



Social dominance correlates and family status in wintering dark-bellied brent geese, *Branta bernicla bernicla*

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In many gregarious species, including ducks and geese, being dominant provides more benefits than costs, because dominants have better access to resources essential for survival or reproduction. In geese, being in better body condition during migration towards the breeding grounds positively influences reproductive success. However, underlying proximate mechanisms linking prebreeding body condition on the wintering grounds to breeding success remain poorly understood. We investigated social dominance correlates and family status, in three consecutive winters, in a free-ranging, migrating, dark-bellied brent goose population. Families with juveniles dominated pairs, and pairs dominated singletons. Dominance rank did not increase with the number of juveniles per family. Males were dominant over females. Social dominance and reproductive status for a given winter were significantly correlated with body mass, body size and body condition during the previous winter, suggesting that body condition in winter also affects subsequent breeding success and hence also dominance. Levels of testosterone and triiodothyronine were not correlated with immediate or later dominance or reproductive status. We discuss the role of family status as a signal of social status in determining reproductive strategies.

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Intraspecific competition for resources exists in all non-solitary species, generally for food by indirect depletion (Sutherland & Anderson 1993) and/or direct interference (Appleby 1980; Ens & Goss-Custard 1984; Triplet et al. 1999), but also for a mate (Dobson 1982). To reduce direct and indirect costs of intraspecific interference, dominance hierarchies provide stability in a group by reducing the intensity and frequency of aggressive interactions (Raveling 1970; Archer 1988). Although this organization is beneficial to all individuals in a hierarchy by increasing the time devoted to foraging activities (Belthoff et al. 1994; Guillemain et al. 2000), it seems that benefits are greater for dominant than for subordinate individuals. Dominance status can enhance individual fitness in various

ways. Dominant individuals may have privileged access to food resources (Appleby 1980; Kotrschal et al. 1993; Stahl et al. 2001) and/or a mate, especially when the sex ratio is biased (Brodsky et al. 1988; Holmberg et al. 1989). Social dominance status is also related to reproductive success (reviewed in Ellis 1995; Côté & Festa-Bianchet 2001). Consequently, social dominance relationships figure prominently in the social behaviour of group-living animals (Sirot 2000; Krause & Ruxton 2002).

For most migratory birds, competition for food is particularly important at wintering grounds where they are gregarious (Ens & Goss-Custard 1984). Food resources are crucial for accumulating fat reserves used both for breeding and during migration (Ebbinge & Spaans 1995; Tamisier et al. 1995) and for replenishing protein reserves lost during migration (Zwarts et al. 1990; Gauthier et al. 1992; Katti & Price 1999). Palaearctic geese feed in large groups in winter quarters that are often characterized by food supplies that are nonrenewable and hence become depleted. Therefore, competition for resources is potentially high (Kotrschal et al. 1993; Carbone et al. 2003; Rowcliffe et al. 2004), in particular when low ambient temperatures increase energy demands (Frigerio et al. 2004a). The efficiency with which resources are ingested

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and/or monopolized is relevant not only in winter, but also for future reproductive success. In barnacle geese, *Branta leucopsis*, females that arrive first at the breeding grounds nest first and have a higher reproductive success (Dalhaug et al. 1996). Furthermore, several studies using individually marked dark-bellied brent geese have shown that females that have offspring when they return in autumn to wintering grounds in Western Europe are heavier at spring departure from the Wadden Sea than those that return without offspring (Ebbinge et al. 1982; Ebbinge & Spaans 1995; Spaans & Postma 2001). It therefore seems important for geese to store enough energetic reserves rapidly, at all stages of their migration, and, in this context, being dominant could be an advantage (Stahl et al. 2001).

If social rank is important for wintering geese, we predict an association in winter between social dominance status and individual morphological, hormonal and/or behavioural traits. Several correlates of social dominance have been explored in birds (reviewed in Piper 1997). For waterfowl, age, sex, reproductive status (paired or single) and body size are all related to dominance status (Hepp & Hair 1984; Lamprecht 1986b; Black & Owen 1987; Hepp 1989). Social dominance is also often associated with pronounced aggressive behaviour and high levels of plasma testosterone (Wingfield et al. 1987; Marler & Moore 1988) which leads to a relation between testosterone (T) levels and social rank in some organisms, including birds (Wingfield et al. 1987, 1990; Guillemin et al. 2000). Thyroid hormones, such as triiodothyronine (T₃), which are important for the regulation of metabolic rate, body temperature and oxygen consumption in birds (reviewed in McNabb 2000) could reflect differential metabolic activity between individuals with different dominance ranks.

Endocrine patterns associated with social dominance in the context of reproductive behaviour have been fairly well studied in geese (e.g. Kotrschal et al. 1998; Hirschenhauser et al. 1999, 2000). However, winter endocrine parameters, to our knowledge, have never been explored as correlates of social dominance in free-ranging populations. Nevertheless (1) T is low in both sexes until late winter (Hirschenhauser et al. 1999), (2) aggression in a nonsexual context does not have to be T-related (Frigerio et al. 2004b), and (3) experimental chronic increase in systemic T in male greylag geese, *Anser anser*, during the winter flock period did not stimulate agonistic interactions (Frigerio et al. 2004b). One dominance-related behaviour affected by T is the 'beak up', a status-signalling display (Frigerio et al. 2004b).

Studies of geese have shown that the best predictor of dominance status is family size rather than individual morphological parameters such as body mass, size or body condition (Lamprecht 1986b; Gregoire & Ankney 1990; Loonen et al. 1999; Stahl et al. 2001). Large families are dominant over small ones, which in turn dominate pairs, and pairs dominate single adults and juveniles. Furthermore, more dominant pairs in winter may produce more offspring in the following summer and return to winter quarters with more young than less dominant pairs do (Lamprecht 1986a, b). These findings suggest that geese use a two-step behavioural strategy to minimize the costs

of maintaining dominance through costly behaviours such as aggression and/or displays. First, individuals in pairs without young should ensure that they are in good body condition in winter to increase their reproductive output during the following breeding season. They could do this by investing more in agonistic interactions in winter to protect essential resources required to build up their energy stores. Second, pairs that reproduced successfully can then rely on their family size to maintain high social status and replenish their energy reserves without investing extensively in costly social interactions.

We investigated dark-bellied brent geese dominance relationships during three successive winters to test the two-step scenario presented above, proximately linking social dominance status and family size with reproductive success. We first verified the role of family size (i.e. reproductive status) in the determination of individual dominance status. We then tested whether social dominance and family size are correlated with other phenotypic traits (morphology, hormones) in current and/or previous winters. If our scenario were correct, we expected to find a strong relation between family size and social dominance status for a given winter, and a significant correlation between dominance/family size in one winter and body condition and T₃ levels (i.e. metabolic activity) during the previous winter.

METHODS

Birds and Study Site

During the winters 2001–2002, 2002–2003 and 2003–2004, we captured 112 dark-bellied brent geese in the wintering area of Oléron Island (45°56'N, 1°21'W, France), by using a cannon net (Bub 1991). We caught the geese on the beach, close to a watering area where brents came in small flocks.

We determined sex by cloacal examination and distinguished juveniles (first-year) from birds in adult plumage (second-year and older) by the white edges of the wing coverts, which produce a 'chevron' (Lambeck 1990a). We marked each bird individually with coded Darvic coloured leg rings that allowed recognition from a distance of up to 250 m with a 20 × 60 telescope. Using these observations, we estimated that about 2% of the individuals constituting the local wintering population were individually marked. Darvic rings have been used for the last 14 years in the European brent network, and no significant negative effect has been reported.

Measurements and Body Condition

We weighed birds (±1 g) on a spring balance and measured tarsus and culmen lengths (±0.01 mm) with an electronic calliper. Wing length was measured (±1 mm) with a ruler. One observer (M.P.) carried out all measurements to minimize observer biases.

We used wing + culmen + tarsus lengths as a body size index and we calculated the ratio of body mass (g) to (wing + culmen + tarsus lengths) (mm) as an index of

body condition (Chastel et al. 1995; Kitaysky et al. 1999; Poisbleau et al. 2005a, b). High values represent individuals that were relatively heavy for their respective body size and low values those that were especially lean for their size. After measurements, birds were kept in holding boxes singly or in groups of up to three individuals before blood sampling (Bub 1991). As the cannon-net procedure leads to long handling times for individual birds (time elapsed between capture and blood sampling: $1\text{ h }53\text{ min} \pm 1\text{ h }19\text{ min}$), and considerable interindividual differences in handling time, we tested the effect of handling time on hormonal levels. Although the effects were not statistically significant (T: $F_{1,36} = 1.903$, $P = 0.176$; T₃: $F_{1,30} = 3.600$, $P = 0.067$), we included handling time in the main analyses.

Blood Sampling and Radioimmunoassays

Birds were bled as quickly as possible following the same standardized technique: a blood sample (around 800 μl) was collected from a brachial vein with a 1-ml heparinized syringe and a 25-gauge needle. Blood samples were put into ice and centrifuged within 1 h. Plasma was subsequently stored at -20°C . Blood sampling had no immediate adverse effects on the geese and we observed no behavioural difference from nonhandled birds during the following weeks.

Plasma T levels were determined by radioimmunoassay with a specific antibody (Lormée et al. 2000; Poisbleau et al. 2005a). Only one assay was carried out and the intra-assay coefficient of variation was 6.5% ($N = 3$ duplicates). The lowest concentration detectable was 0.10 ng/ml. Total plasma T₃ was determined in one assay (Chastel et al. 2003). The lowest concentration detectable was 0.038 ng/ml. The intra-assay coefficient of variation was 2.3% ($N = 6$ duplicates).

Behavioural Observations

We determined the dominance hierarchy of the flock by observing interactions. For a given marked individual, we considered any interactions with any opponent, marked or not. We defined an interaction as a direct confrontation between two birds, ranging from threats with lowered head and neck to active chases with flapping wings (Stahl et al. 2001). We considered an agonistic interaction as being won when the opponents turned and walked or ran away. Conflicts were resolved within seconds. The dominance score was defined as the percentage of interactions won by a focal bird divided by the total number of interactions in which this bird participated whatever its opponent (Ens & Goss-Custard 1984; Lamprecht 1986b). For each winter, we calculated a winter dominance score for each marked individual for which we had seen a minimum number of 26 interactions in order to obtain an error less than $\pm 10\%$ for the estimated score (Poisbleau et al., in press). The more dominant a bird is the closer to 100% is its dominance score. We assigned an individual score for each individual in a familial structure, in contrast to Stahl et al. (2001)

who assigned the same global rank for all family members. Of the 112 individually marked birds available, 62 were involved in at least 26 interactions for one, two or three different winters ($\bar{X} \pm \text{SD} = 93.46 \pm 68.66$, range 26–424).

Because parents and their offspring normally stay together until spring (Lambeck 1990b), we determined mating status and family size from behavioural observations. Family members coordinate their behaviour and stay close together, for example family members move as a unit, and conspecifics that come too close to a family are pecked at or chased away (Gregoire & Ankney 1990).

Statistical Analysis

All measured parameters followed a normal distribution without transformation, and dominance scores expressed as percentages were arcsine transformed, allowing parametric testing (Sokal & Rohlf 1995).

To explore dominance score correlates, we used analyses of covariance on arcsine-transformed dominance scores in adult birds. Mixed-effects models, with 'winter' as a random factor, allowed us to take into account the unpredictable and potentially high variability between winters. When the same birds were used for two or three winters, the individual code was also included as a random effect in the model. Sex, reproductive status (singletons, pairs with or without young), family size, body mass, body size and body condition indexes, T and T₃ levels were considered as factors according to the analysis. We assumed individual adult body size to be constant over years. We also used a mixed model to test correlates of reproductive status and included 'winter' as a random effect. As the body condition index was calculated from body mass and body size, we constructed two models, one including the effects of both body mass and size (model 1 in Table 1), the other including the effect of body condition (model 2).

For all statistical analyses we used SAS software (SAS Institute 1997). Values are presented as means \pm SE for hormonal parameters and as means \pm SD for morphological measurements.

RESULTS

Dominance, Family Status, Sex and Body Size

We investigated the effect of family status on social dominance scores incorporating effects of sex and body size. None of the two-way interactions was statistically significant (all $P > 0.05$). In an analysis of covariance, both family status and sex significantly affected dominance score, but body size did not ($N = 75$; family status: $F_{1,31} = 75.44$, $P < 0.001$; sex: $F_{1,31} = 18.62$, $P = 0.0002$; body size: $F_{1,31} = 0.36$, $P = 0.551$). Sex and family status remained significant when body size was removed from the model ($N = 98$; sex: $F_{1,33} = 27.03$, $P < 0.0001$; family status: $F_{2,33} = 72.49$, $P < 0.0001$). Males were dominant over females, and pairs with offspring were dominant over pairs without offspring, which were dominant over singleton birds (Fig. 1). For pairs with juveniles, number

Table 1. Current and previous winter correlates of dominance score

Effect	Current winter correlates			Previous winter correlates		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Model 1						
Handling time	1,12	1.06	0.323	1,16	5.92	0.027
Sex	1,12	11.80	0.005	1,16	0.58	0.457
Reproductive status	2,12	48.68	<0.0001	2,16	0.08	0.924
Body size index	1,12	0.92	0.357	1,16	4.52	0.049
Body mass	1,12	0.38	0.550	1,16	25.55	0.0001
Testosterone level	1,12	1.94	0.189	1,16	0.56	0.464
Triiodothyronine level	1,12	0.88	0.367	1,16	0.31	0.585
Model 2						
Handling time	1,13	0.73	0.407	1,17	6.77	0.019
Sex	1,13	12.26	0.004	1,17	0.18	0.679
Reproductive status	2,13	54.99	<0.0001	2,17	0.30	0.743
Body condition index	1,13	0.65	0.434	1,17	29.56	<0.0001
Testosterone level	1,13	1.57	0.232	1,17	0.37	0.552
Triiodothyronine level	1,13	0.58	0.458	1,17	0.77	0.392

Results are shown for mixed-model procedures on arcsine-transformed dominance scores (winter *n*) with winter as a random effect and (1) sex, reproductive status, body size index, body mass and testosterone and triiodothyronine levels as factors, and (2) sex, reproductive status, body condition index and testosterone and triiodothyronine levels as factors. For current winter correlates $N = 22$; for previous winter correlates $N = 26$. All interactions were nonsignificant and therefore removed from the model during the backwards stepwise procedure.

of juveniles (from 1 to 5) was not significantly related to dominance score ($N = 20$; $F_{1,2} = 7.47$, $P = 0.112$). The body size effect on dominance score remained nonsignificant when data from males ($N = 41$) and females ($N = 34$) were analysed separately (males: $F_{1,17} = 0.48$, $P = 0.494$; females: $F_{1,11} = 0.05$, $P = 0.833$).

Current Winter Correlates

Body condition and hormonal levels were available only for winter of capture. We therefore initially used a restricted data set including only individuals for which all morphological, behavioural and hormonal characteristics considered were measured during the same winter. Body size and body mass in the first model, body condition in the second model and hormonal levels in both models were not statistically significantly related to dominance score variation (Table 1). Effects of sex and reproductive status on dominance score remained significant in the final model (sex: $F_{1,22} = 75.88$, $P < 0.0001$; reproductive status: $F_{2,22} = 114.25$, $P < 0.0001$). Males were dominant over females, paired adults with juveniles were dominant over paired adults without juveniles, and paired adults without juveniles were dominant over singleton adults.

Previous Winter Characteristics

Sex, reproductive status and hormone levels during the previous winter were not significantly related to dominance score during the current winter (Table 1) but body size and body mass were (final model with only significant variables; body size: $F_{1,22} = 5.89$, $P = 0.0238$; body mass: $F_{1,22} = 22.28$, $P < 0.0001$). Dominant birds were larger and heavier. Body condition during the previous winter

was also strongly positively correlated with dominance score in the current winter ($F_{1,23} = 23.23$, $P < 0.0001$; body condition was the only significant variable in the final model; Fig. 2). The sex effect was not significant in this model (Table 1).

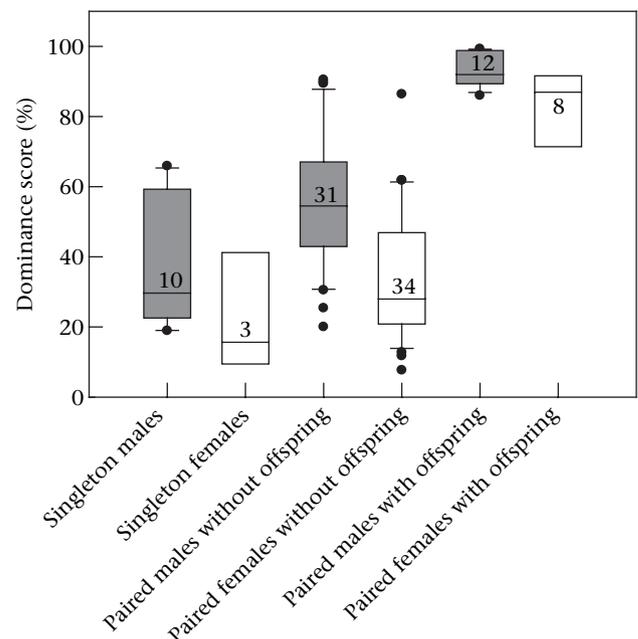


Figure 1. Mean dominance score (%) according to reproductive status (singleton bird, paired bird without offspring, or paired bird with offspring) and sex (grey boxes: male; white boxes: females). Boxes show medians, 25% and 75% quartiles. Whiskers indicate the range between the 10th and 90th percentiles. ●: Data outside the 10th and 90th percentiles. Sample sizes are given in the boxes.

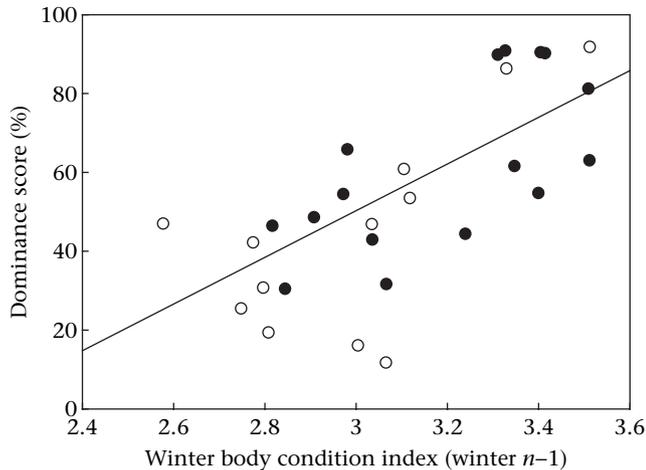


Figure 2. The relation between the adult dominance score (DS, %) during a given winter n and the body condition index (BCI) during the previous winter ($n-1$). First-order linear regression: $r^2 = 0.512$, $DS_{\text{Winter}(n)} = 65.507 \times BCI_{\text{Winter}(n-1)} - 149.161$. ●: males; ○: females.

Reproductive Status Correlates

Body condition index during the previous winter was significantly correlated with reproductive status during the current winter (analysis of covariance with winter of capture/measurements (winter $n-1$) as random effects and body condition index (winter $n-1$) as covariates; $F_{1,31} = 11.33$, $P = 0.002$), that is, adults in families were in better body condition during the previous winter than paired or single adults. T levels during the previous winter were not significantly related to subsequent reproductive status in the current winter ($F_{1,31} = 0.15$, $P = 0.702$). Contrary to our predictions, but consistent with our results on dominance correlates presented above, T_3 levels during the previous winter also did not seem to influence subsequent reproductive status in the current winter ($F_{1,31} = 0.05$, $P = 0.829$).

Reproductive status in one winter was significantly correlated with body condition index during the same winter, and adults in families had better body condition than adults in pairs or alone ($F_{1,49} = 5.79$, $P = 0.02$). Finally, plasma hormone levels were low (males: 0.342 ± 0.103 ng/ml, $N = 46$; females: 0.340 ± 0.148 ng/ml, $N = 37$) and were not significantly correlated with reproductive status during the same winter (T: $F_{1,49} = 0.74$, $P = 0.395$; T_3 : $F_{1,34} = 0.83$, $P = 0.37$).

DISCUSSION

Dominance Correlates

Our results confirmed that families socially dominate both pairs and single birds, consistent with most previous studies (Raveling 1970; Lamprecht 1986b; Gregoire & Ankney 1990). As we did not detect a relation between dominance score and the number of young per family, it appeared that the most pertinent family parameter for acquiring a high dominance status in brent geese was the

presence of offspring, rather than family size per se. The breeding pair effect was additive to a sex effect, with males dominating females. To explain similar findings in semi-captive bar-headed geese, *Anser indicus*, Lamprecht (1986b) proposed the 'co-operative hypothesis', that family members cooperate against opponents, and the 'motivational hypothesis', that males are willing to fight harder in the presence of a mate (see also Scheiber et al. 2005). Gregoire & Ankney (1990) also suggested that the presence of offspring stimulated parent snow geese, *Anser caerulescens*, to be more aggressive, making them more likely to win an encounter. In this process, males could be more dominant than females, as we observed in this study, and adult male rank could determine the social status of the pair or family too. On the other hand, both body condition and body size measures in the previous winter influenced the social status of individual brent geese (i.e. with or without offspring). This finding suggests that bigger birds may have an advantage in conflicts and tend to be more dominant and would also contribute to males dominating females, as males are larger and heavier than females (Cramp & Simmons 1977).

In our study, winter hormone levels did not seem to intervene in the expression of dominance scores and breeding success. The low T levels are consistent with partial atrophy in gonads outside the breeding season (Wingfield & Farner 1993; Hau et al. 2004). However, we observed numerous winter fights in the absence of high plasma T levels. Evidence suggests that dehydroepiandrosterone (DHEA), a precursor of T, can be rapidly converted to T in the brain, and can determine winter aggression in the absence of high plasma T levels (Soma & Wingfield 2001; Soma et al. 2002; Hau et al. 2004). According to the 'challenge hypothesis' predictions, this would allow maintenance of basal T levels without costs and a quick response to aggression when necessary (Wingfield et al. 1990). Our observations are consistent with the findings of Hirschenhauser et al. (1999), who observed minimum plasma T values during summer and autumn, with an increase from January onwards. Perhaps plasma T levels are higher when geese arrive on the wintering areas in early autumn (August–September), possibly related to flock reunification and the termination of photorefractoriness of the reproductive system, and drop to basal levels afterwards.

Familial Status as Signal of Dominance

If the 'motivational effect' promotes success without fighting, the absence or presence of offspring could sometimes signal parental dominance status and influence responses in opponents ('Status-signalling hypothesis', Rohwer 1975). This hypothesis was proposed partially to explain the dominance of paired barnacle geese over singletons in breeding areas (Stahl et al. 2001). In such circumstances, relative social stability and inertia (Guhl 1968) are unlikely to be the result of individual recognition alone (Wiley et al. 1999), which might be difficult in large flocks with a rotating membership, as happens in the wintering areas (Guhl & Allee 1944). Status signalling might

therefore serve to regulate social interactions, with or without restricted hormone-driven signalling, which is often related to testosterone (Archawaranon et al. 1991). The lack of a significant correlation between dominance score and plasma hormonal levels in our study seems to support this hypothesis. Costly hormones and associated costly behaviours (Marler & Moore 1988; Wingfield et al. 2001; Goymann & Wingfield 2004) implicated in the maintenance of social status are probably not required for adult geese accompanied by goslings. The presence or absence of goslings with a pair could thus be considered as an 'honest' signal of pair quality (Caryl 1982), a signal that may help to determine individual social dominance status with a minimum of contests involved. This hypothesis assumes that offspring are costly to produce for geese (initial energetic investment for females but also in time and energy for both parents, Black & Owen 1989; Poussart et al. 2001; Samelius & Alisaukas 2001). Loonen et al.'s (1999) experimental results support this hypothesis: artificial removal of one or more juveniles decreased the familial social status whereas adding one or more juveniles increased it, and pairs with offspring were more dominant without being especially more aggressive than other birds, perhaps because potential opponents might well take the presence of young as a signal. The fact that pairs accompanied by offspring in Loonen et al.'s study were at least as heavy as pairs without offspring suggests that there are no important additional costs of being dominant for parents. There are costs of being dominant (Kotrschal et al. 1998), but the benefits seem to outweigh them by far (Scheiber et al. 2005). In addition, we suggest that the crucial role of good body condition for future reproductive success (Ebbinge & Spaans 1995) should also favour the establishment of signals to show social dominance independent of costly hormonal processes and aggressive behaviours.

Body Condition and Reproductive Strategies

It has been suggested for blue geese, *A. c. caerulescens* (Harvey 1971), and barnacle geese, *Branta leucopsis* (Prop et al. 2003), that females with small winter reserves would be physiologically unable to secure enough food on the wintering grounds and during migration for successful breeding. Our study provides the first quantitative evidence supporting this hypothesis in brent geese, showing a correlation between winter body condition and the breeding success (family status) in the following season. Previous investigations have already found links between female body mass on spring staging areas and breeding success during the same year (Ebbinge et al. 1982; Ebbinge & Spaans 1995; Spaans & Postma 2001).

Both male and female winter body condition affected subsequent breeding success in our study. One potential explanation is that fat storage in pairs determines the timing of migration, with birds that arrive earlier on the breeding grounds having higher breeding success (Prop et al. 2003). In addition, fat reserves may be used for both migration and mate guarding (Teunissen et al. 1985; Prop et al. 2003) at spring staging areas. Successful

mate guarding would then allow females to feed peacefully on spring staging areas; uninterrupted feeding is essential for successful reproduction (Lamprecht 1986a; Ebbinge & Spaans 1995).

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