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Dominance relationships in Dark-bellied Brent Geese *Branta bernicla bernicla* at spring staging areas

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Spring staging is an important period influencing reproductive success for migratory birds. During this period, female geese must accumulate reserves for subsequent migration, egg laying and incubation. They may increase feeding opportunities by being guarded by dominant males protecting a large feeding area and providing feeding time, and/or having themselves a high dominance status. Using paired adults of Dark-bellied Brent Geese *Branta bernicla*, we tested if males had higher dominance scores than females, if larger individuals had higher dominance scores than smaller ones and if dominance ranks of paired partners were correlated. Our results supported the first and third predictions while, once controlled by sex, body size was not correlated with adult dominance status.

Key words: dominance score, body size, spring staging, assortative pairing, Brent Geese

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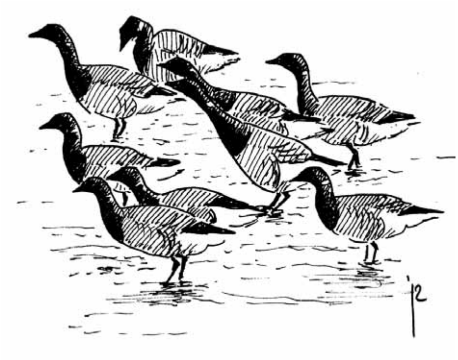

Introduction

Social dominance relationships exist in most, if not all, gregarious animals, from insects (e.g. Tindo & Dejean 2000) to mammals (e.g. Barrette & Vandal 1986). Establishing a dominance hierarchy may limit the costs of interactions with conspecifics, through the reduction of aggressive interactions (Rowell 1974, Archer 1988). For most migratory wildfowl, social dominance organisation may play a particularly important role during the times of year when these birds are gregarious. Body condition of geese in winter and spring affects positively their subsequent migration, breeding success and dominance status during the next winter (see Ebbinge & Spaans 1995, Poisbleau *et al.* 2006b). During migratory stops at staging areas, female geese must accumulate reserves for subsequent egg laying and incubation. The dominance status of the pair during this pre-breeding period, through its influence on foraging efficiency, could thus be a main determinant of future reproductive performance (Lamprecht 1986a, Ebbinge & Spaans 1995). In addition, females may enhance feeding opportunities, optimise food storage and maximise reproductive success when guarded by males protecting a space around the feeding female (Teunissen *et al.* 1985, Spaans *et al.* 2007) and allowing for some extra feeding time. Nevertheless, if determinants and consequences of dominance status are now quite well explored in wintering groups of geese (see for examples Boyd 1953, Raveling 1970, Black & Owen 1989a, Kotrschal *et al.* 1993, Poisbleau *et al.* 2006b), it is less the case at spring staging areas (see Black *et al.* 2007).

Dark-bellied Brent Geese *Branta bernicla bernicla* leave their wintering areas in Britain and France during March and early April and travel from the Atlantic coast to the Taimyr Peninsula, Russia, for reproduction (Green *et al.* 2002). Spring-staging stops may be required in the Wadden Sea (Netherlands, Germany, and Denmark) and White Sea (North-west Russia) to accumulate and restore reserves in anticipation of migration and reproduction events (Ebbinge & Spaans 1995). As for other goose species, the best predictor of dominance status is family size (Lamprecht 1986a,b, Black & Owen 1989b, Gregoire & Ankney 1990, Loonen *et al.* 1999, Poisbleau *et al.* 2006b). However, as in the spring staging period Brent Goose parents chase away their juveniles, most of the pairs act as single pairs (Cramp & Simmons 1977, Lambeck 1990a,b, Boyd 2005). Therefore, this period allows control for social dominance status, independently of the number of juveniles. In addition, a good breeding success may be the result of a higher social dominance status during spring staging and not the cause of it, as is likely the case during winter (Poisbleau *et al.* 2006b). We here analysed some main factors potentially affecting social dominance status in Brent Goose pairs without goslings, during their spring staging on Terschelling Island in the Wadden Sea. In this context and in accordance with a previous study on wintering Brent Geese (Poisbleau *et al.* 2006b), we aimed at testing predictions in Brent Geese that (1) males have higher dominance scores than females, (2) within each sex separately, larger individuals have higher dominance scores than smaller ones and (3) dominance ranks of paired partners are correlated.

Methods

During spring staging on Terschelling Island, the Netherlands, we caught Brent Geese using a cannon net, in May 2002 and 2003. Each bird was marked individually with coded Darvic coloured leg-rings. We determined sex by cloacal examination. Juveniles (first-year) were distinguished from birds in adult plumage (second-year and older) by the white edges of the wing coverts. To minimise observer biases, the same observer measured tarsus and culmen lengths to the nearest 0.01 mm using an electronic calliper, and measured wing length to the nearest millimetre with a ruler.

We studied social interactions at the capture site in May 2003, while the geese were foraging on polder grassland. For a given marked adult, we considered any interaction 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 interaction as being won by an individual when opponent(s) turned and walked or ran away. 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 (Ens & Goss-Custard 1984, Lamprecht 1986b). We calculated a 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 10% for the estimated score (Poisbleau *et al.* 2006c), i.e. for 28 different paired adults. The most dominant bird may reach a dominance score near 100%, the most dominated bird may have a score near 0%.

Using only individuals who were adults when they were captured, we used the first principal component score from a principal component analysis (PC1) of the three morphological measurements as an index of a bird's structural size (Rising & Somers 1989). All dominance scores were arcsine-transformed and all data then satisfied assumptions required by parametric statistical tests (Sokal & Rohlf 1995). Effects of sex and body size on dominance score were analysed using covariance analysis ANCOVA. Because of the restricted sample size, we used non-parametric tests for within-pair comparisons: Wilcoxon paired test to compare average dominance scores between males and females, and Kendall's rank correlation to test for the covariation of dominance scores between mates. All statistical analyses were performed using SYSTAT 7.0 (Wilkinson 1997).

Results

The first principal component (PC1) established from all captured adults ($n = 103$) described a positive correlation in body size variables. Loadings were 0.880 for tarsus, 0.855 for culmen and 0.855 for wing. PC1 had an eigenvalue of 2.237 and explained 75% of the variance of all three morphological variables.

Neither the interaction between sex and body size, nor body size significantly influenced spring dominance score in the initial model (sex x body size: $F_{1,24} = 0.592$, $P = 0.449$; body size: $F_{1,25} = 1.754$, $P = 0.197$). The only parameter significantly affecting dominance score was sex, males being more dominant than females ($F_{1,26} = 11.501$, $P = 0.002$; Fig. 1). However, as males are usually larger than females ($F_{1,101} = 114.501$, $R^2 = 0.531$, $P < 0.001$ from the entire capture database), we separately tested for the effect of size within each sex. For neither sex, larger adults significantly dominated smaller ones (males: $F_{1,15} = 3.539$, $P = 0.079$; females: $F_{1,9} = 0.001$, $P = 0.976$; Fig. 1).

Within-pair comparisons confirmed that males had a higher dominance score than females during spring staging ($n = 9$ pairs, of which both partners were ringed and had a dominance score; $Z = 2.547$, $P = 0.011$). Male and female dominance scores of the same pair were significantly and positively correlated across pairs ($\tau = 0.611$, $P = 0.022$, Fig. 2) whereas their body sizes were not correlated ($\tau = 0.111$, $P = 0.677$).

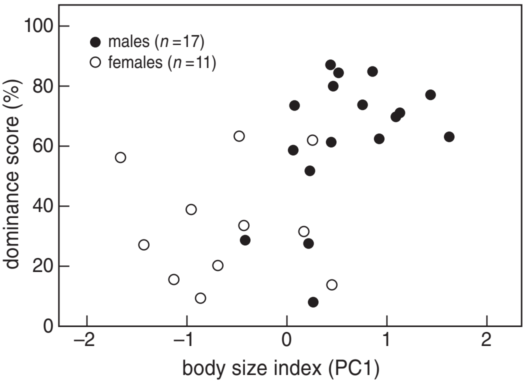

Figure 1. Dominance score (in percentage) of adult male and female Brent Geese during spring staging on Terschelling Island in 2003 in relation to body size ($n = 28$).

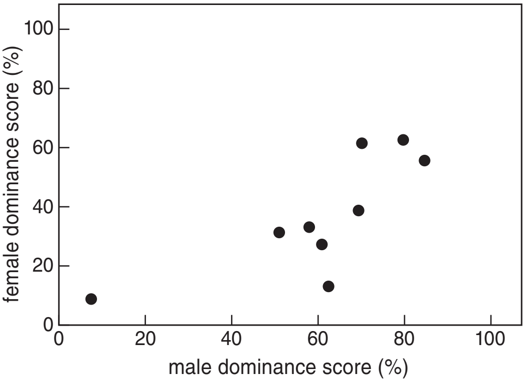

Figure 2. Relationship between male and female dominance scores (in percentage) within Brent Goose pairs during spring 2003 ($n = 9$).

Discussion

The dominance status of Brent Geese during spring staging was explored. Our results confirmed the wintering observations (Poisbleau *et al.* 2006b) that male Brent Geese had a higher dominance score than females both between and within pairs. In addition, as paired birds tended to have comparable dominance scores, we showed that dominance scores of both mates were not independent within a pair during spring staging. Different non-exclusive reasoning could explain these two results. (1) First, the ‘co-operative hypothesis’ (Lamprecht 1986b) proposes that if both partners cooperate against opponents, both will have a rather similar dominance status. We knew and observed that, during spring staging, paired female Brent Geese forage actively while males perform mate guarding by standing next to their female and preventing others from approaching her (Teunissen *et al.* 1985). Indeed, the increase in female body mass during spring and ultimately the subsequent reproductive success of the pair will partially depend on this male protection (Ebbinge & Spaans 1995). Thus, females intervened in a minority of fights while their mates were actively protecting them. However, females were also involved in aggressive interactions without the intervention of their mates when the latter were less attentive and/or occupied elsewhere (pers. obs.). Therefore, the cooperative hypothesis cannot explain the observed dominance score covariation between paired birds. (2) Second, if dominance was correlated to another parameter such as morphology or age, and if Brent Geese tended to pair with mates of similar size or age, we would expect the same relationships. Actual and previous investigations showed no size-assortative pairing in Brent Geese (Poisbleau *et al.* 2006a). Moreover, as the interaction between body size and sex was not significant and body size did not significantly affect dominance score within each sex, the impact of body size on dominance relationships was mainly due to the sexual dimorphism, as males were both more dominant and larger than females, as in numerous other studies (Cramp & Simmons 1977, Lamprecht 1986b). Nevertheless, as we have not been able to test the effect of age, we cannot reject the second hypothesis. (3) Finally, we could suppose that geese directly form dominance-assortative pairs; most dominant males pairing with most dominant females and vice-versa. We cannot verify this hypothesis because this requires the assessment of dominance status of birds both before and after pairing. In conclusion, our results suggest that it is now necessary to quantify male dominance status and mate-guarding efficiency using a larger and longer database integrating data before and after pairing as well as age. According to the importance of body reserves for the migration, egg-laying and incubation (see Spaans *et al.* 2007), it could be now pertinent to verify that females of pairs with high social rank build up a larger amount of body reserves in spring than females lower in rank would. Ultimately, a further monitoring of the same pairs on the breeding and/or wintering areas would be essential to comprehend the implications of their spring dominance status for their subsequent breeding success.

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SAMENVATTING

Bij vogels die in groepen voorkomen, kan op de voedselgronden een sterke concurrentie om voedsel ontstaan. Dat is onder meer het geval bij plantenetende soorten zoals ganzen. Omdat ganzen een groot deel van het jaar paarsgewijs opereren, kunnen partners steun aan elkaar hebben om een gunstige plek in de groep te bemachtigen. Te verwachten is dat de meest dominante dieren toegang hebben tot het beste voedsel. Het percentage gevechten dat een individu wint (de dominantiescore), kan als maat dienen voor de rangorde binnen een groep. In de onderhavige studie, uitgevoerd aan Zwartbuikrotganzen *Branta bernicla* op Terschelling, bleek dat mannetjes hoger scoorden qua dominantie dan vrouwtjes, en dat de dominantiescore van mannetjes gecorreleerd was aan die van hun partner. Tegen de verwachting in werd voor de seksen afzonderlijk geen verband gevonden tussen de dominantiescore en de grootte van het dier. (JS)

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