

Territorial Use and Feeding Behaviour in the Breeding of the Common Shelduck *Tadorna tadorna* L.

by Nigel E. Buxton

1. Introduction

This paper presents a hypothesis for the importance of a good feeding site during breeding and its possible implications for the success of incubation and the rearing of ducklings. The fieldwork was carried out as part of a larger study during the period 1972–1974.

The common shelduck begins to return from its moult migration to the Ythan Estuary, Aberdeenshire in late December or early January. Consequently numbers increase through to May as firstly the older birds arrive, followed later by the immatures. From December through to March or April the birds associate in flocks in specific localities through the estuary. At the onset of breeding there is a change in dispersion as pairs separate from the flocks and occupy favoured areas or feeding territories (HORI 1964, YOUNG 1970, WILLIAMS 1973). The territories are used solely as feeding sites, the nest being generally situated away on Forvie Moor. All the non-breeding birds form a flock frequenting the sand bars in the inner estuary. Upon the hatching of ducklings there is a further change in dispersion as the territories, in the majority, are abandoned and other, usually unrelated, areas taken as brood ranges.

2. Study area

The Ythan Estuary is situated 21 km. north of Aberdeen (Fig. 1) in the north-east of Scotland. It is about 8 km long and averages 300 m wide throughout its length. The substratum is a mixture of muddy shores and flats with patches of sand and gravel. In the lower half of the estuary there are extensive mussel (*Mytilus edulis*) beds and salt intrusion at high tide remains practically undiluted, except during October–December, as far as the Quay (LEACH 1969).

Territories are scattered throughout the estuary, and two areas were selected for detailed study. The Tarty Mudflat is a small isolated mudflat on a tributary stream situated to the south-west of the Sleek of Tarty. The only areas without steep banks are those on the south-west and south-east corners which allow the entry and exit of the burn. The enclosed area is approximately 18 hectares of mud and supports a high density of shelduck pairs. The Forvie Burn Mouth is an area near the main river channel which, at low tide, is approximately 175 metres from the high-tide mark.

Brood ranges occurred mainly throughout the area from Boulder Bay to Logie Buchan.

To the east of the estuary is the Sands of Forvie National Nature Reserve. At the narrow southern-most end, the dunes are mobile but further north there is extensive heather (*Calluna vulgaris*) cover which supports large colonies of rabbits (*Oryctolagus cuniculus*). The majority of nesting shelduck use the deserted burrows of these animals.

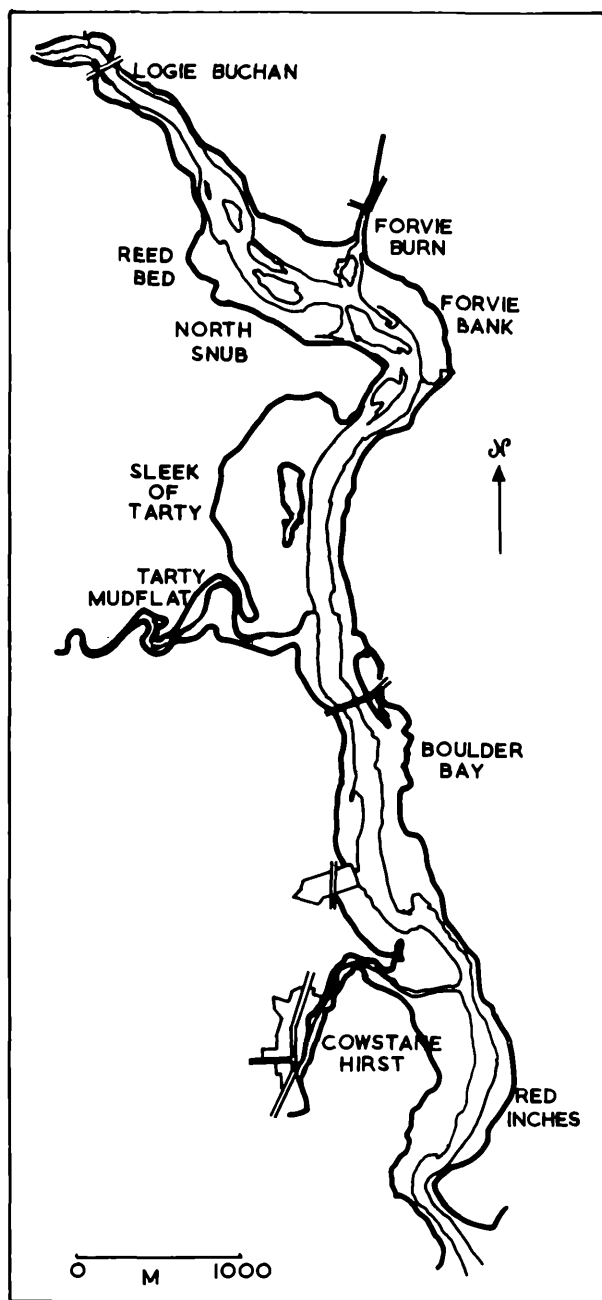


Fig. 1.

Map of the Ythan Estuary showing the main areas used by shelduck.

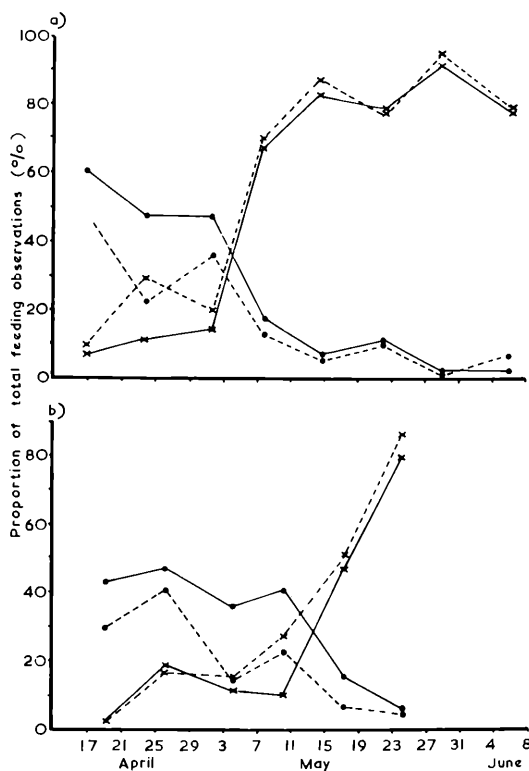


Fig. 2.

Feeding methods used on territories through the breeding season. a) Tarty. b) Forvie Burn.
 × - Pecking ● - Sieving — Male --- Female

3. Results

3.1 Territorial use.

The importance of the territory for feeding was assessed by collecting all the sightings (during the period of territorial behaviour) of the pairs holding territories in 1972 in the study area (excluding high tide roosting and visits to the Moor nesting areas. The sightings on the territory were expressed as the proportion (%) of the total (Table 1).

Table 1. The proportion of sightings of study area pairs on the study area territories.

Locality	No. of pairs	Total individual records	No. on territory	% on territory
Tarty	9	183	178	97.3
Forvie Burn	10	187	181	96.8
Total	19	370	359	97.0

Table 2. Territorial use by males and females.

Locality	Total male records	No. on territory	%	Total female records	No. on territory	%
Tarty	81	78	96.3	102	100	98.0
Forvie Burn	86	83	96.5	101	98	97.0
Total	167	161	96.4	203	198	97.5

Although 6 (32%) of the 19 pairs were, on at least one occasion, noted away from the territory, more than 95% of the individual records were on the territories. There was no difference in the use of the territory by males and females (Table 2).

Unfortunately similar data were not available for 1973 but again only a few pairs fed extensively in areas other than their territory. One pair was known to have used two localities as a territory and another to have gradually abandoned one area in favour of a second. Occasionally pairs were either known or suspected of feeding elsewhere, especially when females were incubating; nest recorders in burrow entrances sometimes showed an absence by females when there was no corresponding attendance at the territory. Since incubating females spent the majority of their time feeding whilst off the nest, it was likely these birds fed somewhere other than on territory whilst absent. Despite these exceptions the majority of pairs were extremely faithful to the chosen feeding sites and once these were selected most birds confined their feeding activities to them.

3.2 Daily attendance patterns at territory

The behaviour of territorial pairs was observed during daylight hours in a series of 20 dawn to dusk watches. The diurnal patterns of attendance by the birds was found to be characteristic of the breeding cycle and thus changed through the season.

a) Prelaying was characterised by the presence of both the male and the female once the pair was in permanent possession of the territory. Initial occupation consisted of short visits.

There was a wide variation in both the percentage of daylight hours spent on territory (attendance) and the proportion of the daylight time on the territory spent feeding (P. S. F.) by both males and females. However there was no correlation between the two for females. The pairs with low attendances were those pairs which were suspected of having spent the early morning at parliaments on the moor. Low attendances were especially prominent when high tide was after midday and pairs also roosted away from the territory.

In the majority of pairs the attendance of the male was similar to that of the female with a mean value of 60% (Table 3). There were slight differences, with the males' attendance being higher, due to their occasionally settling into the territories one or two minutes before the female. Over all this was not significant.

Males did feed for a significantly smaller proportion of the time than females ($P < 0.001$, Mann Whitney U-test). BENGTON (1972) found that female harlequin ducks (*Histrionicus histrionicus*) fed for about 30% more of their time than males prior to laying, compared to 20% in this study.

Table 3. The attendance and P.S.F. by pairs on the territory.

Activity	No. of pairs observed	FEMALE				MALE			
		% Attendance		Proportion of time spent feeding		% Attendance		Proportion of time spent feeding	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Prelaying	52	60.4	17.8–96.7	64.5	31.2–96.4	60.6	17.8–96.7	43.6	12.3–78.9
Laying	12	76.4	29.9–93.1	66.4	50.0–82.9	86.5	35.7–99.1	37.3	25.0–46.4
Incubating	25	21.2	6.5–54.3	82.6	51.4–95.5	85.4	48.0–99.2	34.0	18.4–50.5

The P. S. F. of males was greater than that of their respective mates in only five out of 52 (10%) observations and three of the pairs involved were observed on other occasions when the females fed more. When males did feed for more than their mates it was not extensively so; none had a P. S. F. greater than 8% more than his mate. Some males on Tarty fed for a very small proportion of their time (<25%) but these low levels were not necessarily reflected in the behaviour of their respective females.

b) Laying was the most difficult stage of the breeding cycle to identify since it depended upon a single daily absence of the female. This absence had a mean duration of 2 hrs. 20 min. (range 0 hrs. 30 min – 4 hours 49 min) compared with 2 hrs. 18 min. in an earlier study (WILLIAMS 1973) and 20–30 minutes at Sheppey (HORI 1964). After escorting the female to the nest site the male usually returned to the territory and remained there alone until the female's return.

The feeding behaviour during laying was very similar to that during prelaying (Table 3) but the attendance by both sexes was greater ($P < 0.001$ Mann Whitney U-test). Since nest prospecting had now ceased there were no longer large absences during the early morning, resulting in the increase in attendance. The attendance of only one female was less than 60%, and the attendances of 11 out of 12 males were >70%, but as a result of the egg-laying absence, males spent a slightly longer period of time on the territory than females ($P < 0.05$ Mann Whitney U-test).

The P. S. F. by both males and females varied rather less than during prelaying, but the mean values within each sex were rather similar. Although the mean P. S. F. by the males during laying was slightly less than that during prelaying ($P < 0.05$ Mann Whitney U-test) there was no difference between those of the females. This, together with the difficulty of reliably separating the two stages on a single short absence alone, caused prelaying and laying to be analysed further together as preincubation.

In 8 out of 12 observations on laying birds, females spent 60–80% of their time feeding. On no occasion was the P. S. F. by any male greater than that by his mate, and females fed consistently more to such an extent that even the female with the lowest P. S. F. fed more than any male.

c) Incubation was characterised by the long periods of absence from the territory by the female. Except for females being absent from the territory without exception (confirmed by data from the nest recorders) during the hours of darkness, the attendances were neither diurnally nor tidally orientated. This was noted similarly by HORI (1964). Males took no part in incubation and rarely left the territory except when called by an incoming female or to escort a female back to the nest.

Both the evidence from nest recorders and direct observation showed that the long absences from territory signified incubation. During the two years of study, a total of 19 pairs with the female absent for long periods from the territory were seen to fly back to the moor nesting sites on 26 occasions after feeding bouts. On four of these occasions, females were seen to enter nesting burrows on the edge of the moor, whereupon the male left and returned to the territory. The only exception to this was a pair which was known to have a nest on the west side of the estuary and consequently flew in that direction.

The onset of incubation brought about a large scale change in the females attendance (Table 3) which was significantly lower than that during both prelaying and laying ($P < 0.001$ Mann Whitney U-test). The longest time spent on territory was 8 hours 20 minutes and the shortest 1 hour 06 minutes. The average length of time spent on territory during incubation was approximately $3\frac{3}{4}$ hours which was accomplished by an average of 2.3 attendances. WILLIAMS (1973) suspected that any females appearing for less than 13% of available daylight on territory were likely to fail. From 25 observations during 1972/73 on incubating females, the attendance fell below this on only 3 occasions. However, none of the pairs involved did so consistently and one of the pairs did successfully hatch a brood. The attendance by females was not correlated with their P. S. F. but there was a trend ($P < 0.10$) for the latter to be least when the attendance was greatest. Thus the above female may have been able to compensate although her P. S. F. was only slightly higher (3%) than the mean value.

In contrast, males spent a large proportion of daylight hours on territory (Table 3). This was significantly greater than that by the females. In addition it was significantly greater than that previously by males during prelaying ($P < 0.001$ Mann Whitney U-test) but not during laying.

The high P. S. F. by females emphasised the importance of the territorial attendances. On all occasions except three the females fed for more than 75% of the time. On two of the three exceptions the birds were present for periods longer than the average. The third female spent less than the average on the territory and it is perhaps significant that the pair did not produce ducklings. The high level of feeding was significantly greater than that of prelaying, laying, and that of males during incubation ($P < 0.001$ Mann Whitney U-test). This allowed a minimum of other activities except drinking and bathing, which most females did before returning to the nest.

The P. S. F. by males was lower than that during prelaying ($P < 0.01$ Mann Whitney U-test) but not lower than that during laying.

Thus overall, although attendance and P. S. F. by males changed only slightly from prelaying to incubation, there was a large-scale change in the behaviour of the female.

3.3 Feeding behaviour.

Of 1685 feeding observations made on shelduck flocks 938 (55.7%) involved sieving and only 7 (0.4%) involved pecking. During the occupation of the territories there was a radical change in the feeding method (Fig. 2). Out of 4379 feeding observations on territories, sieving accounted for only 21.0% and pecking for 48.4%.

The change occurred earlier at Tarty but equally rapidly in both areas once it had begun. From mid-May on the Tarty the proportion of pecking reached a high level ($> 80\%$) for both males and females and remained high whilst the birds were territorial.

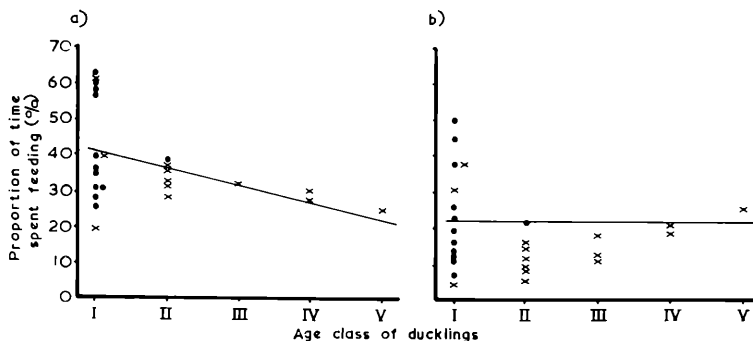


Fig. 3.

Proportion of time spent feeding over the first six hours of a tidal cycle by the parents of broods in relation to the age of the brood. a) Female, $y = 44.87 - 4.61x$. b) Male $y = 24.65 - 0.76x$.
x 1972 • 1973.

The behaviour of the female paralleled that of the male on both Tarty and Forvie, and although the proportions of both sieving and pecking by the females differed from those of the males they were not significantly so.

3.4 Feeding behaviour on the brood ranges.

a) Parents with young broods (<10 days)

The feeding behaviour of broods and their parents was observed for one complete tidal cycle during the first ten days of life. Although there was wide variation in the proportion of a tidal cycle spent feeding by both males and females (Table 4), in general, as on the territories, the latter fed to a greater extent than the males. Overall the proportion of a tidal cycle spent feeding tended to be least in the mid-estuary (Table 5).

In 1973 there was a slight decrease in the feeding by females as the age of the brood increased, although it was not significant. In the instance of Brood 9 being observed twice, the feeding of the female was 10% less after seven days than on the first occasion.

b) Parents with older broods

Data were collected on broods older than 10 days during the two years of study. Using plumage classes defined by WILLIAMS (1973) as a time scale (i. e. increasing time from hatching) the proportion of the tidal cycle spent feeding by the parents of all broods were plotted against duckling age.

Although not significant there was a trend for both parents to feed longer when the broods were younger. The majority (83%) of broods observed over a tidal cycle were of age Classes I and II, which, since leaving the older broods under-represented in the above trend, placed considerable emphasis upon the single observation of a Class IV brood. However, seven broods of which six were Class III–V's were observed for the first six hours of a tidal cycle. Since the feeding of parents watched for the first six hours was highly correlated ($P < 0.001$) with their feeding over the full twelve hours, the

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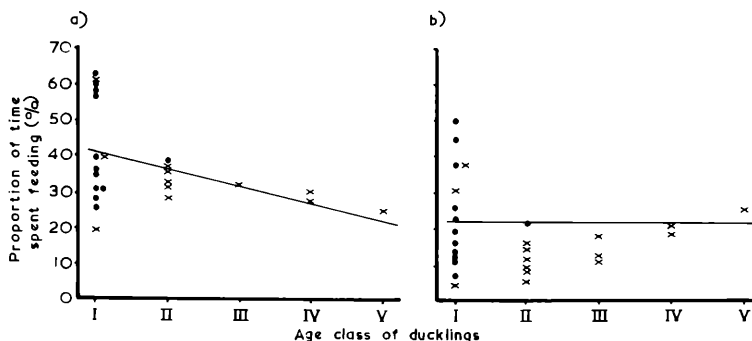


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Table 4. The proportion of a tidal cycle spent feeding by the parents of young broods.

Brood No.	Proportion of time spent feeding by female	Proportion of time spent feeding by male	Age of brood (days)
1	38.2	38.8	—
2	58.2	27.5	—
3	36.8	22.6	8
4	35.4	15.3	6
5	27.6	17.9	6
6	27.3	21.1	8
7	23.6	5.1	5
8	45.1	36.6	6
9	49.3	35.4	10
9	38.9	36.8	3
10	53.4	33.1	2
11	35.0	18.1	4
12	31.5	22.1	5

Table 5. The proportion of a tidal cycle spent feeding in different areas of the estuary by the parents of young broods.

Area	Proportion of time spent feeding by female	Proportion of time spent feeding by male
Boulder Bay	36.8	22.5
Tarty	31.7	16.2
North Sleek	25.4	13.0
North Snub	41.5	36.7
Logie Buchan	33.3	20.1
Average	33.5	21.8

proportion of the tidal cycle spent feeding during the first six hours could be used as a measure of feeding. Again females fed to a greater extent when the ducklings were young ($0.01 < P < 0.02$) i. e. immediately after hatching (Fig. 3).

Further evidence of this is given if the broods and parents are examined within arbitrarily selected areas of the estuary. In all areas the females tended to spend a longer time feeding when the ducklings were young, although the slopes varied (Fig. 4). In the male's feeding there was no relationship with time either in the whole estuary or in any of the separate areas.

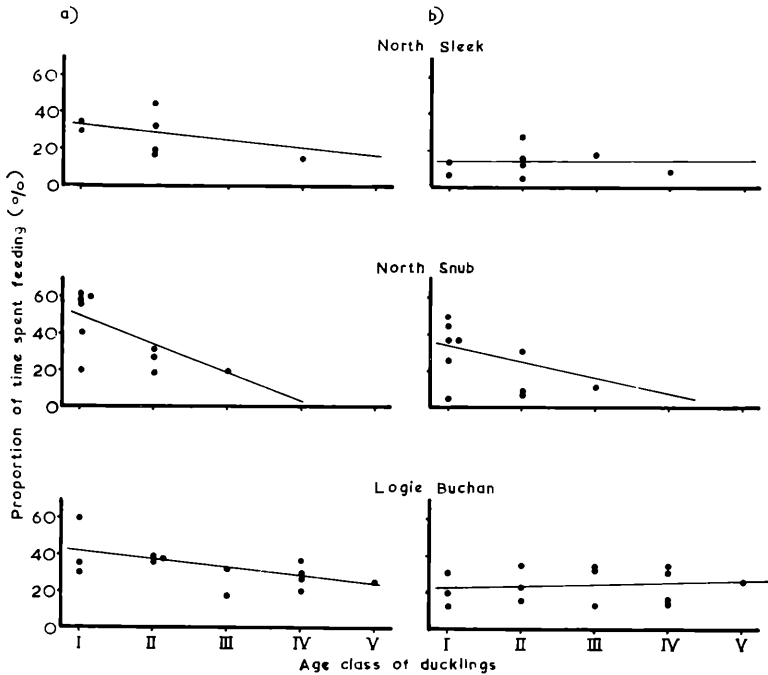


Fig. 4.

Proportion of time spent feeding in different areas of the estuary over the first six hours of a tidal cycle by the parents of broods in relation to the age of the brood. a) Female b) Male.

4. Discussion

What use are territories to shelduck? They certainly do not achieve dispersion of the nesting population since the nests are located at large distances from the territories. LACK (1954) doubted that territories were of value in obtaining food even to those species that fed on their territories. He pointed out that there was no positive proof that each territory contained the approximate quantity of food necessary to breed or even that a territory was of value in finding food.

HORI (1969) concluded that on the Isle of Sheppey, shelduck territories provided isolation for pairs or acted to achieve dispersion. He dismissed food in territories since he said there was an abundance elsewhere which was ignored. However, WILLIAMS (1973) pointed out that since so much time was spent on territory, the territory must contain adequate food. Additionally the food must be available and the particle size of the substrate, water content of the mud and water coverage of the territory may affect this (BUXTON 1975). Therefore not all areas may be equally suitable even though they contain large amounts of food. If it is important at any time to gather food quickly i. e. if time is short, then it may be advantageous to have a good feeding area since this reduces feeding time (BUXTON 1975).

During winter shelduck fed at night and birds on territory were still feeding when darkness fell. If it is assumed that the birds behaved in a similar manner through darkness (except during incubation for the female when the only feeding time was during the day) then the length of time spent feeding by males and females at different stages of the breeding cycle can be calculated (Table 6). This probably under-estimates the feeding of both sexes during prelaying since the % attendance on territory is decreased during the day by prospecting which does not occur at night.

Table 6. The total feeding times over 24 hours by males and females at different stages of the breeding cycle.

Activity	%	FEMALE		%	MALE	
		P.S.F.	Feeding Time (Hrs.)		P.S.F.	Feeding Time (Hrs.)
Prelaying	60.4	64.5	9.4	60.6	43.6	6.3
Laying	76.4	66.4	12.2	86.5	37.3	7.7
Incubating	21.2	82.6	3.0	85.4	34.0	7.0

Whilst prelaying and laying, females spent longer feeding than males by a factor of three to four hours. During incubation the feeding time of females was reduced to three hours which was less than 50% of the time spent feeding by the male during incubation and approximately 25% of the time spent feeding by the laying females.

Early in territorial occupation females were producing eggs which probably necessitated their feeding for long periods of time; KING (1973) estimated that the maximum cost of egg production in anseriforms was 50–70% above the daily energy intake for normal functions without a gain or loss of body weight.

Taking the proportion of time spent on territory in daylight by the laying female (since it is the maximum figure and unaffected by prospecting) and the mean P. S. F. during prelaying and laying (since there is no significant difference between the two) the minimum time spent on the territory and hence the minimum time spent feeding in 24 hours by the female can be calculated.

Time spent on territory = 76.4% of 24 hrs. = 18.3 hrs.
Time spent feeding = 64.9% of 18.3 hrs. = 11.9 hrs.
But KING says this is 150–170% of maintenance requirement.

Maintenance feeding time = 7.0–7.9 hrs.
This is very similar to the 6.3–7.7 hrs. feeding for the male for 24 hours during prelaying and laying.

Hence during incubation feeding is markedly below maintenance feeding time and even allowing for an increase in feeding efficiency with the change in feeding method, a good supply of food would be essential. Females with a brood patch, caught towards the end of the territorial period, were of a lower weight than all summer females and females during winter. Immediately after hatching, the female's P. S. F. was greater than the male's, but it decreased with time, suggesting that the female was regaining condition and needing to feed less. In contrast the male, with plenty of time to feed

whilst on territory, did not need to regain condition and hence did not show a relationship with time from hatching.

Since territoriality spaces the birds through the estuary it may allow the female undisturbed feeding in the defended area during the short feeding time of incubation. Additionally in order that females should retain their body condition as much as possible during breeding it would be advantageous to be aware of a constantly available source of food, i. e. that on a territory. In the estuary as a whole, the food value of any specific locality will vary with the amount of food present and its availability. Thus, although the food value of individual territories can vary, the territorial food supply could be important in the breeding success since overall it would tend to ensure that the female gained as much of her energy requirements as possible during the short feeding spells of incubation. This would enable her to continue incubation and after hatching, be in good condition to care for the brood. This contrasts with the female eider (*Somateria mollissima*) which does not feed during incubation and abandons her brood to other females in order to feed and recover body condition (GORMAN and MILNE 1972). Creching in shelduck may therefore involve broods whose parents are in poor body condition. Hence familiarity with, and the use of, one area as a feeding territory, would facilitate this food collection in a habitat where the food supply is not uniformly available.

The data presented show the varying lengths of time spent feeding through the breeding season by the females and suggest a hypothesis for the importance of the feeding territory. They do not allow the further testing of that hypothesis. Additional research is required to establish the importance of this territorial feeding in breeding. The hypothesis assumes that feeding on a territory is more efficient than feeding in a flock. Further research could show whether flock females lose a significant amount of time in interactions and examine the body condition of territorial females through the breeding season relative to the food value of their territories. This would test the hypothesis by giving an insight into the extent and timing of breeding failures.

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