northern swan was initially separated into arctic-tundra and temperate-zone breeding populations, either in North America or Eurasia. Each of these populations must then have spread out into comparable habitats of the other hemisphere. This would have been readily achieved in the case of the tundra-breeding populations where virtually no barriers to transhemispheric movements once existed, but is much more difficult to imagine for the temperate-latitude forms now represented by the Trumpeter and Whooper Swans. Ploeger (1971) believed that the Whistling and Bewick's Swans' ancestors had a circumpolar distribution prior to the Last Glacial, but were subsequently geographically isolated by glaciation, and have remained so until the present. Such an interpretation would favour the view that the Whistling and Bewick's Swans might best be considered subspecific replacement forms, and that the Trumpeter and Whooper Swans are less closely related to them than to one another, and also should be considered conspecific.

The second possibility is that a single northern hemisphere ancestral swan was initially split into Eurasian and North American components, each of which subsequently developed two populations, a larger form ecologically adapted to nesting in marshes or lakes of temperate grasslands or forests, and a smaller one adapted to breeding on arctic tundra. Presumably the boreal forest provided the initial barrier to their gene pools, but this habitat has been gradually colonized by the more southern populations and has resulted in limited secondary contact to timberline. Such a hypothesis would help to account for the similarities of bill pigmentation in the Old World and New World pairs of forms, and is also supported by parasitological evidence in the form of mallophagan similarities in the swan populations of the same hemisphere (Timmermann, 1964).

If one favours the first argument, then the 'lumper' taxonomy of Delacour & Mayr (1945), as shown in the beginning of this paper, might be the most logical one to follow. However, the second hypothesis would suggest either the recognition of a single Old World species (*cygnus* having priority over *bewickii*) and a New World species (*columbianus* having priority over *buccinator*), or even the more radical view that, inasmuch as geographic isolation prevents a test of reproductive isolation, only a single polytypic species should be recognized. I would support the latter position, and suggest the following technical and vernacular nomenclature:

Cygnus cygnus: Northern Swan
Cygnus cygnus cygnus (L.) 1758. Northern Whooper Swan
Cygnus cygnus columbianus (Ord) 1815. Northern Whistling Swan
Cygnus cygnus bewickii (Yarrell) 1830. Northern Bewick's Swan
Cygnus cygnus buccinator (Richardson) 1831. Northern Trumpeter Swan

This position would allow for acceptance of either of the speciation models described above. It would also emphasize the close anatomical relationships of all of the forms, rather than imply that we know more about the group's phylogeny than is actually the case. If this approach is unacceptable, then a retention of the 'splitter' approach of retaining four separate species would seem to be the most satisfactory interim solution.

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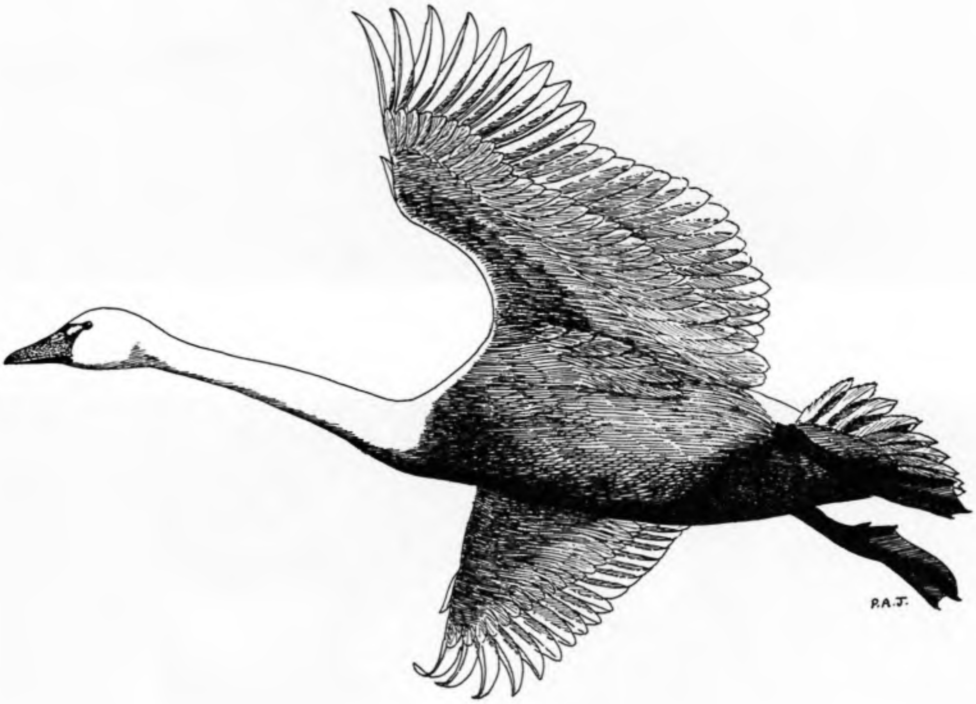
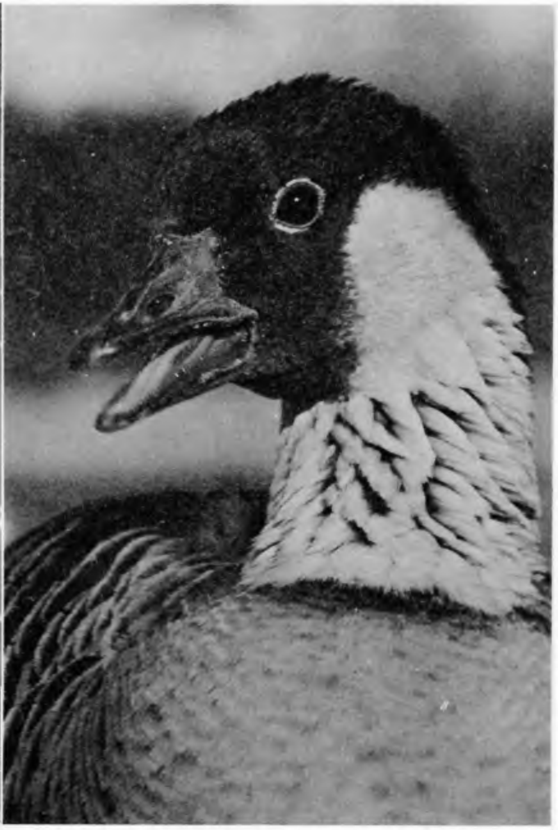


J. Blossom



J. Blossom

Four portrait studies at Slimbridge

J. Blossom

J. Blossom

Research

The Wildfowl Trust's contribution in 1973

The thirty-eight research publications by staff and by those using Trust material and facilities are listed on p. 174.

A complete aerial survey was made of the Greenland population of Barnacle Geese wintering in Scotland and Ireland, while the Spitsbergen population was investigated by a Trust expedition to their breeding grounds (p. 102) and at their Solway winter quarters. Other long-term censuses, counts and ringing of wildfowl continued and are detailed below. Steps were taken towards computer-based methods of analysis of the data. Considerable success was achieved in the new programme of marking Brent Geese to study their dispersal from Foulness, in relation to the Third London Airport plans.

The feeding ecology of geese was further investigated, including the use of experimental grassland management techniques. The long-term studies of Bewick's Swans at Slimbridge, and at Welney, continued. The breeding behaviour of a pair at Slimbridge was closely studied. So was that of a group of White-headed Ducks (p. 56). Exciting new ecological and physiological projects as joint ventures were initiated with Bath, Bristol and Cardiff Universities and with the Royal Aeronautical Establishment, Farnborough. The health of the Trust's collections was again monitored through postmortem examinations and by the development of hygienic techniques and methods of disease prevention.

Wildfowl censuses and counts in Britain and Ireland, 1973–1974

Goose censuses

Arctic breeding populations of geese are subject to considerable annual variations in breeding success. The weather on the breeding grounds, either before laying or during the breeding cycle, plays a large part. The summer of 1973 was clearly a very good one in Iceland and Arctic Russia, but only about average in West and East Greenland and in Svalbard.

Pink-footed Goose *Anser brachyrhynchus*. The annual census was held over the weekend 3–4 November 1973 when 82,000 birds were counted. This is an increase of 9,000 over the previous year which is due to the much better than average breeding success with 29·9% young birds and a mean brood size of 2·35.

European White-fronted Goose *Answer albifrons albifrons*. The peak numbers in Britain came in the second half of January when about 8,000 were counted. This was low considering the very good breeding success for the second year running (44% young birds, mean brood size 2·9). The mildness of the winter will have allowed more birds to remain on the continent.

Greenland White-fronted Goose *Anser albifrons flavirostris*. Breeding success was a little better than the previous 2 years with 15·1% young birds and 2·8 average brood size, and flock size at the main haunts was about normal.

Greylag Goose *Anser anser*. 76,000 Greylags were counted at the annual census held over the weekend of 3–4 November 1973. This is an increase of 8,000 over 1972 which is a result of the best breeding season for 11 years (30·2% young, mean brood size 2·56).

Barnacle Goose *Branta leucopsis*. The count on the Solway wintering grounds of the Svalbard breeding population reached a new record peak of 5,100. Breeding success was moderately good with 21% young birds, but the brood size was low at 1·5. There was no census of the Greenland breeding population this winter but counts on the main haunt of Islay showed a further slight increase to 18,300. Breeding success was about average at 17·4% young, mean brood size 2·5.

Light-bellied Brent Goose *Branta bernicla hrota*. The highest count at Lindisfarne, Northumberland, the only British wintering place of the Svalbard breeding population, was 470. A census of the Greenland/Canada population wintering in Ireland was held in November and 16,000 were counted.

Dark-bellied Brent Goose *Branta bernicla bernicla.* The second successive excellent breeding season (41% young) raised the peak count in Britain to a new record of 41,000 in mid-December.

M.A.O.

Duck counts

Mallard *Anas platyrhynchos.* There was a slight increase in number over last year, but the high figures of the late sixties have still not been repeated.

Teal *Anas crecca.* The seasonal index was the highest since the early sixties, indicating a sudden influx similar to that which occurred then. This latest upsurge has been reflected most strikingly on the Mersey, which had a peak count of 9,580 in January. This estuary held exceptional numbers of Teal last year as well, but the peak this year was slightly earlier. A big increase on the Ouse Washes in March balanced the fall off in numbers on the Mersey.

Wigeon *Anas penelope.* The seasonal index was easily the highest ever, several sites, notably the Mersey, recorded much higher numbers than usual. Over 30,000 were still present on the Ouse Washes in March, when only 9,000 were counted last year.

Pochard *Aythya ferina.* As with Wigeon, the seasonal index is by far the highest ever. Although several other sites often hold very large numbers, the key to the Pochard index is held by the most important site, Duddingston Loch, Edinburgh. On the February 1973 count day the loch was frozen over and no Pochard were present, whereas the February 1974 count reach 8,000, thus greatly inflating the index.

Tufted Duck *Aythya fuligula.* The high level of recent years was continued with several sites holding over 1,000 at some time during the winter.

Shelduck *Tadorna tadorna.* This year's seasonal index was the highest ever. The comparatively few major sites seem on the whole to be maintaining or increasing their numbers.

Seasonal indices 1973–1974
(1959–1960 = 100)

Mallard	93	Pochard	261
Teal	96	Tufted Duck	125
Wigeon	157	Shelduck	148

International Wildfowl Census 1973–1974
The eighth census was held in mid-November 1973 and mid-January 1974.

G. L. Atkinson-Willes
D. G. Salmon

Wildfowl ringing in Britain, 1973

The total numbers of ducks ringed (see Table) was slightly up on the previous year, but yet again mild weather in autumn and early winter meant that the duck decoys did not realize their full potential. However, Borough Fen was back in form and the catch at nearby Deeping Lake was nearly half as large again as in 1972. Nacton and Abberton gave the mixture as before. Caerlaverock began its development as a ringing station. Subsidiary use was made of the trapping stations for research on orientation, measurements and heavy metal contamination of the environment.

Table. Ducks ringed by the Wildfowl Trust, 1973

	Abberton	Nacton	Borough Fen	Deeping Lake	Slimbridge	Caerlaverock	Others	Totals
Shelduck	1						2	3
Pintail	84	139		7				230
Teal	400	114	383	17		3		917
Mallard	1,310	658	883	600	31	44	9	3,535
Gadwall	47	2		10				59
Wigeon	46	181	1	10		1		239
Garganey	9			1				10
Shoveler	42	28		3			10	83
Pochard	44			19			2	65
Tufted Duck	278	1		232				511
Red-breasted Merganser				1				1
Totals	2,261	1,123	1,267	900	31	48	23	5,653

Brent Geese were marked in large numbers, 243, for the first time. Engraved plastic rings proved very successful for their individual identification in the field. These rings were again used on the Bewick's Swans, seventy-eight, caught at Slimbridge, where more than half those marked were in the most valuable, known-age, category. Colonially-breeding Mute Swans, thirty-three, were ringed in Dorset.

M.A.O.

Education

The Wildfowl Trust's contribution in 1973

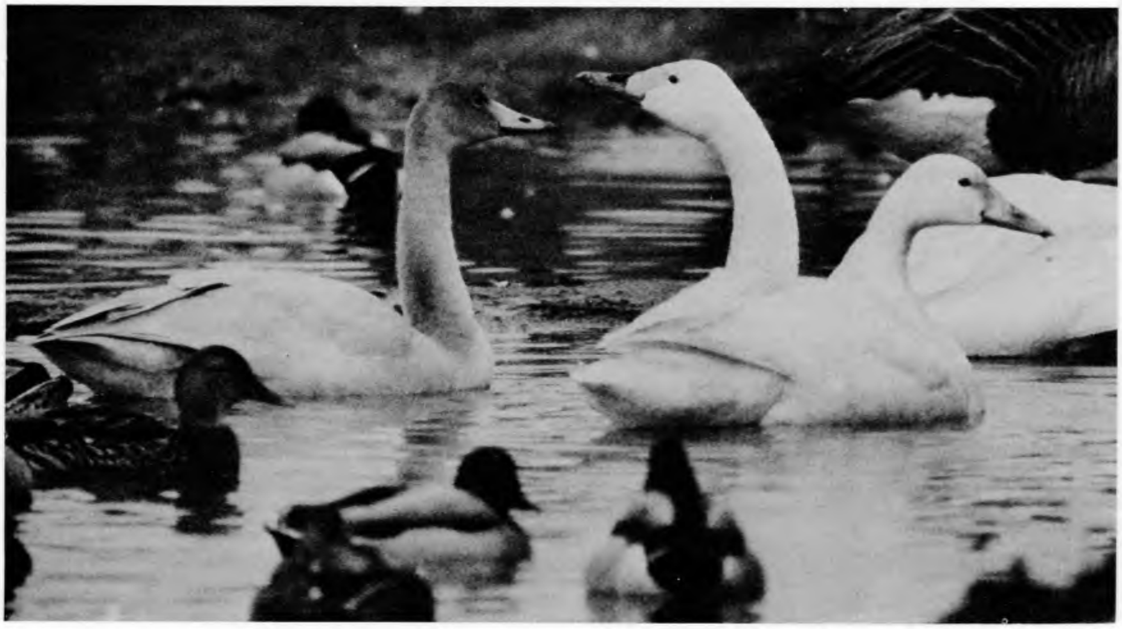
There was a major expansion of the Trust's Education Department in 1973. Mr E. E. Jackson became Chief Education Officer in overall charge of the education department at all Trust centres, and Mr J. Blossom joined the staff at Slimbridge as Education Officer. An Education Advisory Committee was formed during the year and met for the first time at Slimbridge in December. The number of schools using the educational facilities at Slimbridge again increased and over 26,000 children from about 800 schools visited the centre for tuition. The Field Study Courses based on the Slimbridge Youth Hostel became even more popular, and five special courses were run for members of the Young Ornithologists' Club.

Series of lectures were given to the zoology and psychology departments of Bristol and Cardiff Universities by Professor Matthews and Dr Kear. External lectures were given to a large number of natural history and educational organizations. Several displays were also mounted. The annual schools competition was held at Slimbridge in March.

Major new projects undertaken during the year included a completely new Guide Book for Slimbridge and Peakirk, the design and development of a new labelling system for Trust collections, and the start of a new film to replace the highly successful, but now outdated, *Wild Wings*.

E. E. Jackson

'Needham' with his two cygnets, one normal, the other white (see p. 167) *Mary Evans*



Conservation

The Wildfowl Trust's contribution in 1973

Activities at the Trust's own Refuges at Slimbridge, Welney and Caerlaverock are recorded in the following pages. The practical knowledge derived from research was also applied to the wild areas at the developing new centres at Martin Mere, Lancashire, at Washington, Durham, and at Arundel, Sussex. Interventions were made to safeguard the ecology of a number of wetland sites in Britain threatened by various forms of development. Close liason was maintained with the other conservation bodies, official and voluntary, in these matters. The United Kingdom became the third signatory of the Ramsar Convention on the Conservation of Wetlands, and the principle of compensatory reserves for wetlands lost to development was written into a Parliamentary Bill.

The International Waterfowl Research Bureau headquarters remained at Slimbridge and there was participation in Symposia in Belgium and Poland. A 3-day international symposium on Flamingos was organized at Slimbridge and the proceedings will appear in book form. Advisory visits were made, at the invitation of the Governments concerned, to Iran and the Soviet Union. A behavioural study of the Pink-footed Goose in Thjorsarver, Iceland, was assisted. The situation of the Red-breasted Geese in Romania was investigated by a Trust team.

Slimbridge: the wild geese 1973–1974

European White-fronted Geese *Anser albifrons albifrons*
The first arrivals were eleven on 27 September. Numbers built up slowly and there were still only fifty-two by the end of October. On 3 November the total increased to 112 and on 23 November to 253. An influx at the beginning of December brought a count of 2,300 on the 2nd. There was a further rise to 2,500 on the 12th and this level was maintained for the rest of the month. On 9 January there were 3,200 and then on 20 January the winter's peak of 4,500 was reached. The flock stayed at this size until the end of the month when it dropped to 4,000. Further departures took place in mid-February and on the 23rd the count was 2,300, while on the 28th it was 700. There were still 625 on 13 March but only thirty-five on the 14th which were the last seen.

For the second year running the breeding success was high with 44% young birds and an average brood size of 2·9.

Lesser White-fronted Goose *Anser erythropus*
An adult bird was first seen on 2 December (a very early date). It stayed through the winter and was last recorded on 23 February.

Bean Goose *Anser fabalis*
An adult bird was seen on 6 December and frequently through the winter, while on 20 January three were observed. All belonged to the Scandinavian race *fabalis.*

Pink-footed Goose *Anser brachyrhynchus*
Only two were seen this winter, from 20 to 27 January.

Cackling Canada Goose *Branta canadensis minima*
A bird referable to this race was seen among the Whitefronts on 2 December staying until about the 12th. It must be assumed to have been an escape, though not from Slimbridge.

Barnacle Goose *Branta leucopsis*
For the first time for seven winters no wild Barnacle Geese were recorded. Two full-winged birds from the Slimbridge collection spent much of the winter with the wild Whitefronts, however.

Dark-bellied Brent Goose *Branta bernicla bernicla*
A juvenile bird of this race appeared on 27 November and departed with almost the last Whitefronts to leave on 13 March.

M.A.O.

Slimbridge: The wild swans 1973–74

Once again the Bewick's Swans beat their record for the earliest arrival; the first pair, Nijinsky and Caroline, here for their fifth winter, returned to Slimbridge on 13 October, Two days later the intrepid Lancelot flew in, the first swan so far to return for its eleventh consecutive winter.

Arrivals were, however, scarce for the first 12 days. Then there was a gentle build-up to sixty-six. Thereafter there were two major arrival periods. At the beginning of November 104 birds arrived in 5 days. A month later, when N.W. Europe was caught in one of the most severe freezes for many years, 102 swans arrived during the first 3 days of December, bringing the total then recorded for the season to exactly 400. The final figure for the year was 541, and 515 of these had arrived by 31 December. On that date the greatest day total for the year was recorded. This was 294 which, while similar to those in the previous 2 years (325 in 1972–73 and 311 in 1971–1972), was nevertheless the smallest since 1967–1968.

There was no noticeable mass departure in January. Day attendances dwindled to 153 by the 24th, then rose 3 days later to 211. These gradual disappearances and temporary fluctuations were apparently caused by the swans' discovery of the attractions of Walmore Common, 10 km away on the other side of the river Severn. January saw unusually many gales and accompanying heavy rain, with much flooding. Walmore Common became a lake, and was very popular with the swans. However, some of these would turn up periodically at the Trust, presumably when they were disturbed. Indeed for several years now swan attendances have often increased at Slimbridge at weekends, particularly on Sunday afternoons, the traditional walking time of the British public. Numbers continued to dwindle very gently throughout February, so that on the 28th 109 swans were present. Although it was known that swans had started to leave the Slobs in Co. Wexford, and the Ouse Washes, it was still, nevertheless, a shock when attendances dropped right away to none on 3 March! However, after 2 days a few turned up again, although they used Swan Lake only as a roosting place, a complete reversal of their normal behaviour. The last of these left on 16 March.

The cygnet proportion was even better than last year's 19%. This winter it was 24%, comprised of three families with five cygnets, seven each with four and three, twenty-three with two, and twenty-two singles. The mean brood size was 2·1. It was interesting to note differences in behaviour among the larger families. Some pairs were extremely good parents, and wherever they were their offspring were always close by, except at feeding times, when it is difficult to make out individuals in the general mêlée. The daily check of the less organized families was often much more tedious, for the cygnets would be dispersed pursuing various activities. Cygnets are unrecognizable by bill pattern, still unformed, so it was often easier to check off those ringed by their number than wait for parents to assemble their wayward young. Ravens and parrots can discriminate between numbers up to six, but it is not known if Bewick's Swans are similarly skilled. A pair certainly does not appear to become unduly agitated if they lose sight of a cygnet, and it is not within calling distance. Thus one of the families with five cygnets, Daniel and Burnel, dwindled to four, then to three. One female, McJuliet, who had lost her mate, Romeo, nevertheless had two cygnets. These she had also lost by the beginning of January. This difference in parental ability does not seem to be related to experience. Some pairs are also strikingly more tolerant than others of their previous year's offspring when they meet up again at Slimbridge. Some offspring are allowed to rejoin the family group; others are driven off resolutely by the male.

The saddest loss of a cygnet was that belonging to Needham and Ethelrida (*Wildfowl*, 24:61–62). Needham has an abnormal amount of red on his bill, and yellow legs, while Ethelrida is normal. The pair returned to Slimbridge on 3 November with two cygnets, one normally grey, the other white, with pale grey/white legs and a pink bill, i.e. a leucistic bird. We were lucky to get a photograph (p. 165), for the family only reappeared briefly the following day before reverting to their last year's haunt at Walmore Common. There they were identified on 15 November and on several subsequent occasions during the winter. Although the grey cygnet was with them, the white one was never seen again after leaving Slimbridge.

There were only five ringing catches this season, but four of these were, by previous standards, large, and, indeed, one consisted of eighty-four swans. This season more birds (267) were processed than in any other. Eighty-eight were ringed for the first time, and of these forty-eight were cygnets and yearlings in which we are particularly interested since their age is precisely known. So far 558 Bewick's Swans have now been ringed at Slimbridge.

The X-raying of the swans was continued. Of adults X-rayed for the first time, the proportion carrying lead pellets was found to be 46%, which is 2% more than the result of the adults X-rayed over the past three winters. The greater number of 1st and 2nd winter birds X-rayed (47% against 40% in 1970–1973) reduced the overall proportion of birds with shot from 34% to 29%.

This season the tails and wing tips were not marked with yellow dye, which in the past three winters had enabled us to learn much about the migration routes. Aesthetic considerations mainly led to this change of policy, but we had not realized how useful the dye was nearer home. Some smaller mark would greatly have facilitated the observation of the Slimbridge Bewick's at Walmore for instance. If the birds were at a distance in shallow water, it was very difficult to make out their bill markings, or see if they had rings. Nevertheless, thirty-eight Slimbridge birds were recognized out of 107 swans seen there on 24 January, and several interesting sightings were received from other places, often from observers who had previously been alerted to 'Slimbridge' swans by the dyeing policy.

Seven ringed Bewick's were seen on the Slobs, in Co. Wexford, Ireland, and six were identified. Interestingly, four are of known age. They were too young to have mates when at Slimbridge, and apparently do not yet. The other two birds were adults at Slimbridge, again without mates, both then and in this last winter. Three of them had been on the Slobs in 1972–1973, and two of these also in 1971–1972.

One ringed swan was reported from West Cornwall in December, and two from Tealham Moor in Somerset on 17 November. One of these, called Lattice, arrived at Slimbridge on 10 December, and spent the rest of the winter here.

The most comprehensive reporting is possible from Welney on the Ouse Washes in Norfolk, where, as at Slimbridge, the birds are lured to easy viewing distance by regular feeding. Two years ago, when this policy was introduced, it was feared that regular Slimbridge birds might be short-circuited to Welney. In that year forty birds with Slimbridge experience were recorded there. Last year the total was forty-eight. This winter it was only thirty-six. Twenty-six of these did not come to Slimbridge at all, but this included at least eighteen known to have been to Welney before. Five went to Welney, and travelled on to Slimbridge. (None of these were known to have been at Welney before.) Five came to Slimbridge first, then went to Welney. Two of these, both with Welney experience, only stayed at Slimbridge for 1 day, returning to Welney in November. The other three arrived there after swans had already started to evacuate Slimbridge. One, the only cygnet of It and Itma, arrived alone on 27 January. Three days earlier the family had been together on Walmore Common.

Considering that there were 1,100 Bewick's at Welney at the beginning of January, the fact that so few Slimbridge birds are identified there would suggest that it does not pose any threat to the continuity of the study at Slimbridge. A regular check is kept there on ringed birds, so it is most unlikely that any would be missed; and observers from Slimbridge, familiar with the bill patterns, go to Welney several times during the winter to check the swans from that aspect. The return rate at Slimbridge of adults and yearlings from the previous season was 58%.

Sightings from the Netherlands were disappointing in comparison to the previous year. Perhaps the ringed birds simply were not there, but observers were affected by the ban on Sunday driving, due to the oil crisis. Sunday is a favourite day for bird watching, and birds can often be approached closer in a car than on foot. It is possible, of course, that more reports are yet to come. We know so far of seven ringed birds, six identified, and of these four were there last winter as well.

The opportunity arose to check the swans in Germany personally, for the swans' presence there coincided with the opening of an exhibition, in which the Wildfowl Trust was taking part, emphasizing the importance of the lower Elbe for wildfowl. This area is threatened by industrial and agricultural development, and was where Dafila Scott and I found some Slimbridge Bewick's 2 years before (*Wildfowl*, 23: 132–135). Certainly the Bewick's put on a good show this time! The count on 9 March showed 800 on Asselersand, 677 on Allwordene Aussendeich, and 130 at Balje a total of 1,600! Unfortunately time was very restricted, but on that day Sir Peter and Lady Scott found and identified Shiny and Silky and their three cygnets, which had last been seen at Slimbridge on 6 February and Walmore on 1 March. More ringed swans were seen, but I was not able to identify them until the following day, when seven were named from nine ringed. It must be admitted that, when time was short, flocks of this size were scanned for rings, and when one was found the bird was then concentrated on. However, only one was actually identified by ring number. This was a very plain bill-patterned swan, called Fabian, that had not been to Slimbridge since 1970–1971. Three were not identifiable by any means, but would have required much more time! Another seven were identified by bill pattern, and the remaining four were cygnets in association with adults. All identified, except Fabian, had been to Slimbridge in 1973–1974, and all had last been seen there or at Walmore on 1 March—quite a coincidence! Probably also by chance the seven from Slimbridge (the Shiny/Silky family and another pair) were first seen on the 9th; those from Walmore (a single bird and a family with one cygnet) were seen on the 10th. Since then one more bird has been identified by observers there—Odin, last heard of, again in that area of Germany, in March 1972. Three more Slimbridge birds of this year have been identified on the Hauke-Haien-Koog in N. W. Schleswig-Holstein, and another bird has been reported from the river Aller, but the number was not readable.

And so farewell to the Bewick's for another season! Three Whoopers came to Slimbridge during the winter. Two were the same pair as were here in 1969–1970 and 1971–1972, but they only stayed for 2 days in December. The third, a new bird, turned up in January, and again only graced us for 2 days.

Mary E. Evans

Aviculture–1973

This is the last issue of *Wildfowl* in which the tabulated breeding results at Slimbridge and Peakirk are given in full. With the opening of three new collections in 1974–1975, it will be necessary in future to present the results of our enlarged avicultural programme in summary form.

Meanwhile, the 1973 Slimbridge season proved an excellent one: some 1,750 birds were reared, including, for the first time in captivity, the White-headed Duck (see page 00). The season was also an exceptionally long one, the first egg (Egyptian Goose) being laid on 18 January and the last hatch (Black Swans) occurring on 19 November. While these late cygnets were still being hand-reared, wildfowl eggs from South America arrived and hatched, so the winter season was busy also.

The generous grant from the Slater Foundation Ltd enabled us to redesign and re-equip the propagation centre, so that temperature and disease control were adequate for the first time, and looking after the large number of young birds was a comparatively easy task. The flamingos, after the driest spring on record, had a poor season, and only the Chileans produced young. This was disappointing as the first International Flamingo Symposium met in July at Slimbridge, partly because of the Trust's pre-eminence in breeding these birds. One of the aims of this very successful Symposium was to exchange information so that zoos will maintain these birds in conditions where they breed, and the unacceptably large numbers of flamingos captured from the wild can be reduced. Since the Symposium, Copenhagen and London Zoos have presented Slimbridge with their Andean and James's Flamingos which, we hope, will enable us to breed these birds more freely, and the Wildfowl Trust has presented the London Zoo with three young Chilean Flamingos to enlarge their breeding flock of this species.

At Peakirk the breeding season started on 12 February with the first Cereopsis egg and ended with a clutch of Southern Red-billed Whistling Duck which hatched on 21 September. Although a total of sixty species and sub-species laid eggs and thirty varieties were reared, the general results were disappointing due, partly, to cold and wet weather. The major triumph of the season was the successful breeding of the very rare White-winged Wood Duck for the first time at Peakirk. The female was the first captive-reared bird ever to lay in captivity. One point of interest was the length of the breeding cycle of the Maned Goose. The first egg being laid on 24 February and a fourth and final clutch started on 9 July.

The number of captive birds held by, or on loan from, the Wildfowl Trust is now around 4,500. Many of these are full-winged, although they remain within our fox-proof enclosures, and well over 90% have been bred by the Trust. Slimbridge has the largest collection—2,575; Peakirk, 780; Martin Mere, 550; Washington, 150; Caerlaverock, 135, and there are 145 (mostly Nene) on loan to other zoos and breeders. Arundel will receive its first birds in autumn 1974, and at all our new collections, emphasis is being placed initially on sizeable flocks of British species which will act as decoys for wild birds. The small collection at Caerlaverock is entirely British and produced a useful surplus of geese during 1973.

Slimbridge is our only quarantine station, and so all imported birds are first brought there.

Important arrivals during the year include: Andaman Teal, Pink-ears, Maccoa and Madagascar White-backs, as well as many South American species collected as eggs by the Slimbridge Curator, Michael Lubbock. Especially interesting were a number of Black-headed Duck (hand-reared in captivity for the first time) and Kelp Geese.

J. Kear

Welney Wildfowl Refuge, 1973

The Refuge held considerable numbers of duck during both winters but the mild weather probably kept the totals for some species down. Wigeon reached a peak of 25,000 in mid-January, dropped suddenly to 12,000 in early February but climbed again to 17,000 on the 17th before a rapid departure in March. Mallard fluctuated between 800 and 1,500 while both Pintail and Shoveler topped 300. Pochard were present in useful numbers in January and February reaching a peak of 200 in the latter month. As usual it was the swans that provided the greatest spectacle with 600 Bewick's in late January, together with up to twenty-three Whoopers and just over 100 Mutes. The Bewick's stayed in good numbers through February and early March before departing in the middle of the month. Unusual visitors included a Smew, present for most of January, a Hen Harrier in February and up to sixty wintering ruff. Up to sixteen White-fronted Geese were seen in January and February.

The breeding season started very early with the first Mallard nest found on 17 February and the first brood seen the following week. These first broods mostly perished in the cold weather that followed, but later hatchings were more successful with at least seven broods of Tufted Duck, while Shoveler and Shelduck also bred well. Four pairs of Black-tailed Godwits breed successfully, after one early clutch had been taken by Jackdaws. Ruffs were not proved to breed but a lek was established at the end of March and it is thought that as many as four pairs may have bred. A pair of Black Terns hung around for a while but did not nest. A Hoopoe put in an appearance on 18 May and a Spoonbill the day after.

During September Mallard built up rapidly to a peak of 3,000 and after a fall in November reached this level again in December. Wigeon increased steadily through the autumn to about 18,000 at the end of the year. Other duck species were generally below average except for Shoveler which were especially numerous in September and October with a peak of 600, but these had mostly left by December. The first Bewick's Swans arrived in mid-October and there were 800 feeding on the lagoon by the end of the year. Whooper Swans totalled thirty. A single Smew was present from mid-November until late December, while a Bittern was seen many times in the second half of October.

M.A.O.

Eastpark Wildfowl Refuge, Caerlaverock, 1973–1974

Barnacle Goose *Branta leucopsis*

The first geese were seen on 20 September, a party of ten sitting on the Blackshaw Bank. By 30 September thirty-nine were present and a steady influx from 8 to 15 October brought the total to 5,100, another post-war record number. The full flock was present at Eastpark until 25 February except for occasional periods of 2–4 days, during which other Solway areas were visited. After the 25th the birds moved to Rockcliffe but up to 750 returned in early March and at the end of the month 450 were still present. In April the flock size on the Refuge varied between 00 and 0000 geese. The last Barnacle of the winter were seen on 00 April.

Age counts were made of a sample of about 1,100 geese. The proportion of juveniles in the flock was 21%, with an average brood size of 1·5. Both figures are slightly down on last winter.

The average number of Barnacles feeding on the merse and arable fields of Eastpark and also on fields elsewhere on Caerlaverock was noted daily. The amount of time spent on the arable, where the geese are readily observable from the hides and towers, increased greatly compared with last year to about 60% of the total, or close to the level of the 1971–1972 winter.

Four white Barnacle Geese were present throughout the winter. These included the two 1972 juveniles and one separate adult seen the previous winter. The two former geese were caught and ringed in Spitsbergen by members of the Wildfowl Trust team in the summer of 1973. In early October they returned to Eastpark and were by now living separately amongst the flock. The other single adult goose also arrived and a fourth white Barnacle appeared as well. This latter bird was a juvenile. Both its parents were normal-plumage adults and one other normal-plumage juvenile made up the family. It is tempting to believe that the same parents were responsible for the other white geese.

Pink-footed Goose *Anser brachyrhynchus*
The first arrivals were thirteen on 20 September. By 1 October over 1,000 were present and this number increased to 4,000 by the 10th. Up to 1,500 were feeding on the stubble fields in October. A general decrease of Pinkfeet on the inner Solway occurred from late October until by mid-November only fifty to sixty were in the local area.

Numbers rose again to 2,000 by 7 December and in early January over 4,000 were roosting on the Blackshaw and Priestside banks. In late winter numbers of Pinkfeet feeding on the Refuge increased steadily, until by 18 April not less than 5,000 were counted on the merse and fields. The last Pinkfeet of the winter were observed on 00th May.

Greylag *Anser anser*
Numbers in the locality did not exceed 250 and the largest flock seen feeding on Eastpark was forty-nine in early January. Up to sixteen regularly fed and roosted in the enclosure for most of the winter.

Other wildfowl

For the fourth winter a single adult Light-bellied Brent accompanied the Barnacles. An adult Lesser Snow Goose was seen on the inner Solway marshes in early November. On the 17th this bird joined the tame geese in the enclosure and is still present. On 7 December a second Snow Goose was present for one day with Pinkfeet feeding on the fields. One single Greenland Whitefront was observed on two occasions. Up to sixty Canada Geese were on the merse in August.

The first pair of Whooper Swans arrived in the enclosure ponds on 18 October. Up to fifteen, including two cygnets, were present through the winter until 1 April. One wild bird has remained. The first Bewick's Swans came on 26 October, a pair with one cygnet. Five more joined them in the following weeks. Although this is a very small flock by English standards, this is the largest recorded this winter in Scotland. Seven departed on 17 March, one remaining. This particular Bewick's has a slight injury to its wing tip and, although flying quite strongly, seems to wish to remain for the time being. Up to forty Mute Swans spent the winter in the enclosure.

Numbers of duck frequenting the enclosure, both as a daytime roost and night-time feeding area, far exceeded expectations. Up to 800 Pintail and 500 Wigeon were present in early winter for up to 6 weeks. Wigeon numbers throughout the winter were steady at between 200–400. Also present were up to twelve Pochard, six Tufted, three Gadwall, two Long-tailed Ducks, thirty-eight Shoveler, 105 Teal and 250 Mallard. A single male Garganey spent several days in June on the ponds. At times up to 800 Shelduck gathered at high tide on the merse. Wigeon and Pintail numbers both exceeded 1,000 on occasions.

C. R. G. Campbell

Breeding results, 1973

Species	Slimbridge			Peakirk		
	Date of 1st egg	Eggs hatched	Young reared	Date of 1st egg	Eggs hatched	Young reared
Spotted Whistling Duck	8·7	7	7			
Fulvous Whistling Duck	9·4	58	40	25·5	1	0
N. Red-billed Whistling Duck		24	22			
S. Red-billed Whistling Duck		62	57	2·6	7	0
Coscoroba Swan	26·3	1	1			
Black Swan	21·1	4	0			
Mute Swan	6·3	4	0			
Black-necked Swan				3·3	0	0
Bewick's Swan	4·6	2	1			
Whooper Swan	11·4	9	8			
Trumpeter Swan	17·4	3	2	13·4	2	1
Swan Goose	8·4	9	8	10·4	0	0
Western Bean Goose				30·4	0	0
Russian Bean Goose		2	1			

Species	Slimbridge			Peakirk		
	Date of 1st egg	Eggs hatched	Young reared	Date of 1st egg	Eggs hatched	Young reared
Pink-footed Goose		5	5	21·4	0	0
European White-fronted Goose		3	3			
Greenland White-fronted Goose		14	14	22·4	0	0
Pacific White-fronted Goose	30·4	0	0			
Lesser White-fronted Goose		4	3			
Western Greylag Goose	11·3	31	29			
Eastern Greylag Goose	12·4	14	12			
Bar-headed Goose	16·4	5	5			
Emperor Goose		3	3	5·6	0	0
Lesser Snow Goose		8	7	25·4	2	1
Blue Snow Goose		2	1			
Greater Snow Goose		16	14			
Ross's Snow Goose		3	3	13·5	2	2
Atlantic Canada Goose		3	3			
Moffitt's Canada Goose	27·3	0	0	8·4	0	0
Lesser Canada Goose	4·4	12	12			
Taverner's Canada Goose				25·4	0	0
Dusky Canada Goose		4	4	12·5	0	0
Aleutian Canada Goose	30·4	0	0			
Cackling Canada Goose	8·5	4	4	24·4	2	2
Hawaiian Goose	10·2	47	42	21·2	6	4
Barnacle Goose	23·4	50	46	30·4	0	0
Light-bellied Brent Goose	28·6	1	1			
Black Brant		3	3	24·5	0	0
Red-breasted Goose	24·5	4	3			
Ruddy Shelduck	4·4	8	7			
Cape Shelduck	21·4	0	0	28·3	0	0
Paradise Shelduck	6·4	0	0			
Australian Radjah Shelduck	22·7	7	7			
Common Shelduck	11·4	9	8	7·5	5	5
Egyptian Goose	18·1	9	8			
Orinoco Goose	26·3	0	0			
Abyssinian Blue-winged Goose	19·4	4	4	14·5	0	0
Andean Goose	10·4	10	8	27·4	10	9
Ashy-headed Goose	22·4	5	4			
Lesser Magellan Goose				23·4	2	1
Greater Magellan Goose				30·4	2	0
Cereopsis Goose				12·2	1	1
Falkland Island Steamer Duck	30·3	0	0			
Patagonian Crested Duck	20·2	28	28	24·4	11	10
Andean Crested Duck	3.4	4	4			
Bronze-winged Duck	15·3	6	6			
Marbled Teal		45	44	6·5	26	17
Cape Teal		4	4	6·5	0	0
Northern Versicolor Teal	9·4	9	7			
Puna Teal		19	17			
Red-billed Pintail		12	12			
Northern Bahama Pintail		16	16	19·5	8	8
Chilean Pintail	17·4	34	31	25·4	4	3
Northern Pintail		10	10	9·5	11	10
Kerguelen Pintail		1	1			
Chilean Teal		10	10	12·4	16	12
Sharp-winged Teal		16	16			
American Green-winged Teal		3	2			
Falcated Teal		1	1	29·5	0	0
Australian Grey Teal	6·6	14	14			
Chestnut-breasted Teal	18·4	13	10			
New Zealand Brown Duck	25·3	5	5			

	Slimbridge			Peakirk		
Species	Date of 1st egg	Eggs hatched	Young reared	Date of 1st egg	Eggs hatched	Young reared
Hawaiian Duck	12·3	18	17	19·4	0	0
Laysan Teal	13·4	33	33	4·4	16	14
Mexican Duck	3·4	2	2			
Indian Spotbill				24·6	5	1
New Zealand Grey Duck		9	9	1·5	1	1
Pelew Island Grey Duck		7	7			
Philippine Duck		12	12	5·5	0	0
African Yellowbill	18·3	30	29	11·4	14	13
Abyssinian Yellowbill				9·5	8	5
Gadwall	15·4	311	280	7·5	7	7
European Wigeon		32	32	23·5	5	4
American Wigeon		5	5	13·6	5	5
Chiloe Wigeon	18·4	21	19	8·5	0	0
Atlantic Blue-winged Teal		3	3			
Garganey		4	4			
Argentine Red Shoveler	18·4	1	1			
Cape Shoveler		6	6			
Common Shoveler	8·5	5	5	29·4	17	8
Ringed Teal	29·4	61	57			
European Eider	23·4	24	22	23·4	8	7
Red-crested Pochard	1·3	41	40	9·4	19	5
Rosybill	18·4	46	46	11·5	9	8
European Pochard		12	12	24·4	12	7
Redhead		5	5	22·5	4	0
Common White-eye		8	8	20·5	14	9
Baer's Pochard		3	3			
Australian White-eye	1·5	35	33	24·5	5	2
New Zealand Scaup		55	44	1·6	13	0
Ring-necked Duck				3·6	2	1
Tufted Duck		135	128			
Lesser Scaup		15	15	8·6	5	1
European Greater Scaup		9	9			
Lesser Brazilian Teal		8	8			
Greater Brazilian Teal		12	12			
Maned Goose	14·4	0	0	26·2	20	8
Mandarin Duck		62	57	2·4	31	17
North American Wood Duck	29·3	63	62	15·3	58	37
Comb Duck	27·8	1	1			
White-winged Wood Duck	21·4	10	3	30·5	4	2
Muscovy Duck	15·3	42	30			
Barrow's Goldeneye		9	1			
European Goldeneye	12·4	0	0			
American Goldeneye	6·4	0	0			
Bufflehead	5·5	4	3			
Smew	30·4	18	10			
Hooded Merganser	8·4	3	3			
Goosander		6	4			
White-headed Duck	19·7	6	4			
North American Ruddy Duck		32	20	24·5	15	5
Crested Screamer	23·3	1	0			
Chilean Flamingo	19·6	19	14			

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Notice to contributors

Wildfowl publishes, once a year, papers and shorter communications dealing with the biology and conservation of the wildfowl (Anseriformes), of their wetland habitat and of ecologically associated birds, such as waders. Review-type articles on recent progress in the various fields are particularly sought. They, and original papers, should not be highly technical but written so that they are understandable by workers in other fields, and by intelligent laymen.

Contributions should be type-written, double-spaced and with good margins, on one side of the sheet. Tables should be typed on separate sheets together with their titles. Drawings and diagrams should be done in indian ink on good quality drawing paper, or on faintly ruled grey or blue graph paper. Lettering and numbering that form part of the diagram should be entered in pencil, as the publishers will ink these in in the correct style. Titles and captions should be typed separately. Drawings and diagrams should be prepared about twice or three times their printed size and allowance made for this reduction. When laying out tables and diagrams the proportions of the page should be borne in mind. It is preferable for them to fit horizontally on the page, either single or double column width, though exceptionally they may take a full page lengthways.

Authors are particularly requested to follow the conventions of style and layout used in *Wildfowl*. English names of birds should have a capital letter for each word, except after a hyphen, e.g. Tufted Duck, Red-crested Pochard, but group terms should not, e.g. whistling ducks, swans. Scientific names should be underlined (but not put in brackets) and used immediately after the first mention of the English name. Nomenclature and classification should follow *A Coloured Key to the Wildfowl of the World* (Scott, 1957, as revised 1968). Dates should take the form 1 January 1968, and winter seasons the form 1968–1969. It is especially helpful if reference lists are set out correctly, and these should take the form:

Salomonsen, F. 1968. The moult migration. *Wildfowl*, 19: 5–24.

Scott, P. & Boyd, H. 1957. *Wildfowl of the British Isles*. Country Life, London.

References within the text should be in the form 'Salomonsen (1968)' or '(Salomonsen, 1968)'.

A short summary mentioning the main conclusions, and suitable for abstracting, should be given at the end of all papers.

Proofs of all contributions are sent to authors for checking and it would be appreciated if these could be returned promptly. After publication, 25 reprints are offered free to authors of papers; further reprints, charged at cost, can be provided if ordered when proofs are returned.

Photographs of wildfowl (black and white, of good contrast and printed on glossy paper) are welcomed, either as illustrations to papers or for publication in their own right. The latter may be of species rarely portrayed, or interesting action studies of birds, wild as well as tame. Records of birds in eclipse plumage and in their natal down are also solicited. Even if these are not published immediately the Trust seeks to build up a comprehensive reference file of wildfowl photographs for which prints will be gratefully received. Photographers retain the copyright on their work.