Duckling mortality in the Shelduck, in relation to density, aggressive interaction and weather

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Introduction

Nidifugous young birds are very vulnerable soon after leaving the nest and, like most ducklings, those of the Shelduck *Tadorna tadorna* suffer most of their pre-fledging mortality in the first 10 days of life (Patterson *et al.* 1974). Variations in this heavy initial mortality largely determine the number of young which fledge (Williams 1974) and are important in determining breeding output by individual pairs and by the population, particularly if the mortality is density-dependent.

Hori (1964), Williams (1974) and Young (1964) described frequent aggressive interactions between brood parents while Hori suggested that such interactions were more frequent when broods were crowded together. Williams (1974) showed that ducklings from different broods mixed together during interactions between their parents and that ducklings which were involved in such mixing had a significantly higher mortality rate than those which stayed unmixed. Thus it seemed possible that early duckling mortality might increase with brood density through a density-dependent increase in aggressive interaction between the brood parents.

It also seemed likely that early mortality of the ducklings might increase in bad weather, as has been found for a number of duck species (Bengtson 1972; Grenquist 1965; Hildén 1964; Koskimies & Lahti 1964; and McAloney 1973). Makepeace (1973) found in the Shelduck that the daily mortality rates increased significantly with increasing values of a chill factor, calculated from rainfall, wind speed and minimum air temperature.

Adverse weather, if sufficiently extreme, might kill ducklings directly by chilling (Koskimies & Lahti 1964) but may more often have an indirect action by increasing the rate of energy loss. The ducklings' yolk reserves last only for a few days (Kear 1965), during which time the young birds must learn to feed efficiently enough to start gaining energy. Any factor which increases their rate of heat loss will increase the rate at which their food reserves are used up and may in addition decrease feeding time through an increase need for brooding. Low temperature and rain may also decrease the availability of invertebrates on the mud surface (Goss-Custard 1969). When the ducklings' net reserves (energy intake minus losses) become very low, they may die, either through direct starvation or, more probably, by becoming more vulnerable to predation. If chill factors were to increase duckling mortality in this way, through an effect on energy balance, a delay would be expected between a worsening of weather and an increase in mortality. A one-day lag effect has been found in Shelducks (Makepeace 1973) and in the Eider *Somateria mollissima* (Mendenhall 1975).

This study aimed to find whether duckling mortality increased with, (a) higher brood density, (b) with increasing frequency of aggressive interaction and (c) with weather factors which increase heat loss, namely low air temperature, rainfall and high wind speed. As background to (a) and (b), it was necessary to describe the ranging and spacing behaviour of broods and the interactions which occurred between brood parents.

Study area and methods

Study area

This (Figure 1) was the Ythan estuary near Newburgh, Aberdeenshire, (Young 1964; Patterson *et al.* 1974; Williams 1973), the southern end of the Sands of Forvie National Nature Reserve, and several fresh-water pools and lochs within 4 km of Newburgh. The Ythan shelducks were known to be a discrete population (Patterson *et al.* 1974), so most of the ducklings produced each year were likely to have been seen, and these were observed until fledging.

Marked individuals

Adult shelducks were caught in baited funnel traps in winter and were marked with coloured plastic leg rings (Williams

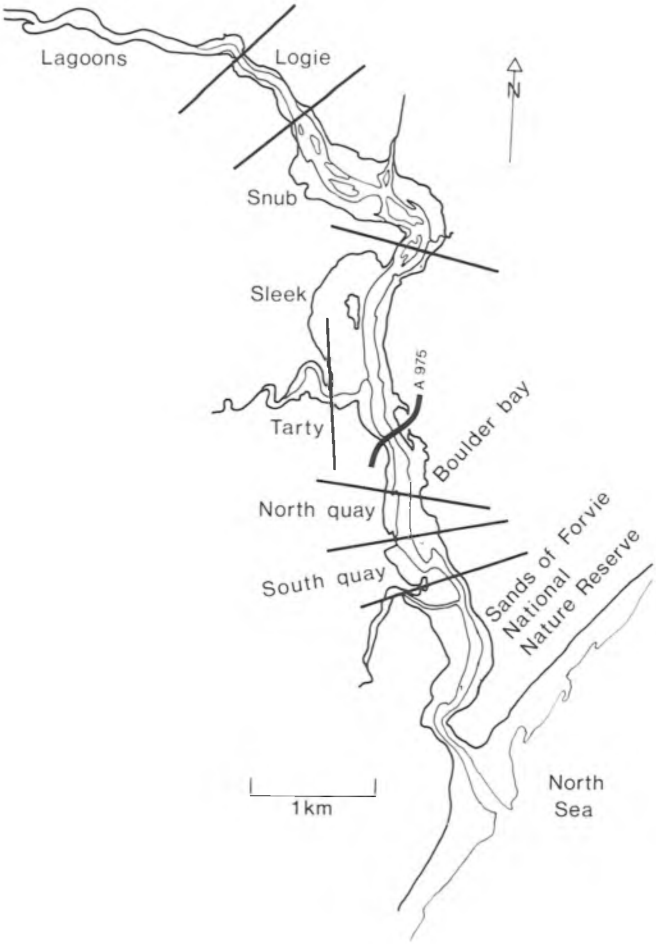

Figure 1. The Ythan estuary, showing subdivisions into nursery areas.

1973; Patterson *et al.* 1974). During the study, 88% of the pairs with broods had at least one parent colour-ringed.

Dyes such as Durafur Black R and yellow picric acid were also used, in five-spot combinations, to identify swimming adults (Patterson 1978). Both dyes remained visible until fledging in July/August.

Broods with unmarked parents could be identified by the facial pattern of the mother, or by their age, number and location. The latter was possible because broods which settled in one nursery area (Figure 1) usually stayed there until fledging (Williams 1974).

Daily brood census

A daily census was carried out from the middle of May when the first broods appeared, to early August when all had fledged. Observations were made at low tide when the broods were most active, starting in the morning if possible. We searched for all known broods, noted new broods, and recorded the number of ducklings in each brood. Disappearance of a duckling was taken to mean mortality. Most analyses were concentrated on the first 10 days of life of the ducklings, when mortality was highest. Since crêching or amalgamation (Williams 1973, 1974) affected the majority of broods we could not estimate the daily mortality rate of an individual pairs' own ducklings, only the rate for the ducklings currently in their care and the rate for all the broods in each nursery area. The data for the whole season were used to estimate overall fledging success, being the percentage of ducklings hatched which reached 40 days of age.

Densities of broods per ha were calculated for each day for each nursery area (Figure 1) separately, and for the whole estuary, from the number of broods present and the actual areas used by the broods that year.

Watches

Broods were watched from a vantage point overlooking a nursery area, preferably at 400 m or more from the nearest brood, to eliminate the possibility of disturbance. The Sleek and the North Snub areas (Figure 1) were most suitable, but some watches were also done at Logie. Watches were organized to coincide with the first 10 days of life. In 1975 a few adjacent broods were selected, but in 1976 all the broods in a nursery area were watched for 2–4 h at low tide by two observers (at high tide the broods usually rested on the shore line). The behaviour of the male, female and ducklings, and the largest and smallest distance between duckling and parent were recorded every five minutes and the mean duckling/parent distance was calculated.

The positions of the broods were plotted each 5 min on a large-scale map and nearest-neighbour distances between broods were measured later. On the North Snub (Figure 1), markers were placed along the shore line at 50 m intervals and the positions of the broods were recorded directly from the markers using two co-ordinates; distance along the shore and distance down the shore towards the waterline.

Detailed descriptions of all aggressive interactions between broods, including attacks on the ducklings, were recorded on Phillips dictaphones and the number of interactions per hour, their duration and the number of attacks on ducklings per hour were calculated.

Weather data

Weather data were mainly from a small meteorological station at the Aberdeen University Field Station at Culterty, 200 m from the lower estuary. Any data not obtainable at Culterty were taken from the Meteorological Office station at Dyce, Aberdeen, 17 km from the estuary. Although the microclimate on the mudflats undoubtedly differed to some extent from that at the meteorological stations, Mendenhall (1975) showed that there was a close correlation between data from the different sites.

The weather factors chosen were as follows:

temperature, to the nearest 0·1°C, at Culterty at 0900 h,
minimum temperature, also to the nearest 0·1°C, at Culterty over 24 h and collected at 0900 h on the next day,
rainfall, to the nearest 0·1 mm, at Culterty over 24 h and collected at 0900 h on the next day and
wind speed, to the nearest 0·1 m/s, at Dyce, using the mean of hourly readings for the 0900–0900 h period.

Since chilling would tend to increase with higher rainfall and wind speed but decrease with higher temperatures, the original temperature data were inverted to measures of 'temperature deficit' by subtracting from 20°C. The original wind speed data were recorded in knots and converted to m/s.

An index of total chill effect was obtained by combining the separate weather factors. Ideally such a measure should incorporate the precise way in which heat loss increases with increase in each of the weather factors (Falkowski & Hastings 1958; Lentz & Hart 1960). However, the effects of weather factors on the rate of heat loss must be determined empirically for each species and this has not been done for shelduck. As a crude first step, a chill index was calculated by adding together the values for three weather factors so that their numerical ranges and maxima were of a similar order, by the following formula:

$$\text{Index} = T + R + (2 \times W)$$

where T = temperature deficit (20 − temperature, °C)
R = rainfall (mm)
and W = wind speed (m/s).

In addition to these measures of daily variation in weather, an overall mean of the daily values was calculated for the main duckling period (15 May to 14 July) for years when an estimate of overall survival of ducklings from hatching to fledging was available. For each year we also calculated the number of days in the duckling season when each weather factor had a higher value than a 17-year mean (from the mid-May to mid-July period, 1960–1976), since a given season's mean could be made up of varying proportions of high and low extremes of weather.

Analysis

The weather data were analysed on the Aberdeen University Honeywell 66 computer, by correlation between weather factors and the percentage disappearance of ducklings in the same 24 h period or, when examining possible lag effects, up to 3 days later. Non-parametric correlation methods (Siegel 1956) were used since some factors (eg. number of broods or date) occurred as ranks of discrete values and so were not continuously distributed and because some of the measurements may not have had a normal distribution. The Kendal Correlation Coefficient was preferred since it allows the use of partial correlation analysis to control for the effect of a third factor on the correlation between two variables, although a statistical significance cannot be assigned to the partial coefficient. Such partial correlation was necessary because many of the variables were intercorrelated. In particular, the weather factors tended to correlate with each other and to decrease together with date. At the same time duckling density tended strongly to increase with date, making it difficult to separate the effects of the various factors on duckling mortality.

For most analyses, S.P.S.S. (Statistical Package for the Social Sciences, Nie *et al.* 1975) programmes were used.

Results

Brood ranges

The likelihood of aggressive interactions between broods may be affected by the pattern of useage of brood ranges. When the broods arrived on the estuary, the parents abandoned their territory and defended a moving area round the young as they fed. The ranges of several broods usually overlapped, but in general broods seemed to avoid each other. Williams (1973) found that older ducklings had larger ranges but in this study, broods tended to reduce their range as they were joined by other broods in the same area. Buxton (1975) found no clear correlation between the size of a range and the food abundance on it.

Birds which had at least three broods during the six years 1972 to 1977 were selected to test whether particular pairs used the same nursery area year after year. Only half of the pairs returned to the area they used the previous year (Table 1), but 90% used only one or two nursery areas out of a possible six. Some pairs were seen to return first to their previous nursery area, but were evicted by an earlier brood and then moved to a second area. If there was a change of mate between years, fewer birds used the same nursery area (Table 1).

Table 1. Fidelity to nursery areas. Data from birds which had at least 3 broods in 1972–1977.

	Number of pairs	Percentage which used the same area in next year
Pairs which stayed together	20	50
Male with a new mate	3	0
Female with a new mate	7	29

None of the differences between categories is statistically significant (Fisher exact test).

Older birds (over 6 years of age) did not hatch their broods earlier, did not tend to use particular nursery areas more and did not rear their ducklings more successfully than did younger pairs. There is no evidence that families of shelducks had a 'traditional' nursery area. Of 23 Ythan-reared females breeding for the first time, 39% returned to the nursery area on which they themselves were reared. This is not significantly different from the expectation if birds returned randomly to the nursery areas available (χ^2 test).

The adults defended their young vigorously from other pairs with broods, from other shelducks, and also from other species. Some of the last were potential predators of the ducklings. In 1975, 72% of 92 shelduck attacks on other species were directed at gulls, mainly Black-headed *Larus ridibundus* and Herring gull *Larus argentatus*. Eleven per cent of the attacks were on other ducks (Mallard *Anas platyrhynchos* and Eiders), and 11% were on waders. The frequency of attacks on other species was one per two hours per brood.

Hori (1964) found that later broods crowded together and crêched more rapidly than early ones, and Williams (1974) found that crêched broods survived less well than solitary broods. It therefore seemed likely that early broods might occupy the remoter areas of the estuary, and that these more isolated broods might be more successful. The first broods often did go to the remoter areas, the Lagoons, Logie and Tarty (Figure 1), but they were frequently joined by later broods, and were not successful in keeping the areas for their exclusive use. The exception to this was Tarty (Figure 1) which was very narrow and relatively undisturbed. The first brood to settle there usually remained isolated and the fledging success of ducklings in this area was significantly greater than that in the other nursery areas (Table 2). In 1975, the only year in which no young fledged in Tarty, three successive broods were present in the area at once, giving an initial total of 18 ducklings, all less than three days old. There are, however, statistical problems in these data since the chance of survival of one duckling in a brood is not independent of the chance of survival of others in the same brood. The percentage of broods which produced some fledgelings did not vary significantly between areas (Table 2). Tarty thus differed from the others only in having a larger number of fledglings per successful brood.

Aggressive interactions between brood adults

Aggressive interactions usually occurred when broods were less than 100 m apart (Figure 2). Fights between brood adults (Hori 1964; Williams 1974) were usually the result of a brood, often a new one, moving into the area occupied by another. The first sign of aggression was hunching of the back, a posture adopted mainly by the males, the head lowered and the back feathers raised. This was commonly followed by Head-pumping by the males and Inciting by the Females as the two broods converged. One of the broods might then move away and hostilities would die down. However, if the broods got closer, the interaction could escalate into one where the adults made attack charges without any actual contact, or one where attacks and fights with contact occurred. Males nearly always attacked and fought the male of the other brood and the most violent clashes occurred with all four birds fighting, male with male and female with female. Birds were pecked (often with feathers pulled out), beaten by wings, pushed under water or held down on the ground, but no serious injuries were recorded. Some possibly redirected attack was seen when brood adults suddenly left the fight for a few minutes and attacked an uninvolved nearby bird.

The outcome of some interactions was clear cut; the winner stood his ground, and the loser retreated. Occasionally both broods moved apart at the same time, especially when the broods had already had frequent encounters with each other. Both brood parents appeared to be necessary for success. A female alone was never seen to win against an attacking male, and so could not defend her ducklings. A male alone could win fights but seemed to be unable to keep the ducklings with him (the females did all the calling together of ducklings). Males also were never seen to shelter very young ducklings from bad weather by brooding them.

Attacks on ducklings

Attacks were also made upon ducklings, usually by the parents of another brood, but sometimes by their attendant adults. Interactions frequently started by ducklings being attacked by adults of another

Table 2. Fledging success in different nursery areas. Data from 1975, 1976 and 1977 combined.

	Total hatched		Percentage fledged	
Area	Broods	Ducklings	Broods	Ducklings
Tarty	10	56	50	57*
Sleek	17	122	47	34
Snub	28	189	46	33
Logie	14	130	43	35
Lagoons	12	86	33	33
Pools	14	117	43	32

* Percentage of ducklings fledging, Tarty vs other areas; $\chi^2 = 6{\cdot}7\text{–}9{\cdot}3$, $p < 0{\cdot}01$. None of the other differences is significant.

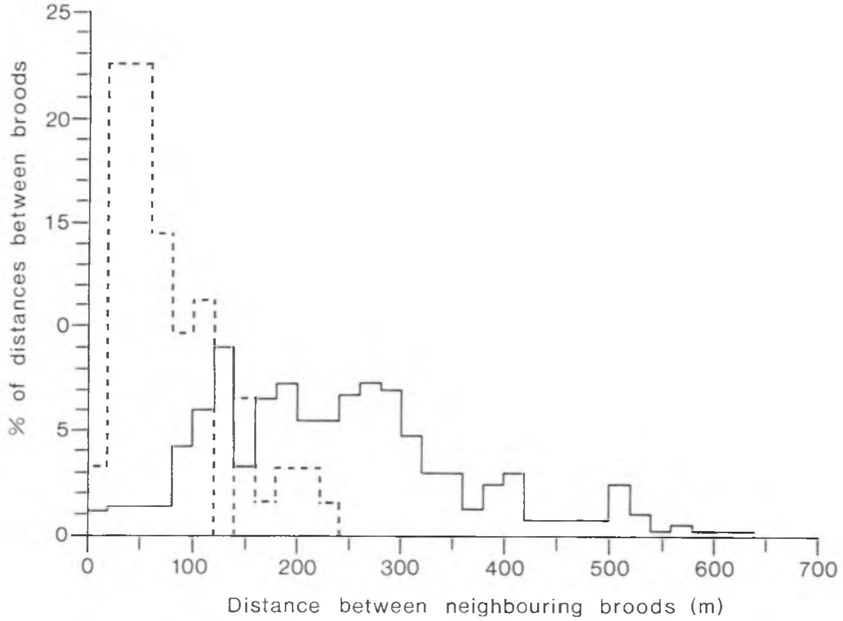

Figure 2. The distribution of nearest-neighbour distances between broods 5 min before an aggressive interaction (dotted line, n = 62) and when no interaction took place (solid line, n = 398). No statistical test is possible since consecutive distances were not independent of each other.

brood who were in turn attacked by the parents. Attacks on ducklings by adults could be severe. Ducklings were run down and bitten, picked up and beaten on the ground, or repeatedly pushed under water where they usually dived to escape. No duckling was seen to be killed. Such attacks occurred in 21–24% of all interactions (1975 and 1976).

Ducklings from different broods could mix together while their parents were fighting and attacks on ducklings by the accompanying adults were then common (Williams 1974). When the resultant crêche contained ducklings of differing ages and sizes the accompanying pair of adults singled out the 'foreign' ducklings for most of the attacks (Young 1964). When the ducklings in a crêche were all of similar size, the adults seemed unable to discriminate between the ducklings and all were attacked. An extreme example of this was seen in 1975 where all of a crêche of 20 ducklings, 6 of whom had been acquired the day before, were hounded for three and a half hours by the accompanying adult female. The male of the pair tried to defend the ducklings, and frequently attacked his own female when she attacked a duckling.

Adults attacked ducklings in their care in 10·6% and 4% of the total interactions in 1975 and 1976 respectively. Although such attacks were almost invariably associated with crêche formation, one incident was recorded in 1977 where there was no question of the brood having been involved in crêching. A new brood repeatedly approached an established brood then faltered, and both the male and female started pecking their own ducklings for a few minutes before retreating. It is possible that aggression was re-directed to the ducklings because the parents were afraid to attack the other pair of adults. Such attacks were not seen to drive ducklings away from the brood (see also Williams 1974).

The distance between the ducklings and their parents often changed during an interaction. In the brood being attacked there was a slight increase in the mean distance for older ducklings but none for younger ones (Figure 3). In some cases, the ducklings ran together in a tight group close to their parents after being physically attacked by other adults. In the attacking brood, especially with older ducklings, there was a considerable increase in the mean distance between the young and their parents during an interaction (Figure 3), largely through the adults leaving their brood to make the attack. Occasionally, single ducklings became separated from the rest of the brood and had to run or

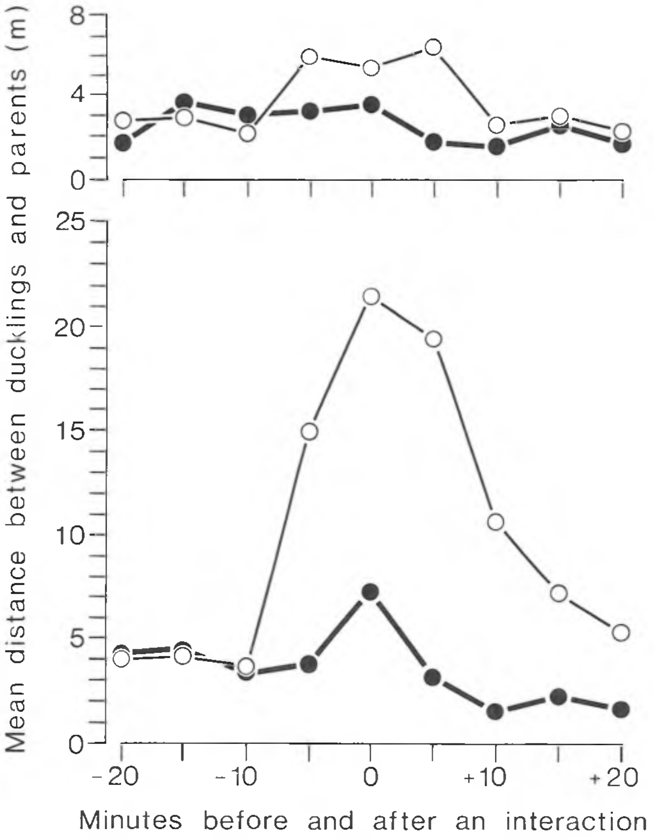

Figure 3. The mean distance between ducklings and their parents before, during and after aggressive interactions with other broods, in the attacked brood (upper figure) and the attacking brood (lower figure). The closed circles refer to ducklings less than 10 days of age and the open circles to older ducklings.

swim over 100 m to re-join it. This increase in distance from the parents might increase the risk from predators and one duckling was seen taken by a gull.

Duckling mortality factors

In 554 brood-hours of watching (plus some hundreds of hours spent on brood censuses over the three years) only two cases of predation were actually seen. In both cases a Herring Gull swooped and grabbed one of a group of well scattered ducklings on a mudflat. Only two dead ducklings were found during the three years, one being in a field 100 m from the estuary.

Hori (1964) considered Great-black-backed Gulls *Larus marinus* to be important predators in north Kent, and Jenkins *et al.* (1975) blame gulls and stormy weather for the deaths of ducklings at Aberlady Bay near Edinburgh. One ringed female (and one duckling) disappeared from a brood in 1977, and the female's body was subsequently discovered outside a known fox den.

Females were found to rear significantly fewer young to fledging in the season following a change of mate. There was no such relationship for males (Table 3).

Duckling mortality in relation to density

On the estuary as a whole, the percentage of ducklings under 10 days of age which disappeared in each 24 h period increased significantly with increasing number of broods present in 1976 and 1978 (Table 4). In both years there was a sudden increase in the daily mortality rate, from usually under 4% to over 10%, at the highest densities in that year (Figure 4A). The increase occurred above 18 broods in 1976 and, more strikingly, above 7 broods in 1978. In 1975 and 1977 there was no such relationship (Table 4) and daily mortality rates varied erratically, with no tendency to increase at high density (Figure 4B).

The difference between years remained when correlations between daily duckling mortality and weather factors were allowed for by partial correlation; indeed the coefficients were increased in 1976 and 1978 and reduced in 1975 and 1977, so accentuating the differences (Table 4). Even in the year with the best correlation (1978) the coefficient was not large; a Pearson correlation suggested that under 40% of the variation in duckling mortality could be explained by brood density ($r = +0{\cdot}62$; $r^2 = 0{\cdot}38$; DF = 32).

Table 3. Breeding success in relation to change of mate between years. Data from 1972–1977 combined.

	Number of ducklings hatched	Percentage of ducklings fledged
Males:		
Same mate as previous year	117	58
New mate	32	72
$\chi^2 = 1{\cdot}5$, $p > 0{\cdot}05$		
Females:		
Same mate as previous year	155	51
New mate	64	15
$\chi^2 = 12{\cdot}9$, $p < 0{\cdot}001$		

Neither the total number of ducklings present on the estuary nor the number of broods had a consistently higher correlation with disappearance of ducklings. Indeed the number of ducklings was so highly correlated with the number of broods (Kendal tau = 0·63 to 0·89; $p < 0{\cdot}001$ in all years), that these two factors could not easily be separated.

The lack of correlation between duckling density and mortality, in two of the four years, might have resulted from ignoring local variations in density. Consequently the main nursery areas, Sleek, Snub, Logie and Lagoons (Figure 1) were analysed separately in 1975, 1976 and 1977. Within any one area, the number of ducklings present at any one time was small, so that mortality had to be calculated for ducklings of all ages, not just for those under 10 days of age.

In none of the resulting 9 sets of data was there a significant correlation between duckling mortality and density (largest Kendal tau (Lagoons, 1977) = + 0·20; DF = 30; p = 0·11).

A number of other analyses also failed to show any correlation between duckling disappearance and density in 1975 and 1977.

There was similarly no evidence of a lag effect. Correlations between the disappearance of ducklings and density on the previous day, or one or two days earlier,

Table 4. Correlations and partial correlations between percentage of ducklings which disappeared from the estuary during each 24 h period and the number of broods present at the start of the period.

Year	Mean and maximum number of broods	Kendal Correlation Coefficient (tau)	Partial Correlation controlling for weather variable
			Temperature
1975	7·5	tau −0·09	−0·03
		DF 28	27
	11	p = 0·26	
			Minimum temperature
1976	12·7	tau +0·38	+0·45
		DF 44	43
	20	p = 0·001	
			Temperature
1977	14·1	tau −0·13	−0·002
		DF 38	37
	20	p = 0·13	
			Wind
1978	8·5	tau +0·53	+0·55
		DF 32	31
	12	p = 0·001	

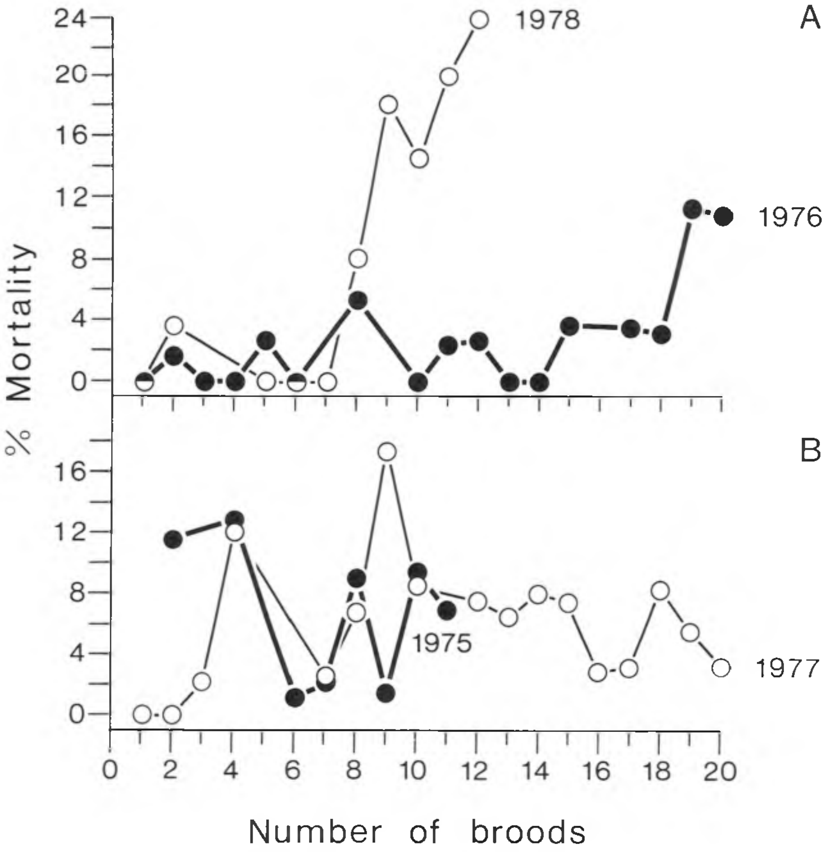

Figure 4. The percentage of ducklings under 10 days of age which disappear in each 24 h period, in relation to the total number of broods on the estuary at the start of the period.

were not consistently higher than correlations between the two variables measured in the same 24 h period.

The possibility that density might only be important in years with high brood density can probably be excluded. The two years with a high number of broods (1976 and 1977) included one year with a significant correlation between duckling mortality and density (1976) and one year with no correlation (1977) (Table 4). The two years with a lower number of broods (1975 and 1978) showed a similar variation.

Frequency of aggressive interaction between broods in relation to density

The frequency of aggressive interaction between broods increased significantly with increasing density of broods in both 1975 and 1976 (Table 5). The frequency of interactions which involved physical attack on the ducklings of either of the broods also increased to some extent with brood density in both years although the correlation was barely significant (Table 5). Partial correlation, controlling for seasonal changes in density and interaction frequency reduced the correlations to some extent, particularly the one between density and physical attack on ducklings in 1976.

Experimental manipulation of brood density

In an area of the estuary containing 4–5 broods, the density was increased experimentally on two occasions by a person moving upstream to push the nearest broods closer together for three hours. The experimental session was preceded and followed by undisturbed control sessions on adjacent days with the same total number of broods and with similar weather.

Table 5. Correlations and partial correlations between the frequency of aggressive interactions among broods and the density of broods per ha in the observation area.

Year	1975		1976	
Measure of aggression	Kendal Correlation Coefficient	Partial Correlation controlling for date	Kendal Correlation Coefficient	Partial Correlation controlling for date
Total interactions, per brood per hour	tau +0·51 DF 16 p = 0·004	+0·40 15	+0·42 20 0·004	+0·35 19
Physical attacks on ducklings, per duckling per hour	tau +0·33 DF 16 p = 0·053	+0·27 15	+0·29 20 0·050	+0·17 19

Since only the broods nearest to the disturbance were likely to be affected, the measurement of density over the whole area would be misleading and was replaced by estimates of mean nearest-neighbour distance between broods, measured from plots of the position of each brood every 5 min. Mean values for nearest-neighbour distance and frequency of interaction were calculated for each hour of observation.

The presence of a person at one end of the area did result in the mean nearest-neighbour distance of the 2 broods nearest to the disturbance being significantly reduced relative to the mean distance between broods without disturbance.

The frequency of aggressive interaction between the artificially crowded broods was significantly higher than that between control broods (Table 6). The frequency of all aggressive interactions in a given hour of the experiment also increased significantly with decreasing mean nearest-neighbour distance between the broods ($r = 0{\cdot}558$, $n = 59$, $p < 0{\cdot}001$).

Thus the experimental crowding of broods showed clearly that aggressive interaction between broods did increase with increasing brood density, and so confirmed the observational data.

Table 6. Mean frequency of aggressive interaction between broods during crowding experiments. The samples (n) are one-hour observation periods.

	Control periods	Experimental periods
Mean interactions per brood per hour	0·23 ± 0·10 n = 8	1·30 ± 0·17 n = 5
Mann-Whitney U = 1, p < 0·002		

Duckling mortality in relation to the frequency of aggressive interaction between broods

In areas of the estuary containing several broods, the percentage of ducklings which disappeared was measured for 24 h periods which contained a 3 h observation of the frequency of aggressive interaction between broods. In 1975, disappearance of ducklings increased significantly with increasing frequency of interaction, though not with increasing frequency of physical attacks on ducklings (Table 7). In 1976 there was no correlation between mortality and frequency of interaction and in neither year were the results greatly affected by partial correlation to control for any effect of density.

An alternative analysis of the same data, based on the individual broods, was possible in 1976 but not in 1975 when too few separate broods were observed. Since the interactions involving a particular brood were not independent of those of the neighbouring ones, a different measure of interaction, the number of physical attacks suffered by the ducklings of each brood, was used. The percentage of ducklings in a brood which disappeared during their first 10 days of life increased significantly with increasing frequency of physical attacks suffered by the ducklings (Table 8). This result differs from that of the previous analysis for 1976 (based on all interactions and disappearances in whole areas) but the difference is difficult to interpret since the two analyses differ in the way they use the data. The difference is unlikely to be caused by density effects since again the correlations were only slightly reduced by partial correlation analysis (Table 8).

The results provide only qualified support for the original hypothesis that increasing brood density would lead to an increase in the frequency of aggressive interaction which in turn would lead to increased mortality of ducklings. The first difficulty for the hypothesis is that the predicted increase in duckling mortality with increasing density occurred in only 2 of the 4 years and was not shown within individual nursery areas, even when the possible influence of weather was excluded by partial correlation.

The predicted increase in aggressive interaction with increasing density did occur in both of the two years examined, although this relationship did not extend to the frequency of physical attacks on ducklings when seasonal effects were controlled. However, the increase in frequency of interaction with density was confirmed by experiment. Perhaps the most serious difficulty is the lack of a consistent increase in duckling mortality with increasing frequency of aggressive interaction between broods, so that in 1976 measurement based on mortality within areas showed no such relationship while measurement based on losses from individual broods showed a significant one. Of these two conflicting results, the one based on broods is probably the less reliable since mortality was measured over a 10-day period which may have included only one (though usually more) 3 h observation of the frequency of aggression.

Thus, due to inconsistencies between years, brood density and aggressive interaction cannot completely explain variations in the disappearance of ducklings. The importance of other factors must be considered and of these, weather was thought to be the most likely to affect duckling mortality.

Overall duckling survival in different years, in relation to weather

There was no significant correlation between overall duckling survival from hatching to fledging in a given year and the mean value of any weather factor for that season (highest Kendal tau (temperature) = 0·34, p = 0·088). However, duckling survival increased significantly with increasing number of warm days in the season, i.e. num-

Table 7. Correlations and partial correlations between the percentage of ducklings which disappeared from an area in 24 h and the frequency of aggressive interactions between broods, in the same area in a 3 h observation during the same period.

Year	1975		1976	
Measure of aggression	Kendal Correlation Coefficient	Partial Correlation controlling for date	Kendal Correlation Coefficient	Partial Correlation controlling for date
Total interactions, per brood per hour	tau +0·51 DF 16 p = 0·004	+0·38 15	−0·05 20 0·396	−0·13 19
Physical attacks on ducklings, per duckling per hour	tau +0·02 DF 16 p = 0·462	−0·15 15	−0·01 20 0·485	−0·04 19

Table 8. Correlations and partial correlations between the percentage of ducklings which disappear from a brood in their first 10 days and the frequency of attacks suffered by the ducklings of that brood in at least one 3 h observation during those 10 days (data from 1976 only).

Measure of attack	Kendal Correlation Coefficient	Partial correlation, controlling for broods per ha
All attacks on ducklings, per duckling per hour	tau +0·47 DF 18 p = 0·004	+0·37 17
Physical attacks on ducklings, per duckling per hour	tau +0·46 DF 18 p = 0·006	+0·33 17

ber of days when the daily mean temperature was above the overall mean for the 17 years from 1960 to 1976 (Figure 5a, Table 9). Similarly, overall duckling survival decreased significantly with increasing number of windy days in the season (Figure 5b, Table 9). There was no significant correlation between duckling survival and the number of rainy days in the season or the number of ducklings hatched that year (Table 9).

The correlations were not substantially altered by partial correlation analysis and the correlation between duckling survival and temperature was increased when controlling for rain (Table 9). There was some mutual effect between temperature and wind, presumably because windy days tended also to be cooler giving a negative correlation between the number of warm days and the number of windy days in the season (Kendal tau = − 0·41, p = 0·053).

There is thus some evidence that overall duckling survival was affected by overall weather in the season, which raised the possibility that daily mortality might be related to the immediate weather.

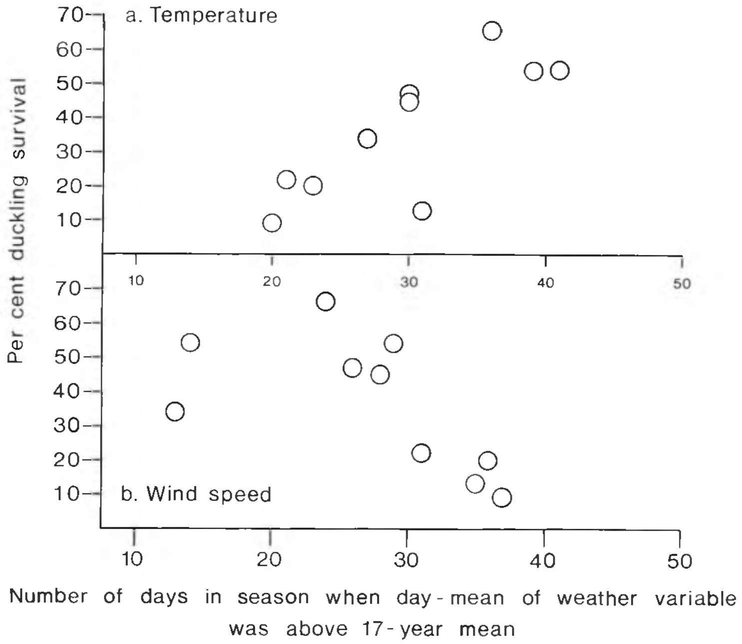

Figure 5. Overall duckling survival (per cent fledging of those hatched) in relation to the number of days in the season (15 May to 14 July) when the day-mean for a weather variable was greater than the 17-year mean from 1960 to 1976. Survival data from 1962–1964 and 1970–1976.

Table 9. Correlations and partial correlations between overall duckling survival in a year and the number of days in the season when each weather variable was above a 17-year mean value.

Variable	Kendal tau*	p	Partial correlation, controlling for:
Temperature (0900)	+0·61	0·007	wind, +0·51; rain, +0·66
Wind	−0·58	0·010	temp., −0·47; rain, −0·56
Rain	+0·30	0·131	temp., +0·43; wind, +0·22
Number of ducklings hatched	+0·32	0·104	

* 8 degrees of freedom in all cases.

Daily duckling mortality in relation to weather

There was considerable variation between years in the extent to which daily duckling mortality was correlated with weather, in which of the factors were involved and in the degree of lag between weather changes and subsequent changes in mortality (Table 10). In 1975, the daily disappearance of ducklings increased with lower temperature at 0900 h on the same day and with increasing wind speed two days before. In 1976, none of the weather factors was significantly correlated with duckling mortality except if brood density was controlled by partial correlation, when mortality increased with lower minimum temperature one day before. Duckling mortality in 1977 increased significantly with lower temperature at 0900 h on the same day, with lower minimum temperature two days before and with both higher wind speed and higher values of the combined weather index three days before. However, the correlation between mortality and the weather index was greatly reduced by partial correlation controlling for brood density (Table 10). In 1978, duckling mortality increased significantly with increasing wind speed on the same day, and with lower temperature at 0900 h, lower rainfall and lower values of the weather index one day before. Altogether, 9 significant correlations were found among the 16 possible combinations of 4 weather factors in 4 years.

Thus, in each of the 4 years, variations in the daily disappearance of ducklings were significantly correlated with daily variation in one or more of the weather variables, although different ones were involved in different years. Low temperature, either at 0900 h or the 24 h minimum, was involved in each year and wind in 3 of the 4 years but rain was important only in 1978 as was the combined weather index. Most of the correlation coefficients were only slightly reduced when the effect of brood density was allowed for by partial correlation analysis and two, between mortality and minimum temperature in 1976 and wind speed in 1978, were increased.

There was evidence of a lag effect, in that several of the correlation coefficients reached their maximum values when mortality was related to weather on the previous day rather than to weather in the 24 h period when the ducklings had actually disappeared. More of the coefficients reached a maximum with a one-day lag, compared to longer lags of 2 or 3 days.

The difference in the lag periods of different factors explains why the combined weather index was rarely correlated with duckling mortality at any given lag. Indeed, allowing for density effects, the weather index was significantly correlated with duckling mortality only in 1978, which was the only year when even two of the weather factors (temperature and rain) reached their maximum correlation coefficients with the same degree of lag.

The results show clearly that the daily rate of disappearance of ducklings tended to increase significantly in poorer weather. The inconsistency between years is perhaps not surprising, since the mean values of the

Table 10. Correlations and partial correlations between the percentage of ducklings which disappeared in each 24 h and weather factors in the same period or in earlier periods (lag). Non-significant correlations have been omitted.

Year and factor	Lag (days)	Kendal Correlation Coefficient			Partial coefficient, controlling for broods per ha
		tau	DF	p	tau
1975, temperature	0	+0·26	45	0·029	+0·24
1975, wind speed	2	+0·23	45	0·048	+0·23
1976, min. temperature	1	+0·14	54	0·107	+0·30
1977, temperature	0	+0·24	58	0·019	+0·20
1977, min. temperature	2	+0·32	58	0·002	+0·24
1977, wind speed	3	+0·26	58	0·011	+0·20
1977, weather index	3	+0·22	58	0·028	+0·10
1978, wind speed	0	+0·21	57	0·043	+0·27
1978, temperature	1	+0·36	57	0·002	+0·28
1978, rain	1	+0·34	57	0·005	+0·27
1978, weather index	1	+0·41	57	0·001	+0·35

weather factors varied considerably between years. For example, the mean daily rainfall in the duckling period was 4 times higher in 1978 than in 1975 or 1976 (Table 11a), and a given weather factor may not have any effect on mortality until it exceeds a threshold value. This was tested by comparing the distribution of significant correlations between mortality and weather with the distribution of mean values for the weather variables in the different years (Table 11a). There is a highly significant tendency for duckling mortality to increase with poorer weather only in years when that weather factor was worse than the mean for the four years (Table 11b). There were no exceptions to this in 1977 and 1978 and the exceptions in the other years were either close to significance (min. temperature, 1975), only significant when controlling density (min. temperature, 1976) or the year mean values were close or equal to the overall mean (temperature and wind, 1975). Thus it appears that weather factors were not correlated with duckling mortality in years when the factor was 'better' than average, which might indeed suggest a threshold below which the factor has no effect.

A one-day lag effect of weather on duckling mortality is consistent with the hypothesis of indirect action of weather chill on mortality by increasing the rate of energy loss and thereby increasing the chance of mortality some time later. The possibility that bad weather might kill ducklings directly and quickly, say by 'exposure', is largely excluded. It is difficult, however, to explain why different factors had lags of different length and especially why the same factor differed in its lag between years. One possibility is that the degree of lag may depend on the severity of the factor in any given year, since this is known to vary (Table 11a).

Discussion

Since the mortality of young shelducks increased to some extent with brood density and aggressive interaction and also with adverse weather, we might ask which of these factors has the most important effect and to what extent they jointly explain variations in mortality.

Duckling mortality increased with increasing density in only 2 years out of 4 and with increasing aggressive interaction in only one year of two, whereas mortality increased with adverse weather factors in all 4 years studied. The significant Kendal Correlation Coefficients (tau), controlling for other factors, were +0·45 and +0·55 between mortality and density, +0·38 between mortality and frequency of aggression and ranged from +0·20 to +0·35 between mortality and weather factors,

Table 11. Correlations between weather factors and duckling mortality (*) in relation to mean weather for the duckling period in each year (mean values greater that the 4-year mean are underlined). Temperatures are deficits (from 20°C).

(a)

Weather factor	Mean over 4 years	1975	Mean in: 1976	1977	1978
Temperature (°C)	7·2	6·9*	6·6	7·6*	7·7*
Min. temperature (°C)	11·9	13·4†	11·1(*)	12·1*	11·6
Rain (mm)	1·5	0·8	0·8	1·3	3·2*
Wind speed (m/s)	4·3	4·3*	3·6	4·8*	4·7*

(*) Only significant when controlling density.
† p = 0·053.

(b)

		Correlation between weather and mortality: significant	non-significant
Weather factor mean value in relation to 4-year mean;	above mean	6	1*
	below mean	2	6

Fisher exact test; p = 0·032

* p = 0·053.

with similar sample sizes. Thus although density and aggressive interaction did not have a consistent effect on duckling mortality, in years when there were significant correlations, these tended to be higher than those between mortality and weather.

The extent to which variations in both density and weather could together explain variations in duckling mortality can be estimated from multiple regression analysis, though the results must be viewed cautiously since parametric statistical methods may not be valid with these data. The proportion of the variation in duckling mortality (r^2) which was explained by a combination of density and three weather variables was 15, 33, 6 and 47% in the 4 years, 1975 to 1978 (Table 12). This analysis confirmed the earlier ones in showing that density was important only in 1976 and 1978, when it explained 15 and 38% of the variation in mortality, compared to 2 and 0·1% in 1975 and 1977. Conversely the weather factors were more important in 1975 and 1977, although in these years less of the variation in duckling mortality was explained by all the factors together (Table 12). Again, this analysis confirmed that weather factors tended to be less well correlated with mortality than was density (when significant), and explained only 6 to 18% of the total variation in mortality.

It is clear that in all 4 years, and especially in 1975 and 1977, there were other important factors affecting duckling mortality. We have no data on other mortality factors, but there are a number of possibilities. Mendenhall (1975) has suggested that the frequency of predation may vary with changes in the number of predators and variation in their alternative food supplies. It is also possible that duckling food supply varied in ways not related to brood density or weather. Although the identity of other mortality factors is not clear, we can probably eliminate those which varied seasonally. When the effects of brood density and weather factors were controlled by partial correlation, any apparent correlation between mortality and date in the season disappeared completely (tau = −0·002 to −0·06).

Since simple effects of weather on duckling mortality are not likely to change with brood density and since density effects on mortality did not occur every year, it does not seem likely that density-dependent mortality is consistently important in limiting the production of fledglings in the Ythan population of shelduck.

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Table 12. Multiple regression of the percentage of ducklings disappearing in 24 h on brood density and weather variables.

Year and weather factor		Multiple regression coefficient, r	r^2	Increase in r^2
1975	rain	0·30	0·09	0·09
	wind	0·35	0·12	0·03
	temperature	0·36	0·13	0·01
	density	0·39	0·15	0·02
1976	density	0·38	0·15	0·15
	min. temperature	0·57	0·32	0·17
	rain	0·57	0·33	0·01
	wind	0·57	0·33	0·003
1977	temperature	0·21	0·04	0·04
	wind	0·23	0·05	0·01
	rain	0·24	0·06	0·01
	density	0·24	0·06	0·001
1978	density	0·62	0·38	0·38
	wind	0·69	0·47	0·09
	rain	0·69	0·47	0·003
	temperature	0·69	0·47	0·0002

Summary

The daily mortality rate of ducklings of the Shelduck *Tadorna tadorna* increased significantly with density of broods on the Ythan estuary, Aberdeenshire, in two of four years (1975–1978). Aggressive interaction between broods increased significantly with brood density in both of two years and this was confirmed by crowding experiments. The daily mortality rate of ducklings also tended to increase with increasing frequency of aggressive interaction between broods.

The overall survival of ducklings in any year increased significantly with increasing number of warm days in the season and decreased significantly with more windy days. There was no correlation between survival and either the number of rainy days or the number of ducklings hatched.

The daily mortality rate of ducklings increased significantly with adverse weather in all four seasons. Although different weather variables were involved in different years, duckling mortality increased significantly with low temperature in all four years, with high wind speed in three, but with rainfall in only one year. Duckling mortality tended to increase with worsening weather only in years when that weather factor was more severe than average and the mortality tended to follow one day after a worsening of the weather, rather than occurring immediately.

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