Bill knob size and reproductive effort in Common Shelducks *Tadorna tadorna*

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Male Common Shelducks *Tadorna tadorna* with large bill knobs were more effective at defending spring feeding areas in the Severn Estuary, southwest England, against other males than those with small bill knobs. Their female partners were consequently able to devote more time to feeding and less to walking and being alert. Most of the walking by pairs in which the males had small bill knobs was undertaken in order to avoid interactions with other pairs. All males, except those with the smallest knobs, made a significant investment in reproduction by spending more time being alert than females, allowing them to gather food resources for egg formation and incubation more quickly. By selecting male partners with large bill knobs, females thus increased their feeding time and decreased their energy expenditure. These observations are consistent with Patterson's (1982) contention that territorial behaviour has been selected for in Common Shelducks because it provides an undisturbed feeding area for the female.

Key Words: Common Shelduck, feeding territories, bill knobs, secondary sexual characters, sexual selection

Male ducks generally provide little or nothing by way of parental care since the pair bond is broken before hatching (Maynard Smith 1977; Ogilvie 1975). The Common Shelduck *Tadorna tadorna* is an exception in that the pair bond is maintained for several years, and the male accompanies and guards the female, both when she is gathering resources for egg formation and when she is feeding between incubation shifts. He also assists during chick rearing (Patterson 1982). Since males contribute directly to breeding success in these ways, it is important for females to select a partner whose contribution will be maximal.

Common Shelducks of both sexes with more immaculate chestnut breast bands tend to be more numerous at good feeding and breeding sites in the Severn Estuary, southwest England, to mate assortatively, achieve better body condition and produce greater numbers of surviving offspring (Ferns & Lang 2003). However, the breast band is not the only feature contributing to the conspicuous appearance of this species. An equally obvious secondary sexual character is the knob that develops on the bill of males in the early spring. In this paper, correlational studies of Common Shelducks are used to determine whether the bill knob might play any rôle as an indicator of individual quality in males, especially in relation to his direct contribution to breeding.

Study Area and Methods

Common Shelducks were studied in spring (April and May) in the Severn Estuary at a time when pairs defended feeding areas (usually referred to as feeding territories), on the intertidal mudflats, and the females were forming eggs. None of the females had started incubating, however, since they were present throughout the low tide period. The study was a purely observational one and did not involve any colour-marked individuals. The time budgets of individual males with different bill knob sizes, and their mates, were compared during the most important feeding period – the 3 h before, and the 3 h after, low tide – between Cardiff and Newport on the Welsh shores of the Severn Estuary in 1994, 1999, 2001 and 2003. This region contains many good quality feeding sites for Common Shelducks (see e.g. Fox & Salmon 1994; Musgrove *et al*. 2003), supporting over 200 territorial pairs each year. To minimise the possibility of studying the same pairs in different years, sections of shore that were at least 1 km apart were selected each year.

Pairs that were individually recognisable from day to day were selected. This was deduced on the basis of the location of their feeding areas, their breast band and bill knob scores, and any other recognisable plumage or behavioural differences. The activity of each of the individuals in up to six different pairs was recorded continuously for 3 min in each hour, and each pair was observed again for a further 3 min in each subsequent hour. The activities recorded were feeding, walking, swimming, alertness, preening, interacting and sleeping. Feeding activity was further divided into the categories used by Bryant & Leng (1975), the commonest of which, in this study area, were scything through wet

mud, digging, and feeding in water by dipping and upending. Information for a total of 49 different pairs was collected in this way.

Time budgets were compiled for most of the remainder of the tidal cycle (total 10 h), but specific individual pairs could not be recognised for more than 3 h on either side of low tide, because the rising tide caused them to leave their main feeding areas and concentrate on successively smaller areas of shore.

Bill knob size was determined using the categories shown in **Figure 1**, in which a score of 4 corresponds to the largest knob illustrated in Young (1970). The bill knob increases in size from February to April, and once it is fully grown there is a strong positive correlation between knob size and testis size (Young 1970). The repeatability of bill knob score, based on observations of the same individuals made by four different observers, was moderately good ($r = 0.583$, $F_{5,18} = 6.60$, $P = 0.001$). Plumage quality was measured using the criteria in Ferns & Lang (2003), as was body condition (see **Figure 2**), the latter being based on similar body profiles to those used on geese by Owen (1981), and which have proved reliable (Black & Zillich 2002).

There are two problems in analysing time budgets statistically. The first is the potential lack of independence in the amount of time (expressed as a percentage) spent in a specific activity in successive time intervals. The second is the lack of independence in the amount of time spent in different activities that sum to a fixed total (100%). The first problem was overcome by testing successive hourly observations for independence using autocorrelation and only analysing those that lacked serial dependence. Bootstrapping (10,000 times) with Resampling Statistics 3.0.7 was used to test for differences between the sexes and sites. The second problem was overcome by only testing those components of greatest value in elucidating the different roles of the sexes (feeding, alertness and interaction). These accounted for 70–80% of the overall time budget. Correlations between bill knob size and the five main categories of activity in the 6 h around low tide were examined (feeding, walking, alertness, preening and interacting). Bonferroni corrections were applied when testing such correlations for significance, and $P = 0.01$ was therefore used as the critical level for the rejection of null hypotheses. Exact non-parametric ordinal tests were computed using StatXact 4.0.1.

Results

The commonest male bill knob size class was 3, which contained 47% of the males, with a further 37% in class 4, 12% in class 2 and 4% in class 1 ($n = 49$). There was a significant tendency for males with larger bill knobs to have more immaculate plumage scores (Jonckheere-Terpstra test, $P = 0.002$), and their body condition was better, but not quite significantly so (Jonckheere-Terpstra test, $P = 0.075$). Neither was there any significant difference in the plumage immaculateness or the body condition of their female partners (Jonckheere-Terpstra tests, $P > 0.200$).

Figure 1. Bill knob scores of male Common Shelducks.

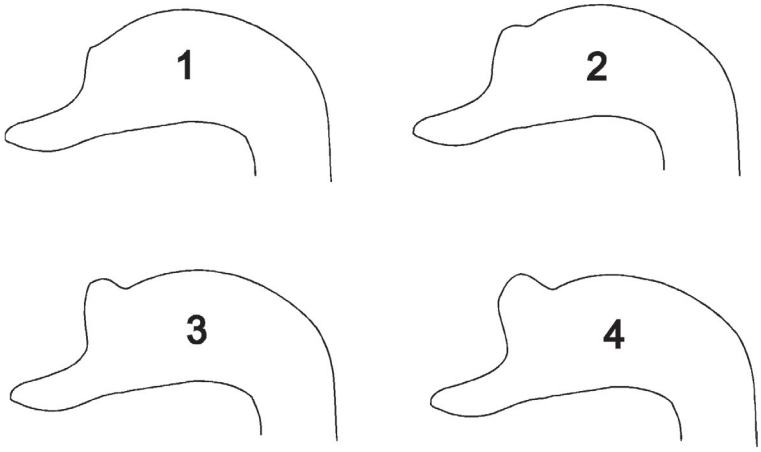
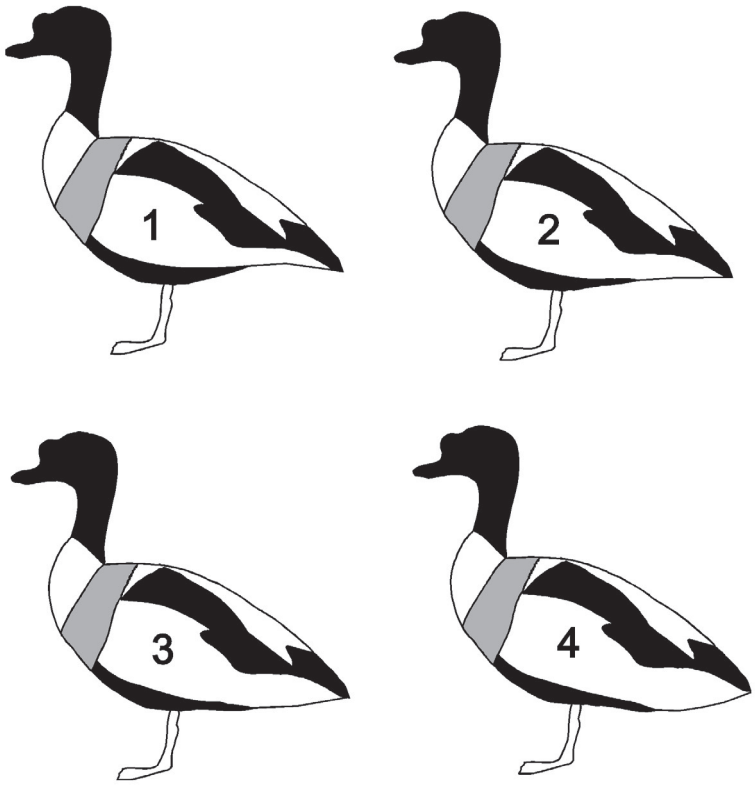


Figure 2: Body condition scores of male Common Shelducks.



Females whose partners had large bill knobs spent significantly more time feeding (ANOVA, $F_{3,45} = 3.07$, $P = 0.037$) and less time walking ($F_{3,45} = 3.11$, $P = 0.036$) (**Figure 3**), either because other pairs avoided them, or because food supplies within their feeding areas were more concentrated, i.e. their territories were of better quality. It is not easy to discriminate between these two possibilities directly, but the correlations described below provide some circumstantial evidence. The amount of time spent feeding was highly correlated within pairs ($r = 0.880$, $P < 0.0005$), as was the amount of time spent walking ($r = 0.410$, $P = 0.003$). There was also a strong negative correlation between the amount of time spent walking and feeding in both females ($r = -0.736$, $P < 0.0005$) and males ($r = -0.420$, $P = 0.003$).

Most of the preening that took place in the period of 6 h around low tide appeared to be associated with display rather than plumage maintenance. This can be deduced from the fact that it usually took place when pairs were approached by other individuals, and it was overtly associated with an increase in the number of interactions with other individuals. Thus, the correlation between the amount of time males spent preening and interacting was highly significant ($r = 0.452$, $P = 0.001$). The amount of time males spent preening was even more closely correlated with the amount of time their partners spent interacting ($r = 0.945$, $P < 0.0005$).

Visual inspection of the hourly time budgets indicates that both sexes spent most of their time feeding (**Figure 4**). However, the absolute amount of time devoted to this activity in males was lower, mainly because of the large amount of time they spent being alert. However, there was no significant difference in the amount of time devoted to alertness in different bill knob categories, the averages being 3% in those with a score of 1, 36% in 2, 28% in 3 and 26% in 4. The low figure of 3% in males with very small bill knobs should be treated with caution since it is based on only two birds.

Males also spent more time interacting with other individuals than did females, but this difference turned out not to be significant (see below). The majority of preening that took place around the high tide period, in contrast to that around low tide, appeared to be genuinely associated with plumage maintenance since it was not preceded or followed by social interactions.

Autocorrelation of the overall time budgets (compiled for the 5 h before and 5 h after low tide) revealed no statistically significant dependence of the amount of any activity in one hour and the amount in the previous hour. Male interaction with other Common Shelducks came closest ($r_{\varphi} = 0.533$, $P = 0.050–0.100$), with a slight tendency for more interactions to occur during the first few hours of the falling tide. The difference in the time spent in interactions for males and females was in any case not quite significant (**Table 1**). Power is low in a test in which n = 10, so if it is assumed that any serial autocorrelation that accounted for 10% of the variance in activity from one hour to the next rendered a test suspect, this would only lead to the rejection of cases in which $r > 0.32$. This does not apply to either of the significant results in **Table 1**. The risk

Figure 3*:* Time spent (a) feeding, and (b) walking, by female Common Shelducks on the Severn Estuary, southwest England, in relation to the bill knob size of their mate (+1 SE bar). The lower graph shows the sample sizes (number of pairs) for both (a) and (b).

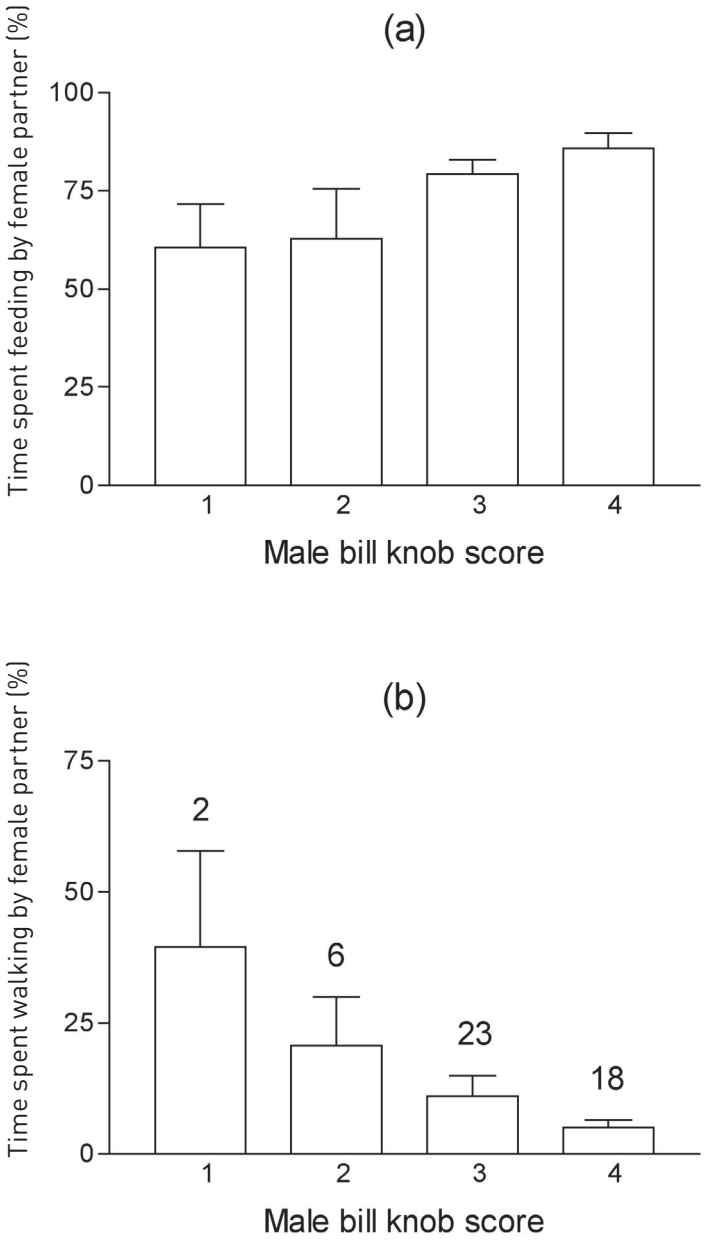
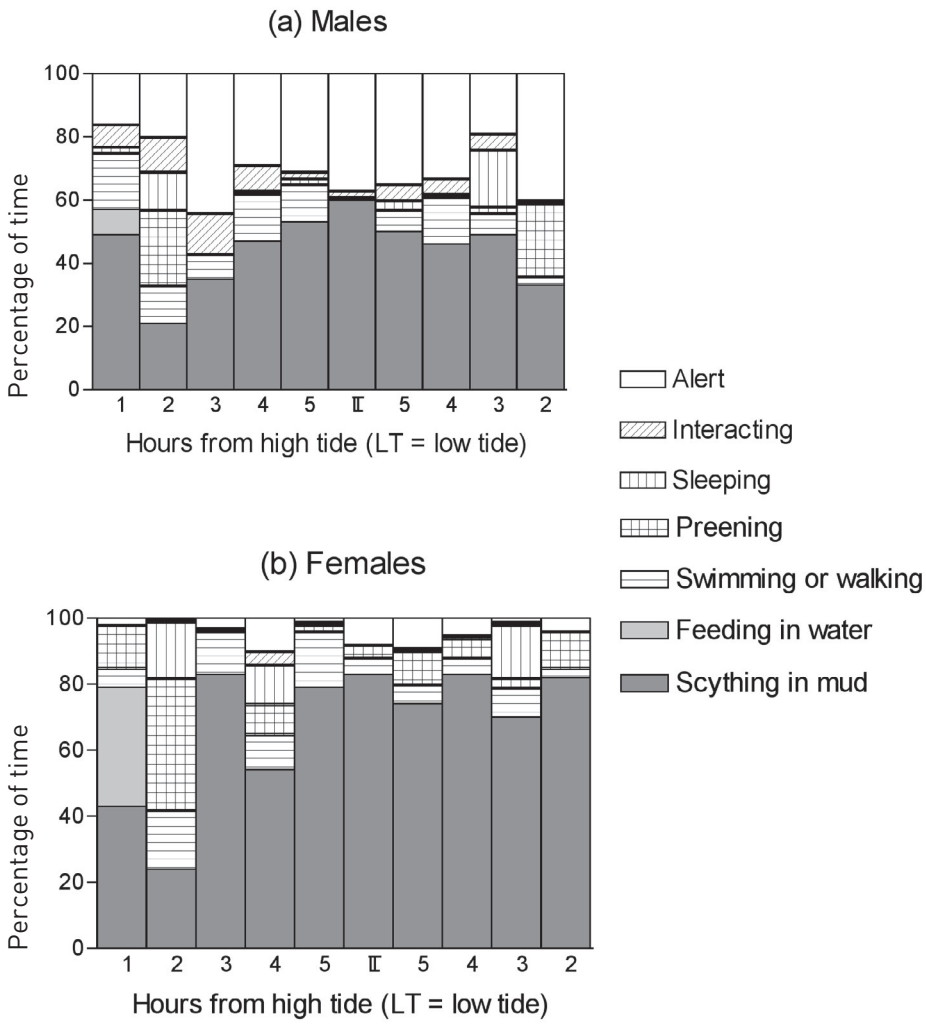


Figure 4: Time budgets of (a) male, and (b) female, Common Shelducks at Rumney Great Wharf, Severn Estuary, during a period of neap tides.



of making a type I error (equivalent, in this case, to finding a spuriously significant difference in activity) is thus low. Females spent significantly longer feeding than their male partners (**Table 1**). In fact, they fed for 63% longer than males and continued doing so for most of the tidal cycle, at least on neap tides, despite having to upend in order to reach the mud at high tide. Males spent seven times as long as females being alert, and this difference was highly significant.

Males with a bill knob score of 1 were only capable of providing inferior protection, since their females had

Table 1. Percentage of time spent in different activities by male and female Common Shelducks in the Severn Estuary, southwest England, during the 10 h centred on low tide during the pre-breeding period (*P* = probability of a difference as large as this being due to chance, based on resampling the hourly percentages, - = not tested). The figures in brackets are the serial hourly autocorrelations of the activities within each sex. These need to exceed a value of 0.60 to indicate a significant lack of independence at the 5% level with the observed sample size of 10.

Activity	Males	Females	*P*
Feeding	44.3 (0.25)	72.1 (0.13)	0.0015
Swimming and walking	9.8 (0.04)	9.3 (0.09)	-
Preening	5.6 (0.10)	9.8 (0.20)	-
Sleeping	3.2 (0.22)	4.6 (0.48)	-
Alert	30.4 (0.13)	4.3 (0.03)	<0.0001
Interacting	5.9 (0.53)	0.9 (0.14)	0.05–0.10

to walk far further before being able to continue feeding. Although these females managed to spend nearly as long feeding (61%) as those whose partners had bill knob scores of 2 (63%), they had to walk for almost twice as long (i.e. for 40% of the time, instead of 21%) in order to do so (**Figure 3**). By contrast, the partners of males with a bill knob score of 4 walked for only 5% of the time, and were able to feed for 86% of the time during the main feeding period before and after low tide (**Figure 3**).

Discussion

There was a close association between a male's bill knob size and his ability to defend a feeding area and protect himself and his female partner from harassment by other pairs. Those with the smallest bill knobs (score = 1) were only marginally able to defend feeding territories at all in the face of competition from other pairs. They spent so much time walking away from other Common Shelducks that they had little time left for anything else, including feeding and being alert. One consequence of this was that their territories were poorly defined. Thus it is not surprising that it was only possible to observe two such males that managed to maintain feeding territories and breeding partners for the duration of the observations.

Pairs in which the males had a bill knob score of 2 also tended to avoid other pairs. The females of such pairs, however, spent much less time walking than those of the poorest males. They also spent more time preening than any other group of birds (13%), and consequently had only marginally more feeding time than the partners of the poorest males. Both sexes have a "preening-behind-the-wing" display associated with aggressive interactions (Johnsgard 1965). The large amount of time spent preening on the feeding areas by females whose partners

had a bill knob score of 2 may thus reflect display activity, perhaps in an attempt to discourage encroachment by other pairs, rather than plumage maintenance. Their mates, on the other hand, devoted little time to either interacting with other individuals or preening (total 1%). They did, however, spend more time alert than other males.

Males with a bill knob score of 3 spent much more time feeding (56%) and less walking (12%). Pairs in which the males had a bill knob score of 4 spent very little time walking (5% in both sexes) and much more feeding. These relationships explain the significant negative correlation between time spent feeding and time spent walking in both sexes. Only a small amount of time was spent overtly interacting with other Common Shelducks by males in all bill knob categories, probably because the well-established social hierarchy in this species means that inferior individuals simply avoid confrontation by walking away (Paterson 1982). Williams (1973, cited by Patterson 1982) found that females spent 0.4–1.4% of their time in aggressive behaviour on the feeding areas, and Pienkowski & Evans (1982) found that feeding time was interrupted by aggressive encounters, but this study is the first to indicate that more interruptions are suffered by males with smaller bill knobs.

It can thus be concluded that a good deal of the walking undertaken during feeding in Common Shelducks is to avoid confrontation with other pairs, rather than to find better feeding places. However, it would be surprising if the better quality pairs did not tend to occupy feeding areas with the densest food resources, and the possibility that pairs in which the male has a small bill knob also had to walk further simply to find suitable feeding places in poor territories cannot be ruled out.

Bill knob size was an effective indicator of those males able to provide females with high quality protection that minimised the effort that females had to expend on walking during foraging. This guarding activity of males, reflected in the large amount of time they spent being alert, allowed females to concentrate on feeding, spending much less time on the lookout for danger, as well as for possible harassment by other pairs. Guarding thus represents a major investment in reproduction by males, enabling their partners to forage more efficiently. Males contribute to an increased food intake of females (by being alert on their behalf) and, in the best individuals, by reducing the females' energy expenditure on walking. This is despite the fact that the time devoted to alertness actually declines slightly in the males with the biggest bill knobs, probably because such individuals do not have to spend as much time monitoring the position and movements of their neighbours, since they have little to fear from them. They none the less still spend more than a quarter of their time alert, since they must still keep a lookout for predators on behalf of their partners.

Well-guarded females (i.e. those whose partners had bill knob scores of 3 or 4), spent at least 16% more time feeding than other females. This in turn provided them with more resources to compete for the best nest sites, nest earlier, lay larger clutches

and incubate more closely. Although it has been demonstrated that birds with more immaculate plumage produce more surviving chicks (Ferns & Lang 2003), it was not possible to measure breeding success in relation to bill knob size because the bill knob has begun to shrink by the time the chicks reach the feeding areas and there were no marked individuals to monitor. Males with large bill knobs did have more immaculate plumage, however, and are therefore highly likely to have been more successful breeders.

Males spent 3.7 h per tidal cycle feeding, equivalent to about 7.4 h per 24-h period. This is very similar to the 7.7 h recorded for males in the laying period on the Ythan Estuary found by Buxton (1975, cited by Patterson 1982). The present figure of 12.0 h per 24-h period for females in the Severn Estuary is also remarkably close to the 12.2 h on the Ythan. On the other hand, the figures for alertness are much higher than the 8–13% recorded by Williams (1973, cited by Patterson 1982). The amount of time spent feeding is higher in laying females than it is during pre-laying (9.3 h), or incubation (3.0 h) (Buxton 1975, cited by Patterson 1982), suggesting that foods ingested during laying, as well as prior to it, contribute to the formation of the clutch. In this respect, the Common Shelduck is probably closer to the Mallard *Anas platyrhynchos*, which is mostly an 'income' breeder, than to the Eider *Somateria mollissima*, which is entirely a 'capital' breeder (Meijer & Drent 1999). This helps to explain why there were no significant differences in the body condition of females whose partners were in different bill knob categories. Most females in pairs capable of defending feeding areas (i.e. those whose males were in bill classes 2–4) were in sufficiently good condition to be able to form eggs.

The size of the bill knob is thus an efficient indicator of male quality, especially in relation to that most critical factor for females – protection from interference when feeding. One reason why the Common Shelduck's bill knob may be such a good signal is that, prior to pair formation, males that are able to devote more time to feeding (unharassed by all other Shelducks) are able to grow larger bill knobs. It certainly provides an effective indicator of those males best equipped to contribute high-quality care to their female partners during the early breeding season. The major components of this care are alertness to danger and the prevention of interruptions to feeding caused by other pairs.

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References

Black, J.M. & Zillich, U. 2002. Body mass and abdominal profile index in captive Hawaiian Geese. *Wildfowl* 53: 67-77.

Bryant, D.M. & Leng, J. 1975. Feeding distribution and behaviour of Shelduck in relation to food supply. *Wildfowl* 26: 20-30.

Buxton, N.E. 1975. *The Feeding Behaviour and Food Supply of the Common Shelduck Tadorna tadorna on the Ythan Estuary, Aberdeenshire.* Unpublished PhD thesis, Aberdeen University.

Ferns, P.N. & Lang, A. 2003. The value of immaculate mates: relationships between plumage quality and breeding success in Shelducks. *Ethology* 109: 521-532.

Fox, A.D. & Salmon, D.G. 1994. Breeding and moulting Shelduck *Tadorna tadorna* of the Severn Estuary. *Biological Journal of the Linnean Society* 51: 237-245.

Johnsgard, P.A. 1965. *Handbook of Waterfowl Behavior*. Constable, London.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25: 1-9.

Meijer, T. & Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding birds. *Ibis* 141: 399-414.

Musgrove, A.J., Langstone, R.H.W., Baker, H. & Ward, R.M. (eds.) 2003. *Estuarine Waterbirds at Low Tide: the WeBS Low Tide Counts 1992/92–1998/99*. WSG/BTO/WWT/RSPB/JNCC, Thetford.

Ogilvie, M.A. 1975. *Ducks of Britain and Europe.* T. & A.D. Poyser, Berkhamsted.

Owen, M. 1981: Abdominal profile – a condition index for wild geese in the field. *Journal of Wildlife Management* 45: 227-229.

Patterson, I.J. 1982. *The Shelduck*. University Press, Cambridge.

Pienkowski, M.W. & Evans, P.R. 1982. Breeding behaviour, productivity and survival of colonial and non-colonial Shelducks *Tadorna tadorna*. *Ornis Scandinavica* 13: 101-116.

Williams, M.J. 1973. *Dispersionary Behaviour and Breeding of Shelduck Tadorna tadorna on the River Ythan Estuary.* Unpublished PhD thesis, Aberdeen University.

Young, C.M. 1970. Shelduck parliaments. *Ardea* 58: 125-130.

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