Clutch parasitism and nesting interference between Shelducks at Aberlady Bay

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Introduction

Several studies have shown that productivity of Shelducks *Tadorna tadorna* decreases as nesting density increases (Jenkins *et al.* 1975; Patterson *et al.* 1974), and that far fewer young per adult fledge from birds nesting in 'colonial' situations than from more dispersed breeding pairs (Pienkowski & Evans 1982). At Aberlady Bay, in SE Scotland, and probably also at the Ythan estuary in NE Scotland, most of the reduction in productivity is due to reduced duckling survival at high densities. There are indications, however, that high nesting densities also lead to a reduction in the number of ducklings hatching per pair (Patterson *et al.* in press; Pienkowski & Evans 1982). Shelducks apparently try to avoid other Shelducks when prospecting for nest-sites (Patterson & Makepeace 1979), and interference in nesting activities early in the season may be the cause of reduced hatching success, particularly if more than one female lays in a single nest.

As Shelducks nest in holes in the ground, investigation of interference in nesting is generally difficult. At Aberlady, most nests are in burrows of Rabbits *Oryctolagus cuniculus*. However, some birds used artificial nest-boxes fitted with inspection hatches. These were first installed by Jenkins *et al.* (1975) and later modified by Taylor (1976) and ourselves. This paper describes the nesting biology of the ducks, with particular reference to intra-specific interference.

Study area and methods

Aberlady Bay is one of several tributary estuaries, with intertidal areas, of the Firth of Forth. Shelducks breed in 'colonies' there and at Tyninghame Bay and the Almond Estuary, as well as at 'isolated' sites and spread along linear shores on the East Lothian coast and on the inner parts of the Firth.

Birds feeding on Aberlady Bay nest mainly in adjacent sand-dunes and golf-links at Gullane (Figure 1). Smaller numbers nest in the valley of the Peffer Burn, which flows into Aberlady Bay. Such 'inland' nesters were more common during the study made by Jenkins *et al.* (1975). Adults (128) and well-grown ducklings (95) had been individually marked by colour-rings in their study and in the intervening period until our work began in 1976. We marked a further 111 adults and 109 well-grown young at Aberlady and one adult and 65 ducklings at nearby sites. Often, two to three years elapsed before marked ducklings joined the breeding population. Also some adults caught in winter did not stay to summer at Aberlady. Therefore, the proportion of marked adults in the summer population at Aberlady (about 60 pairs) did not increase as rapidly as the marking figures imply. It rose from about 30% at the start of the study in 1976, to about 70% in 1978 and 1979.

From March to June, visits were made around dawn and a few hours afterwards to areas where Shelducks from Aberlady prospected for nest-sites and often formed small gatherings ('communes' of Hori 1964 and 'parliaments' of Young 1970b). Where possible, colour-ringed individuals were identified at each area.

In April, May and June, watches were made to identify actual nest sites of individuals. Colour-ringed ducks could be identified with difficulty as they quickly entered or left their concealed nest-burrows. More were identified by pairs of observers, in the dunes and on the Bay, linked by two-way radios. Thereby, ducks were identified when they returned to the Bay after incubation spells, and drakes when they returned to feeding areas on the Bay after accompanying females returning to their nest sites.

A total of 88 nest-boxes were installed from 1971 to 1977 in Gullane dunes and links. The design varied but tried to mimic natural burrows as much as possible (Taylor 1976). During the breeding season, the boxes were inspected regularly. If they were in use, checks were made only while they were unoccupied, and eggs numbered, measured and weighed. After hatching or desertion, any remaining eggs were examined by Dr K. F. Laughlin.

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Figure 1. The study area with inset showing location. Shelducks nested in highest concentrations in the dunes between Aberlady Bay and Gullane. Lower densities of nests occurred in the dunes NE along the coast, in Gullane and Luffness links, and in the valley of the Peffer Burn.

On several occasions during the laying and incubation periods of the Shelducks in 1978 and 1979, certain nest-boxes were watched throughout the day from concealed positions in the dunes, and the activity of all Shelducks in the area monitored.

Results

Behaviours recorded at early morning gatherings in the dunes near Aberlady, and when prospecting for actual nest-sites, were very similar to those described by Patterson & Makepeace (1979). Females walked around the area inspecting and entering rabbit burrows. Their mates tended to follow them (but not into the burrows), remaining alert and often chasing other Shelducks which came near. As the numbers of Shelducks in an area increased, individuals appeared to prospect less, but this was not quantified. Marked individuals at Aberlady tended to nest in the same areas of dune from year to year, but not necessarily in the same nest-sites.

On the basis of distances from nearest neighbouring nests, observations of birds present at the sites, and shape and weight of eggs laid, most clutches were judged to have been laid by a single duck. The mean interval between egg-laying in such nests was 1·8 days in 1974 (26 eggs in 3 clutches—calculated from P. Hall, unpublished data) and 1·6 days in 1976 (30 eggs in 4 clutches—calculated from Taylor 1976). The latter found that 73% of eggs laid the day after the previous egg were lighter than the previous one, and that 75% of eggs laid after missing a day were heavier than the previous one.

Eggs were usually left in the bare sand or soil in the nest until laying was almost complete. Then the eggs were surrounded with down, most of this appearing within a day. Observations at the nest-box and examination of failed clutches suggested that incubation often started before the last one or two eggs were laid.

The mean size of 16 clutches, each believed to have been laid by a single duck, was 8·94 ± s.e. 0·41 (range 7 to 12), and the mean incubation period of 13 such clutches 32·0 ± s.e. 0·6 days. Overall, 97

(92·4%) of 105 eggs hatched from nests which survived until hatching.

In some nests, however, more than one female contributed to the clutch. This was determined (i) by direct observations of females entering the burrow, combined with examination of nest-box contents before and after a duck had entered, and /or (ii) by a laying rate greater than one egg per day over some periods. Often such clutches contained abnormally large numbers of eggs at completion, and eggs of different sizes and weights (before incubation). Only one female was recorded as incubating at any one nest. However, apart from ducks visiting the nest of another to lay eggs, unpublished observations in the dunes, in 1978, by A. C. Read and F. G. Burton and, in 1979, by J. Owen, P. Simm & S. Watson showed that ducks also frequently entered nests of other birds, whether or not a laying or incubating duck was already inside, as also reported by Hori (1969).

Between one-third and one-half of clutches examined had been laid by more than one female. Of clutches not lost to human or other predators, 13 (59%) of 22 multiple-layings observed were deserted at some stage, a significantly higher proportion than the 7 (27%) of 26 single layings ($\chi^2_1 = 4{\cdot}09$, $P < 0{\cdot}05$). The desertions of single layings resulted from burying of the clutch by a burrowing rabbit or human disturbance of the nest-box (at least 4 cases). Two of the 13 desertions of multiple-layings occurred before incubation started; a third shortly after other ducks had been observed to visit a nest; two more after a new egg had been laid (presumably by a different female) several days after incubation had started (in both cases, the eggs already present had been laid by more than one female); and one after incubation had proceeded about 5 days longer than the normal incubation periods of 32 days. In this last case, the clutch consisted of 22 eggs laid by at least 3 ducks. The incubating bird was unable to cover all the eggs and, at times, 1–3 were pushed outside the main group. Even shortly after an incubation spell, the outer eggs of the main group were sometimes noticeably cooler than the inner ones. All the eggs probably cooled faster than normal while the duck was away, as there was insufficient down to cover them. After desertion these eggs were examined. Those pushed out of the nest showed no development but the remainder held embryos at development states equivalent to 23 to 26 days of normal incubation, far less than the actual incubation period of about 37 days. 'The eggs appeared to have lost insufficient water for their age. This may indicate very humid nest conditions or generally cool incubation conditions' (Dr K. F. Laughlin, in litt.). The nest was not particularly humid but, as indicated above, egg temperature was probably lower than usual.

In several other multiple clutches at Aberlady, eggs were also pushed out of the incubated group (e.g. in 1979, 2 from a clutch of 15 and 5 from one of 17). Incubating ducks sometimes excluded their own eggs, not just those of others (judged by egg-dimensions).

Apart from the laying of eggs in active nests of other ducks during laying or incubation, single eggs were also laid in three, otherwise empty, nest-boxes, and eggs added to already deserted clutches in at least two cases.

Eggs which failed to hatch in otherwise successful clutches, in 1977–1979, contained embryos equivalent to the following periods of days of normal development: 7, 15, 15, 16, 17, 19, 20, 20, 22, 22, 23, 23, 23, 26. Deserted clutches, examined in 1977–1979, contained eggs as follows: clutch of 22 reported above; clutch of 10 with 8 at 18 days, 1 at 15 days, and 1 showing no development (one egg had appeared in this nest more than two weeks after incubation of the others had started. Therefore, clutch-parasitism may have caused desertion—see Jenkins *et al.* (1975) for other examples of this); clutch of 9 fertile but undeveloped; clutch of 9 in which 1 examined and found to be fertile but undeveloped (others taken by predator after desertion); 1 of a clutch of 20 in same state (rest taken by predator after desertion); clutch of 17 with 1 fertile but undeveloped and 1 of 4 days development (rest taken by predator; there was some evidence at this nest of laying after initial desertion); clutch of 11 with 6 fertile, 1 infertile and 4 unidentifiable.

Because of the different nature of nest-boxes and natural sites, and the difficulty of distinguishing egg-predation by humans from more natural predators, it is not possible to give quantitative estimates of the rate of predation. However, brown rats *Rattus norvegicus*, stoats *Mustela erminea* and weasels *M. nivalis* were present in the area and some nests showed signs of losses to one or other of these. Local gamekeepers and rangers also reported nests dug out by foxes *Vulpes vulpes* (A. Mathieson, W. Watt, pers. comm.). Dead adult female

Shelducks were found in the dunes during the breeding season on three occasions in three years but the causes of death were not known.

Ducklings remained in the nest for up to about one day after hatching, the time depending somewhat on the time of hatching, as parents tended to lead their young from the nest in the early morning, between 0400 h to 0940 h according to Taylor (1976). Generally both parents conducted the brood to the Bay, but in one case the duck returned to the territory 9 times during 4 hours to fetch the drake, since each time she entered the burrow he returned to the territory. Eventually she led the brood to the Bay herself (S. Kingman & S. Leader, unpublished).

Discussion

Clearly, the exclusion of eggs from large clutches, the lowered average incubation temperature and consequent prolonged incubation period required, and the increased chances of desertion of clutches arising from multiple layings, lead to depressed nesting success and a lower proportion of eggs hatching in successful multiple nests (*contra* Hori 1964). Pushing of eggs out of nests also occurred at Loch Lomond, where some nests in natural sites, under rocks and fallen trees, could be examined (Bignal 1980). As Shelducks at Aberlady sometimes excluded their own eggs, they were presumably unable to identify these by size alone in the dark nest chambers, unlike Ostriches *Struthio camelus*, in which incubating females tend to exclude those laid by other females (Bertram 1979).

Why interference or clutch-parasitism may cause desertion by Shelducks is unclear, as the costs to the deserting bird in lost production appear to be large. Possibly signs of interference at a nest by an intruding duck are difficult to distinguish from those left by a potential predator. As Shelducks are long-lived birds, reduction of danger to the duck probably heavily outweighs the loss of one clutch. Bignal (1978) describes cases of predation of adults and clutches, and desertions apparently associated with feral American mink *Mustela vison* at Loch Lomond. There was, however, no direct evidence of predation of adult Shelducks at Aberlady.

Several possible reasons for egg-dumping can be envisaged:

(i) some (possibly young) females may be capable of producing eggs but incapable of sustaining incubation until hatching, perhaps because their body reserves at the start, or feeding rates, are too low;

(ii) some females may lose their nests during laying and not have time to find another suitable site;

(iii) nest sites could be in short supply;

(iv) females incubating their own clutch could 'spread the risk', or increase the number of their own eggs which can be incubated, by laying additional eggs in the nests of others;

(v) some females may specialize as 'cuckoos', not incubating a nest of their own but laying all their eggs in the nests of others.

Because of the high frequency of nest parasitism, (ii) seems unlikely as a *sole* cause, and (iii) seems improbable in view of the large number of rabbit burrows and unused nest-boxes available (more than 70 of the latter). Most of the scant evidence points to (iv). Taylor (1976) observed a bird which laid normally in one nest for three days, but failed to lay at this nest until after a further six days, when one egg was laid; then, after another four days, it laid three more eggs over four days and began to incubate. Presumably she may have laid elsewhere on some of the intervening days. Visits by this duck, and by others known to have their own nests, to nests not their own were commonly observed in all years of our study. In 1978, A. C. Read & F. G. Burton (unpublished) noted that a female laying in another's nest was absent from her territory for much of the season, in the manner expected of an incubating duck. Thus she is likely to have laid a full clutch elsewhere.

The only indirect evidence for type (v) was a duck which, in 1978, laid in another's nest but was seen on her territory throughout most of the summer, and was therefore not incubating. However, it is possible that she had lost her own clutch during laying. Further, in the following year, she did incubate a clutch; perhaps this could be taken as slight evidence for possibility (i), or for (iv).

Intra- and inter-specific clutch parasitism is fairly common in ducks, particularly in those species nesting in concentrations. In Shelducks, it has been reported by Hori (1964), Patterson *et al.* (1974) and Bignal (1980), from various parts of Britain, as well as at Aberlady. Reduction in hatching success in large multiple clutches of Tufted Duck *Aythya fuligula*, for reasons similar to those advanced above for Shelduck at Aberlady, was reported by Newton & Campbell (1975).

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Summary

Intra-specific nesting interference in Shelducks *Tadorna tadorna* was studied, using nest-boxes, at Aberlady Bay, SE Scotland, where the ducks normally nest in rabbit burrows. The mean size of non-parasitized clutches was 8·9 eggs and the mean incubation period 32 days. At least one-third of clutches investigated were laid by more than one female. These had a significantly higher chance of desertion than clutches laid by one duck. Large numbers of eggs in one clutch also led to exclusion of some, and to a reduction in the incubation temperature (and delayed development) of those remaining. The possible reasons for clutch-parasitism are discussed.

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