

Pre-breeding behaviour affects condition, assessed by abdominal profile, and hence breeding success of Canada Geese *Branta canadensis*

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A population of Canada Geese in southern England was studied in the pre-breeding and breeding seasons of 1983 and 1984, and abdominal profile (AP) was recorded as a measure of stored reserves. Female APs increased during the pre-breeding period, and overall females had higher APs than males during this period. Having allowed for the effects of season and time of day, AP 50 days after 1 January (AP_{50}) was calculated for each female to give an estimate of condition in the middle of the pre-breeding period. AP_{50} was correlated with % time feeding in the pre-breeding period, as expected since stored reserves are derived from processed food. Female AP_{50} also correlated with her mate's size, as assessed by tarsal length, in accordance with the mate protection hypothesis, and females with higher AP_{50} nested earlier, as expected if breeding is contingent on the acquisition of sufficient stored reserves. Early nesting correlated with both hatching and fledging success. The simplest interpretation of our results is that breeding success was strongly influenced by the reserves acquired by the female, indicating there was a premium on effective feeding in the pre-breeding period, promoted as necessary by protection by her mate.

The reserves acquired by female Canada Geese during spring fattening serve to fuel migration, egg production during laying, and some 30 days of incubation, without further feeding (see e.g. Aldrich & Raveling 1983) - an impressive and extreme reproductive strategy. It seems clear that these reserves must play a crucial role in determining breeding success, an idea formalised as the 'condition hypotheses' (Lack 1956, 1963, 1967, Ryder 1970, see Newton 1977 for a review). The relationship between nutrient reserves and clutch size has been demonstrated directly for Lesser Snow Geese *Anser caerulescens caerulescens* (Ankney & MacInnes 1978, Wypkema & Ankney 1979) and Raveling (1979) concluded that depletion of protein reserves is the proximate factor causing cessation of laying in Canada Geese. Aldrich & Raveling (1983) suggested that the importance of stored reserves acquired during the pre-breeding period is that they allow more eggs to be produced. They also allow females to be more attentive to their nests, thereby reducing the chance of egg predation (Harvey 1971).

Rate of acquisition of reserves during spring fattening and rate of depletion during

breeding have been extensively studied by carcass analysis of geese shot at different times in the annual cycle (see e.g. Hanson 1962, MacInnes *et al.* 1974, McLandress 1979, Raveling 1979, McLandress & Raveling 1981b for work on Canada Geese), and by repeated weighing of captive birds (Akesson & Raveling 1981). Carcass analysis has shown that female and male Canada Geese increased body weight before migration by 36-46% and 26%, respectively, above average winter weights (Raveling 1979, McLandress & Raveling 1981). The weight gain of females was composed of 61% lipids, 10% protein and 21% water, and this was presumably reflected in changes in abdominal profile (see below). McLandress & Raveling considered that these lipid and protein stores were sufficient for the production of eggs and the fuelling of maintenance during incubation, although females might have to obtain minerals from food sources on the breeding grounds.

Here we examine the key feeding-breeding relationships in a non-migratory population of free-flying Canada Geese, descendants of birds introduced in Britain some time in the last 300 years (Blurton Jones 1953). The lack of pre-breeding migration means that body

reserves for breeding are not limited by the amounts that individuals can carry in long migrations, as has been proposed for the migratory arctic-nesters (Ryder 1970). However since breeding females do not eat during incubation (Johnson 1986), there is still reason to expect that pre-breeding body reserves will play an important role in determining breeding success.

In an earlier study (Johnson & Sibly 1990) we suggested that protection by their mates allows females to feed more during the pre-nesting period, and we suggested that this allows her to increase her rate of gain of nutrient reserves, as in White-fronted Geese *Anser albifrons* (Fox & Madsen 1981). Here we are able to examine in detail the relationships between feeding rate and body reserves, assessed by abdominal profile (Owen 1981), between abdominal profile and nesting date, and between nesting date and breeding success.

Because of the key role of spring fattening in female geese, and because carcass analy-

ses of geese in other areas have shown that reserves increase in the pre-breeding period, more so in females (see above), we predicted that if AP is a good estimator of stored reserves, then during the pre-breeding period:

1. Female AP would increase; and
2. Female AP would exceed that of males.

We further predicted that if nesting is dependent on an adequate store of reserves, as discussed above, then

3. Nesting date should be correlated inversely with female AP during the pre-breeding period.

Lastly, if this population of Canada Geese follows the general bird breeding pattern, as shown by, for instance, Great Tits *Parus major* (Perrins 1963, 1965), Pied Flycatchers *Ficedula hypoleuca* (Lack 1966), Pink-footed Geese *Anser brachyrhynchus* (Inglis 1977) and Lesser Snow Geese (Hamman & Cooke 1989), then

4. Earlier nesters should have higher breeding success.

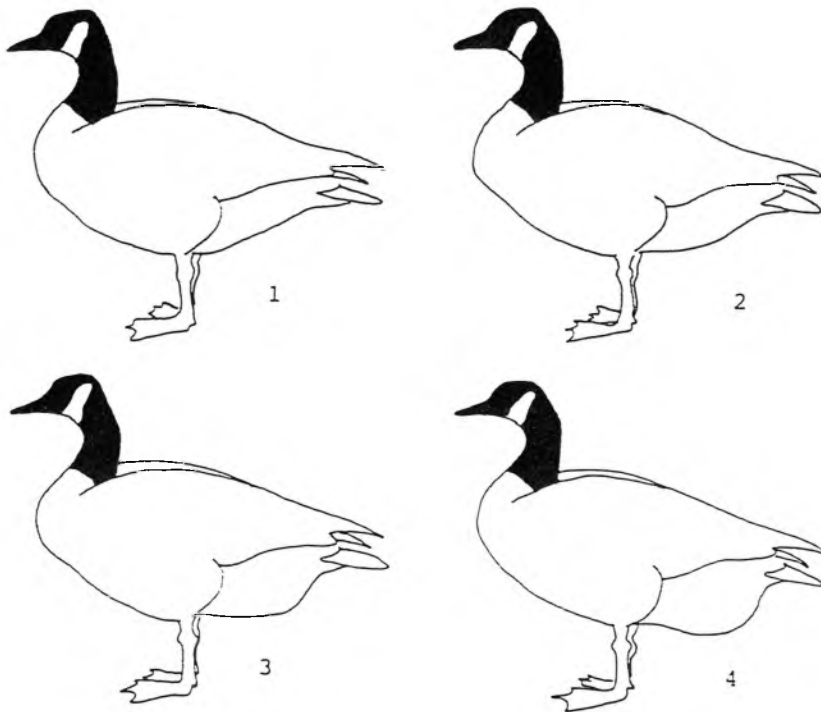


Figure 1. Abdominal Profile (AP) was assigned to Canada Geese on the basis of the roundness of the belly (i.e. the region between legs and tail covered by the white under-tail coverts) on a scale of 1-4 as illustrated (after Owen 1981). Intermediates were scored as half points.

Methods

The study population consisted of some 40 pairs of non-migratory Canada Geese living around Elvetham in north Hampshire, UK, described in detail in Johnson (1986) and Johnson & Sibly (1990). The study was carried out in 1983 and 1984, but BTO ringing data were available from 1977 onwards. The population was rounded up during the moult and neck collars attached to adults as described in Johnson & Sibly (1989). Measurement was made on each bird of maximum length of *head and bill*, and *tarsus length* with the foot flexed at right angles to the leg. Ages of adult birds were generally known from ringing data, but where exact age was not known the minimum estimate of age was used. Previously unringed birds were not included in the age analysis. Goslings were marked with metal web tags before they left the nest.

Observations of neck-collared adults were made between January and April, here referred to as the *pre-breeding period*. *Abdominal Profile* (AP hereafter) was noted using the method of Owen (1981), assigning each bird a score on a scale running from 1 (thinnest) via 1/2 points to 4 (fattest), while it was standing in the head-up position facing at ninety degrees to the observer (Fig. 1). Repeat observations were found to give similar scores.

% *time feeding* was recorded as % time feeding during continuous observation periods of 5 (1984) or 10 (1983) minutes. Feeding was defined as bill below level of base of neck and pointing downwards, the bird either pecking or uprooting food or scanning ground in between bouts of pecking. *Position in flock* was categorized as Middle, Intermediate or Edge as defined in Johnson & Sibly (1990).

Nests were generally conspicuous and easily found by visiting likely sites at intervals of one to five days throughout the breeding season. Forty-eight were located in 1983 and 28 in 1984, a year when there was some disturbance at the nesting sites. Start of incubation was taken as the day when the eggs were first noted to be at a greater than ambient temperature, or, if the nest was first visited after the clutch was complete, 28 days before hatching (Newton 1977, Owen 1980, Lessells 1982). To control for seasonal variation, *nesting date* was defined as the date on which incubation commenced relative to the first nest of that season. *Clutch size* was defined as the

number of eggs present at the start of incubation, although this was thought to be subject to error due to the existence of egg dumping by 'parasitic' females. The existence of egg dumping was inferred from the appearance of eggs in unattended nests constructed in previous years, and from the appearance of eggs in attended nests several days after the start of incubation. It proved impossible to establish the identity of parasitic females, or to estimate the magnitude of error in the assessment of clutch size caused by egg dumping.

The number of eggs lost from the nest during incubation, and the number hatching, were recorded during visits to the nest. Clutch size, eggs lost from the nest during incubation, eggs hatching and goslings fledging (here meaning present at round-up) were known for 69 nests, for 51 of which the date on which incubation commenced was also known.

Results and discussion

A total of 231 observations of Abdominal Profile (AP) was made on ten pairs in 1983 and 14 in 1984. In our first analysis we began by calculating the average AP for each of these birds. Females had higher average APs than their mates in the pre-breeding period in both years in accordance with prediction 2 (1983: 3.1 *v* 1.7, matched-samples t-test, $n = 10$, $t = 13.6$, $P < 0.0001$; 1984, 2.8 *v* 2.0, $n = 14$, $t = 4.5$, $P < 0.0006$: note that a t-test is appropriate when used on averaged scores as here, however a Mann-Whitney test gives the same result). This fits also with our earlier finding (Johnson & Sibly 1990) that females feed more than males in this period.

The 1984 data set was larger and was obtained over a longer time period (31 January–3 April) and was therefore used in analysis of the effects of date. Female AP correlated with both date ($r_{63} = 0.36$, $P < 0.01$), in accord with prediction 1, and time of day ($r_{63} = 0.29$, $P < 0.05$, these analyses ignore individual identity). For males neither correlation was significant, although there was an increasing trend with time of day ($r_{70} = 0.23$). AP is probably influenced more by fat than by protein reserves but is also affected by the quantity of food in the bird's gut, as in Owen's (1981) data on Barnacle Geese *Branta leucopsis* which is why it is lowest at the start of the day when the gut is empty, and highest at the

end when the gut is full. There is probably more pressure on successful feeding in females, as discussed above, and this may be why the correlation was only significant in females.

Could the increase in female AP with date be a result of increased gut fill? Observations of the behaviour of whole flocks and multiple regression analysis on data for focal individuals both indicated that % time feeding declined in the pre-breeding period (multiple regression analysis allowing for the effects of sex and position in the flock, .19% decline per day, $F_{1,284} = 6.2$, $P < 0.05$). This was probably because individuals that fed more nested earlier (see below), and so were not available for observation later on (correlating mean observation date with mean % time feeding for all focal individuals gave females: $r_{12} = -0.66$, $P = 0.01$; males: $r_{12} = -0.14$, n.s.). Examining seasonal data for individual females we found that seven increased and seven decreased % time feeding over the pre-breeding period. Hence gut fill would not have been increased by changes in % time feeding, but we are not in a position to evaluate the possible effects of longer days or changing food quality. On balance, however, we think that the increase in AP with date does represent a real increase in stored reserves. Owen (1981) found a simi-

lar increase in AP in the pre-breeding period in Barnacle Geese.

Since date and time of day both affected female AP it was desirable to allow for their effects in computing a 'corrected average' AP for each female, to be used in subsequent analyses. For this purpose we used the partial regression coefficients from a multiple regression of the 1984 data. This gave correction factors of .012 for date and .038 for time of day, and these were used to estimate comparable APs for noon on day 50 after 1 January (AP_{50} hereafter) for all females in both years of the study. In the following analyses, data from both years are lumped, but trends in individual years were in the same direction as those reported. AP_{50} correlated with % time feeding in the pre-breeding period ($r_{22} = 0.40$, $P < 0.05$), showing that increased % time feeding does result in increased stored reserves, as assessed by AP_{50} .

In an earlier study (Johnson & Sibly 1990) we showed that mate protection by males allows females to feed more, and Lessells (1982) suggested that females with large, experienced mates might benefit by improved feeding opportunities. In the present study, male age was not correlated with either the % time their mates spent feeding ($r_{21} = -0.13$, n.s.) or with their mates' AP_{50} ($r_{21} = -0.20$, n.s.),

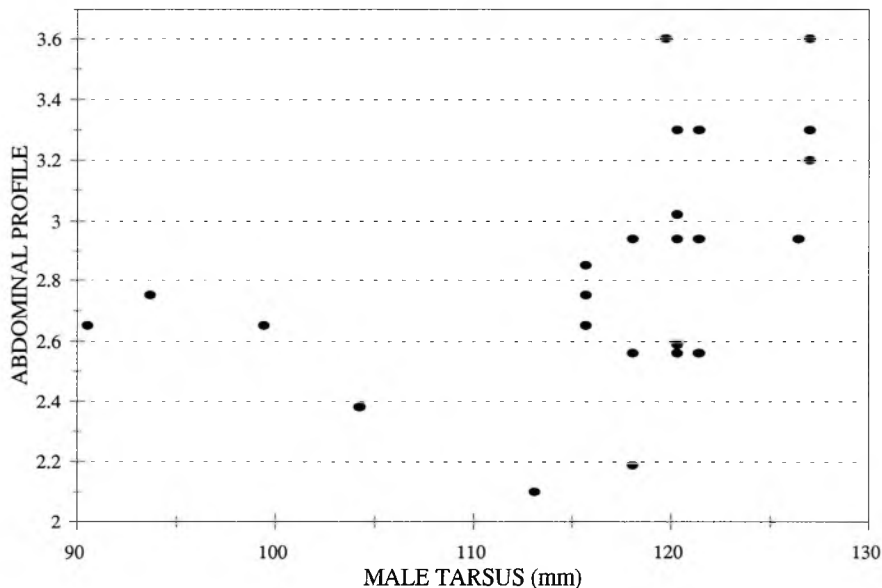


Figure 2. Abdominal Profile of female Canada Geese (AP_{50}).

but male size, as assessed by tarsal length (but not head and bill length) was correlated with his mate's AP_{50} ($r_{22} = 0.41$, $P = 0.05$, Fig. 2). This suggests that females with large mates do benefit in terms of feeding opportunities, as proposed by Lessells (1982), and lends weight to the mate protection hypothesis.

Stored reserves and nesting date

Of the 24 pairs observed feeding in this study, only 13 were subsequently found nesting, and the date of nesting was only known for 12. Despite this small sample, female AP_{50} was inversely correlated with nesting date ($r_{10} = -0.63$, $P < 0.05$, Fig. 3), in accordance with prediction 3. The association with % time feeding in the pre-breeding period was in the expected direction, though not statistically significant ($r_{10} = -0.48$, n.s.), perhaps because of lower precision in the measurement of feeding time than in the measurement of AP_{50} .

Nutrient reserves for breeding are of particular importance for female geese, which incubate for long periods with very little food and lose a large proportion of body weight in this period (as discussed in the Introduction, see also Lessells *et al.* 1979). So, prior to breeding, female geese need to obtain fat and protein reserves not only for egg production but also to sustain the female through incubation. Prediction 3, supported by the present data, suggests that nesting does not occur until an adequate store of such reserves has been obtained.

Nesting date and breeding success

Nesting date was negatively correlated with both hatching success and fledging success (Table 1; hatching and fledging success were defined for each nest as the number of eggs hatching, and the number of goslings recaptured at round-up, respectively). This finding, that pairs nesting early in the breeding season hatched more eggs and fledged more young than later nesting birds, is in accordance with prediction 4. Many other bird studies have reported similar findings, as discussed in the Introduction.

In some species this can be partly explained by older birds laying earlier and also laying larger clutches, e.g. Barnacle Geese (Owen 1980) and Great Tits (Lack 1966). Decreasing clutch size in later nests has also been reported for Snow Geese (Finney & Cooke 1978) and Greylag Geese *Anser anser*

Table 1. Correlation of nine factors with Canada Goose breeding success (data from 1983 and 1984).

	Hatching success	Fledging success
Male age	0.170	0.165
Female age	0.207	0.224
Male tarsus	0.050	0.181
Male head and bill	0.030	0.188
Female tarsus	0.146	0.259
Female head and bill	0.185	0.078
Clutch size	-0.113	-0.141
Mean egg weight	-0.040	-0.060
Date of nesting	-0.270*	-0.362**

* $P = 0.05$, $df = 49$

** $P = 0.01$, $df = 46$

(Newton & Kerbes 1974). In the present study maternal age affected date of nesting in 1984 ($r_{10} = -0.57$, $P = 0.05$) but not in 1983 ($r_{20} = 0.01$, n.s.). However there were no relationships between maternal age and clutch size ($r_{20} = -0.07$, n.s. and $r_{10} = 0.00$, n.s. for 1983 and 1984 respectively), and no significant relationship between maternal age and fledging success (Table 1). This contrasts with Raveling's (1981) study of Giant Canada Geese *B. c. maxima* in Manitoba, in which he found that older geese (4+ y) were more than twice as successful in raising at least one young to fledging as were younger birds. Errors were, however, possible in our estimation of clutch size (see Methods). Distribution of clutch size is shown in Figure 4. Clutches of over ten eggs, probably laid by more than one female (see Methods), produced very few goslings. Generally, clutches of 5-8 eggs produced the most goslings, and these were also among the commonest clutch sizes.

Egg and gosling mortality

Of 371 eggs laid, 114 produced fledged goslings, a mortality of 69%. Most of this (41%) was due to nest desertion, with egg predation and breakage (9%), hatching failure (10%) and gosling mortality (9%) taking roughly equal numbers. Nearly 10% of eggs laid were lost from the nest during incubation, presumably as a result of accidental loss or predation by fox *Vulpes vulpes* or badger *Meles meles*. Eighty-one percent of study pairs nested on islands, and island eggs were significantly less likely to be lost or broken during incubation ($\chi^2 = 10.8$, $P = 0.001$). A possible cause was cattle trampling, observed at three mainland nests in 1983. Nineteen point seven percent of eggs present at the end of incubation failed to hatch. This is a much higher fail-

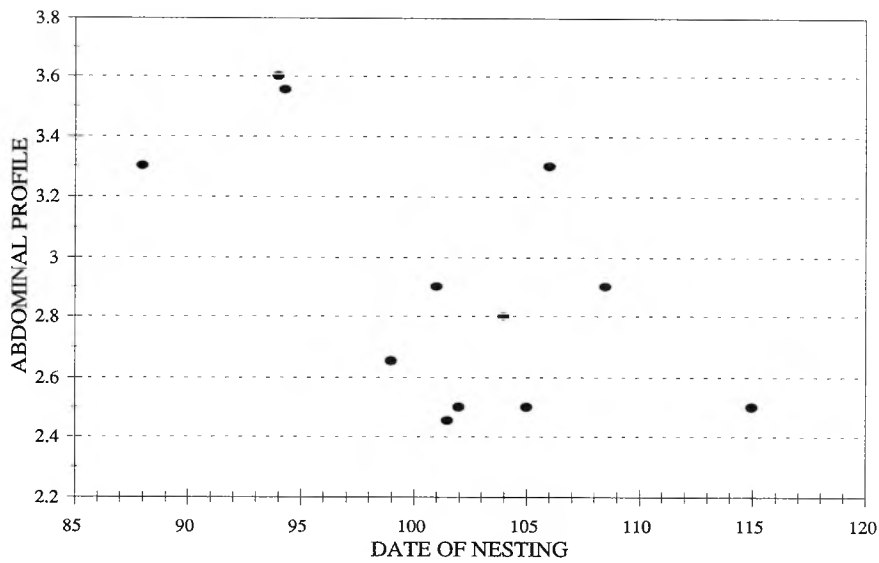


Figure 3. Early nesting female Canada Geese had higher Abdominal Profiles (AP₅₀) ($r_{12} = -0.63$).

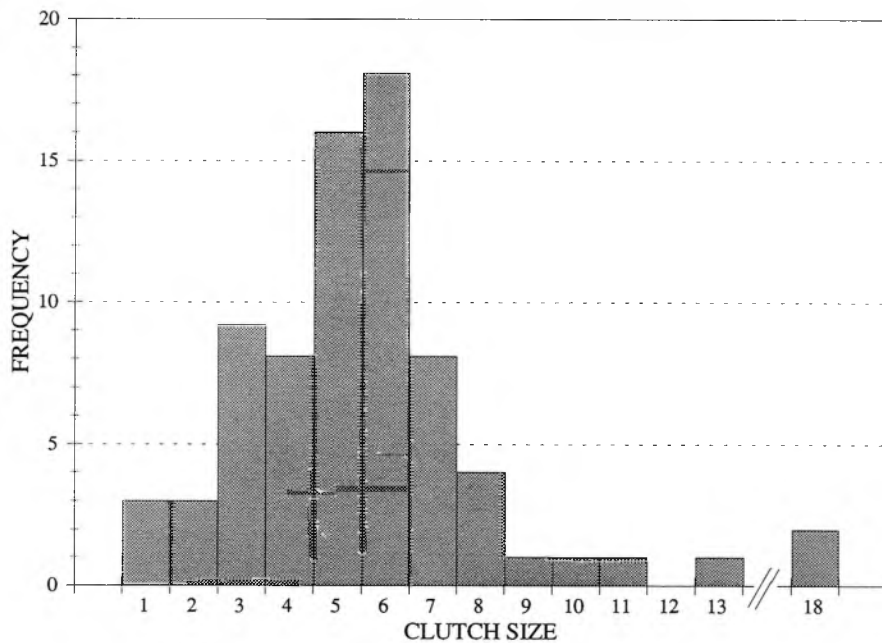


Figure 4. Clutch size frequencies (total $n = 75$) of Canada Geese.

ure rate than that recorded for Greylag (6%, Newton & Kerbes 1974) or Ross's Goose *Anser rossii* (6%, Ryder 1967). Of a small sample of 16 unhatched eggs which was examined, 87% contained developing embryos, all but one of which were nearly fully developed. Mortality was, therefore, probably due to nest abandonment when the first gosling hatched. Possibly the females were close to starvation at this late stage of incubation (e.g. Harvey 1971, MacInnes *et al.* 1974, Raveling 1979) and left the nest to feed. Alternatively it may be the hatching period was protracted due to nest parasitism (see Methods).

Gosling survival was high in both years, with 77% surviving from hatch to round-up, and only one out of 32 pairs hatching eggs failing to fledge any goslings. Causes of gosling mortality were not identified. MacInnes *et al.* (1974) found that 97% of Canada goslings in the McConnell River delta, Canada, survived to five weeks of age if they were alive at one week, and Owen & Norderhaug (1977) estimated that 85% of week-old Barnacle Geese in Svalbard survived to their first winter.

General discussion

This study links explicitly individual feeding performance in the pre-breeding period with the resulting stored reserves, and shows how these in turn affect breeding success. The study was, however, carried out on an atypical non-migratory population for which the constraints and pressures of migration were lacking. Females which fed faster pre-breeding stored reserves faster, and so bred earlier (Fig. 3) and more successfully. Males probably contributed to their breeding success by protecting their mates during the pre-breeding period, so allowing her extra feeding.

Stored reserves were here estimated using Owen's (1981) Abdominal Profile (AP). Hanson (1962) had prepared the ground for such a study by pointing out that the abdomen of Canada Geese enlarges when large amounts of fat are present. AP is thought, on the basis of carcass analysis, primarily to indicate fat reserves (Hanson 1962, Owen 1981, and see Introduction). As stressed by Owen, no other method of estimating condition in the field has yet been developed. Without assessment of Abdominal Profile it would have been impracticable for us to study the effects of feeding on condition, and of condition on breeding success, in marked individuals.

Owen (1981) considered that AP gave a good guide to the condition of geese in winter and spring, a view with which we concur.

AP increased with date and time of day in females, but this was allowed for using regression to obtain an index, AP_{50} , which was used in between-female comparisons. A useful next step would be to check the correlation between AP_{50} and stored reserves in females. This might involve killing a number of females on day 50, or alternatively a condition index based on weight and size could be used (see e.g. Evans & Smith 1975, Halse & Skead 1983). We did not find an increase in male AP with date. Male reserves are important in allowing males to defend larger territories in colonial nesting arctic geese (Ryder 1975, Owen & Wells 1979, Mineau & Cooke 1979), but in our study area males did not defend feeding territories.

Here we have suggested that stored reserves influence nesting date and that this in turn is associated with breeding success. We did not find a direct correlation between reserves and clutch size, although this might be a result of error in the estimation of clutch size due to nest parasitism, as discussed above. Many other studies, however, have found that stored reserves affect both laying date and clutch size (e.g. Ryder 1970). Hamman & Cooke (1989), in a study of Lesser Snow Geese, found, as here, that nutrient reserves (assessed by carcass analysis at the onset of laying) correlated negatively with laying date; they also reported that laying dates (and clutch sizes) covaried within individuals between breeding seasons.

Several studies have suggested that males protect their mates in the pre-breeding period (e.g. Hanson 1953, Raveling 1970, Inglis 1976, Nastase 1983), thereby allowing them to acquire more food, and eventually to breed more successfully. Male Barnacle Geese begin defending feeding areas around their females when vegetation growth begins in spring, thus enabling the females to gain weight more quickly (Owen 1981, citing Owen, Gullestad & St Joseph 1977 unpubl. report, Wildfowl Trust), and male White-fronted Geese in Greenland are thought to defend their mates in the pre-nesting period, thus allowing them to feed for the longest possible time (Fox & Madsen 1981).

In a companion study (Johnson & Sibly 1990), we showed that mated birds associated closely within the flock in the pre-breeding period, and we suggested that male vigi-

lance may protect the mate from potential predators (particularly at the edge of the flock) and from interference from conspecifics. The present study suggests

that larger males provide more effective protection, since male size, assessed by tarsus length, correlates with his mate's AP_{50} .

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