The Shelduck population of the Ythan estuary, Aberdeenshire

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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

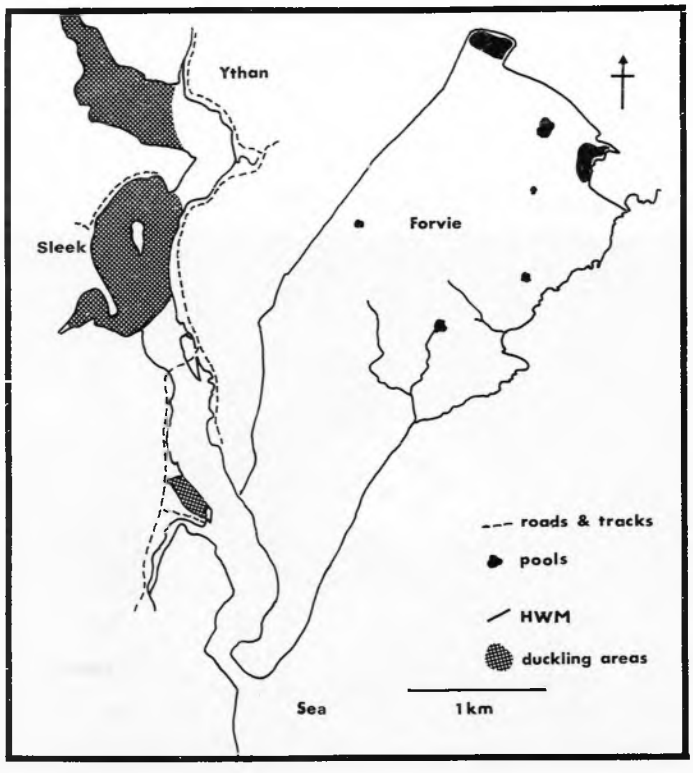

Figure 1. The Ythan estuary and Sands of Forvie National Nature Reserve, showing the areas of the former used by Shelduck broods.

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

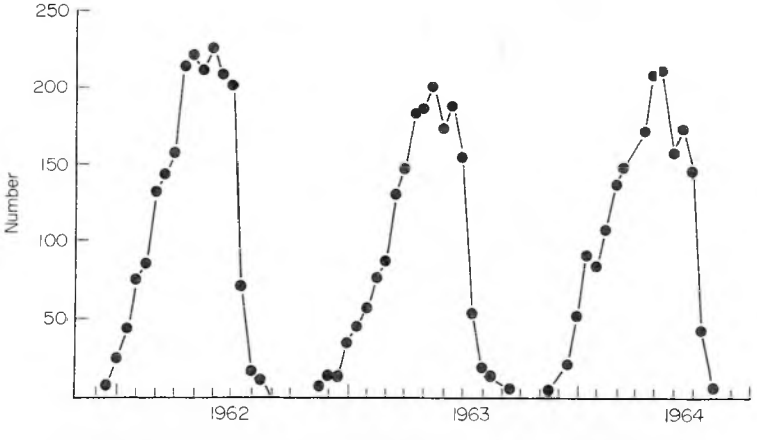

Figure 2. Seasonal changes in the total number of adult Shelduck on the Ythan estuary.

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.

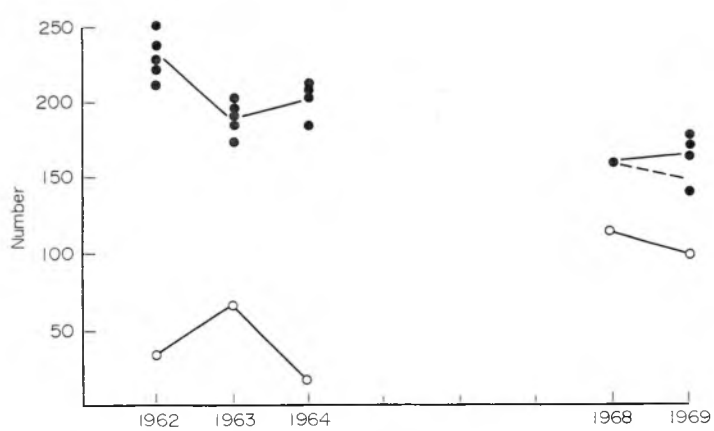

Figure 3. Changes in the Ythan population between years. The points show the total birds present in separate counts in May and the solid line joins the means. The dotted line indicates the 1969 mean total when birds away from the river are excluded. ●, Total adults; O, young fledged.

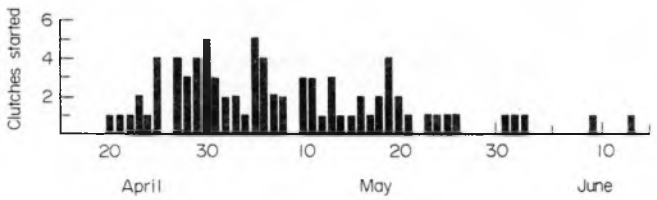

Figure 4. Date of laying the first egg of each clutch.

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

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.

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.

Clutch size

Clutches varied from five to eleven eggs with an overall mean of 8·1 (Table 4). Clutches in

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

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 ($\chi^2 = 6{\cdot}41$, $P < 0{\cdot}05$). 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.

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

Brood size	No. of Broods	Age class and (age in days) 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

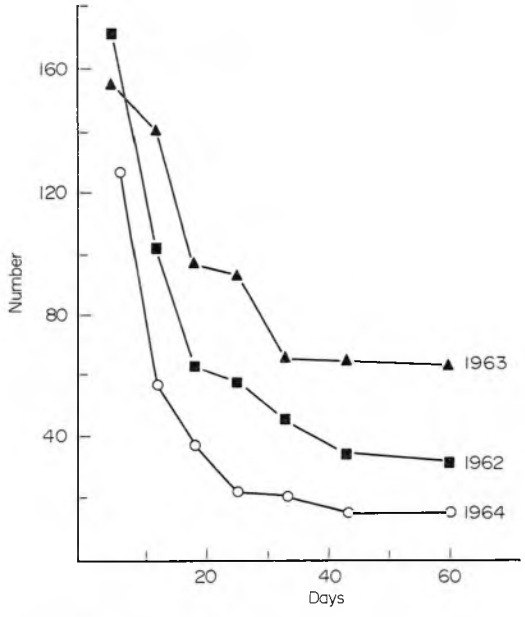

Figure 5. Survival of ducklings on the Ythan. The points show the number of ducklings alive at each age. Dates from Table 9. ▲, 1963; ■, 1962; O, 1964.

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		Survival per year (%)
	a	b	
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

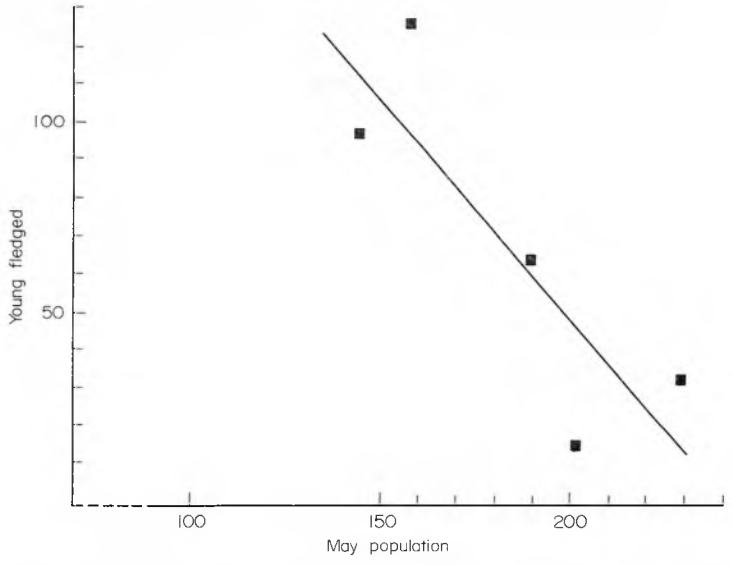

Figure 6. The relationship between the population size in May (river only) and the number of fledged young produced. The line is the calculated regression; $y = 274{\cdot}7 - 1{\cdot}13x$, $r = 0{\cdot}841$, $(0{\cdot}10 < P > 0{\cdot}05)$.

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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