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# Preservation of winter social dominance status in Brent Geese *Branta bernicla bernicla* within and across winters

**Maud Poisbleau · Noël Guillon · Hervé Fritz**

**Abstract** Dominant and subordinate individuals in a group may benefit from the stability of the social dominance organisation, avoiding excessive waste of time and energy in aggressive interactions and reducing injury risks. Nevertheless, the likely evolutionary incentive for individuals to become, and furthermore to stay, dominant may destabilise such dominance hierarchies. In this context, the relative importance of fixed (e.g. sex, morphological size) and fluctuating (e.g. body condition, mating status, reproductive success, social unit size) traits influencing the establishment and preservation of dominance relationships could play a key role in group structure. We investigated the relative role of fixed and fluctuating traits on social status in Dark-bellied Brent Geese *Branta bernicla bernicla* which form large fairly unstable groups both within and across winters. We compared individual dominance scores of ringed Brent Geese during four consecutive winters. Brent Geese conserved their dominance score within a given winter irrespective of their age but were generally unable to conserve it across consecutive winters. As winter dominance scores correlated best with social unit size, dominance status thus appeared to be mostly a by-product of a fluctuating trait: breeding success in the previous summer. When we considered only adults that had the same social unit size during two consecutive winters, we observed a significant preservation of dominance scores. This result suggests that a fixed trait such as sex or morphological size may still play a role in setting dominance status.

**Keywords** Social dominance status conservation · Wintering · Age class · Social unit size · Flock dynamics

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## Introduction

Social dominance organisation occurs in most gregarious species (see Krause and Ruxton 2002 for examples), probably because the benefits of such an organisation outweigh the costs. Indeed, a social organisation based on dominance relationships allows the reduction of costs associated with gregariousness. It also provides social stability through a predictable social environment, mostly by structuring access to limited resources, such as food or a mate (Rowell 1974; Bernstein 1981; Archer 1988). This stable hierarchy avoids an excessive waste of time and energy in aggressive interactions and reduces injury risks, especially between individuals that differ considerably in dominance status. However, although both subordinate and dominant individuals in a group may benefit from a stable social organisation, there is probably an evolutionary incentive for individuals living in groups to access and retain dominant status (Krause and Ruxton 2002).

When a social dominance hierarchy is established within a group, the outcome of subsequent aggressive interactions is often predictable from previous encounters in the short term (Rowell 1974), but also possibly from one year to the next (Lamprecht 1986b). In the long term, the preservation of dominance status may only be possible within groups undergoing few changes in composition. If a group remains

stable (without immigration or emigration), we could expect that its social organisation also remains stable because, once established, social dominance hierarchy between members could be conserved by social inertia (Guhl 1968; Archawaranon et al. 1991; Wiley et al. 1999) when no environmental change affects members' social behaviour (e.g. Sloman et al. 2002). On the other hand, stability of dominance hierarchies may depend on the phenotypic traits influencing individual social dominance status, such as fixed (e.g. sex, morphological size) or fluctuating characteristics (e.g. body condition, mating status, reproductive success, social unit size; see Piper 1997) of the individuals constituting the group. In unstable groups and fluctuating environmental conditions, individuals may conserve their social status if fixed traits influence social dominance more than fluctuating ones. However, if dominance status depends mostly on fluctuating individual traits, individual dominance status in time could be constantly reconsidered and stability within the group may be impossible. In free-living animals, preservation of dominance status may thus depend on group structure, environmental conditions and individual phenotypic traits involved in the expression of dominance status. The relative importance of fixed and fluctuating traits determining dominance status and its preservation should therefore be a key issue when investigating gregarious species.

During winter, goose populations live in large groups for several months. Even if site fidelity provides a relatively stable group composition (Spaans and Postma 2001; and authors' unpublished data), groups are not always stable both within and across winters, due for instance to constant exchanges of individuals between wintering sites and processes related to local recruitment, emigration and immigration. In geese, sex, age, mating status (paired or single) and reproductive success (number of juveniles) have been found to be variously related to dominance status (e.g. Lamprecht 1986b; Black and Owen 1987; Stahl et al. 2001; Poisbleau et al. 2006a, 2008). Stahl et al. (2001) found that social dominance increased with age for female Barnacle Geese *Branta leucopsis* whereas it was less obvious for males in a group of non-breeding moulting individuals. By contrast, Lamprecht (1986b) noted a better correlation between dominance and male age in winter flocks of Bar-headed Geese *Anser indicus*. These results pointed out that individual dominance status may normally increase progressively through life. However, both sex and age are good integrators of various parameters potentially determining social dominance status within a class of social unit size. For instance, sex is strongly related to morphological size and body mass, while age is correlated with experience, mating status, reproductive success, morphological size and body mass. Pairs of Bar-headed Geese improved their dominance status after successfully completing the breeding season

(Lamprecht 1986b). Dominant White-fronted Geese *Anser albifrons* lost their hierarchical position after losing their partner, and decreased their dominance score to the level of unpaired individuals (Boyd 1953). When the brood size of Barnacle Geese changed as a result of natural events or experimental manipulation, social dominance status changed too (Loonen et al. 1999). Moreover, Barnacle Geese that remained with young for the longest period bred more successfully the next year than those with shorter periods of parental care, and females returning to the winter area with a brood were heavier than those that had nested but had no young in winter (Owen and Black 1989; Black and Owen 1989b). For wintering Dark-bellied Brent Geese *Branta bernicla bernicla*, social dominance for a given winter was significantly correlated with body mass, morphological size and body condition during the previous winter (Poisbleau et al. 2006a). Hence free-living goose populations are a pertinent model to test dominance preservation and explore the relative role of fixed and fluctuating factors in setting social status within and across winters.

We investigated dominance relationships in Dark-bellied Brent Geese *Branta bernicla bernicla* during four consecutive winters. For the first time, we tested preservation of social dominance status within and across wintering periods using ringed individuals. Previous investigations on geese showed that the best predictor of dominance status in geese was social unit size (Lamprecht 1986a, b; Gregoire and Ankney 1990; Loonen et al. 1999; Siriwardena and Black 1999; Stahl et al. 2001; Poisbleau et al. 2006a). However, the individual reproductive success of Brent Geese seems to vary significantly across years, mostly due to changes in predation pressure and climatic conditions at the Arctic grounds (Ebbinge 1989; Underhill et al. 1993; Spaans et al. 1998; Bêty et al. 2002). We therefore expect a strong influence of these stochastic events on individual dominance status. We predict that dominance preservation should be high within a given winter but may vary across winters. Whenever environmental constraints are of prime importance, we predict that the preservation of dominance status should be poor between successive winters. If individual characteristics partly override the effects of fluctuations in environmental constraints, we then expect dominance status to be conserved between winters. We therefore investigated the effect of fixed (sex and morphological size) and fluctuating (social unit size) individual characteristics on dominance status.

## Methods

### Birds and study site

During winters between 2001 and 2005, we captured 127 Dark-bellied Brent Geese in the wintering quarter of

Oléron Island (175 km$^2$, 45°56′N, 1°21′W, France) using a cannon net (Bub 1991) but no bait or decoy (Weatherhead and Ankney 1984). We caught birds on the beach, close to watering areas where Brent Geese came in small flocks. We ringed birds immediately following capture and released them together as soon as possible (less than 4 h after capture). We assumed that family integrity was not affected by capture and manipulations (Bowler 2003).

We determined sex by cloacal examination (Hochbaum 1942). Juveniles (first-winter) were distinguished from birds in adult plumage (second-winter sub-adults and older) by the white edges of the wing coverts (Lambeck 1990a). We measured tarsus and culmen lengths to the nearest 0.01 mm using an electronic calliper and wing length to the nearest millimetre with a ruler. One observer (M.P.) carried out all measurements to minimise observer biases. We used wing + culmen + tarsus lengths as a body size index (Poisbleau et al. 2006a). We marked each bird individually with coded Darvic leg-rings, which we could identify from a distance of up to 250 m with a 20 × 60 telescope. Using the same colour combination for each bird, we avoided potential inter-individual differences in the colour-band effect within the studied birds (see, for examples, Burley 1986; Cuthill et al. 1997). The European Brent Geese network have used Darvic rings for the last 14 years and reported no significant effects on the ecology and survival of this species.

Behavioural observations

Each winter, we conducted behavioural observations from arrival to departure of Brent Geese on Oléron Island (i.e. from late September to late March). We determined the social dominance organisation of the flock by observing interactions (see also Poisbleau et al. 2006a, b). For a given ringed individual, we considered any aggressive interactions with any opponent, marked or not, and noted the outcome, while the geese were foraging or drinking on *Zostera* spp. and *Enteromorpha* spp. beds along coastlines. 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 that an individual won an aggressive interaction when its opponent turned and walked or ran away (Stahl et al. 2001). The social dominance score was defined as the percentage of interactions won by a focal bird divided by the total number of interactions in which the bird participated (for method, see Ens and Goss-Custard 1984; Lamprecht 1986b). We calculated a dominance score for each marked individual with a minimum total number of 26 interactions in order to obtain an error of less than ±10% for the estimated score (Poisbleau et al. 2006b). The more dominant a bird is, the closer to 100% is its dominance

score. Thus, we assigned an individual winter dominance score for each observed ringed Brent Goose if involved in at least 26 interactions. During the winter 2003–2004, we assigned a monthly individual dominance score between October 16 and March 16 in order to test social status preservation across months and finally used all interactions to calculate the global winter dominance score.

Because parents and their offspring normally stay together until spring (Lambeck 1990b), we determined the size of ringed birds' social units using behavioural observations. Family members coordinate their behaviour and stay in proximity, i.e. family members move as a unit, and conspecifics coming too close to the family are pecked at or are chased away (Gregoire and Ankney 1990). For adults, social unit size was the combination of mating status and breeding success where 1 meant unpaired bird, 2 meant paired bird without juveniles, 3 meant paired bird with one juvenile, etc. In this dataset, no juvenile was observed with only one parent or only with siblings but some were seen alone. Therefore, juveniles' social unit size could be 1 (juvenile alone) and otherwise ranged from 3 (juvenile without siblings) to 7 (juvenile with four siblings).

Statistical analysis

Dominance scores were percentages, hence were arcsine-transformed to conform to the normal distribution requested for parametric tests (Sokal and Rohlf 1995). To test the correlation of individual dominance scores between different periods and the general trend within the studied population, we analysed the dominance score preservation between consecutive periods (months or winters) using a linear regression between each pair of consecutive periods. If the linear regression was significant, we first tested that the slope did not differ from one, and then that the intercept did not differ from zero, using a hypothesis test for intercept (Scherrer 1984). For instance, if the slopes are the same, but the intercept increases winter after winter, it could be an indication of an increase in score with age, irrespective of the initial position of the individual in the hierarchy.

To explore the dominance score correlates for juveniles, we used a General Linear Model with sex as a fixed factor and social unit size and morphological size as covariates. Because 5 of the 16 juveniles came from the same two families, we randomly included only 1 juvenile from each family in this analysis. To investigate the relative contribution of fixed (between-individual components: sex and morphological size) and fluctuating (within-individual component: social unit size) traits in the variance of adults' dominance scores, we performed two General Linear Mixed Models with social unit size as a random variable, sex as a fixed factor and morphological size as a covariate. Because

sex and morphological size were not independent for adults ($F_{1,118} = 95.852$, $P < 0.001$), we used sex in a first model and morphological size in a separate, second one. We performed all statistical analyses using SPSS 10.0 software (SPSS 1999), and present values as means ± standard error.

## Results

### Dominance score preservation within winter

The individual dominance score appeared to be conserved within a given winter, as all the linear regressions on social dominance scores between consecutive months were significant (Table 1). No slope was significantly different from one, and no intercept was significantly different from zero. The correlation between the first month (just after the arrival on winter areas) and the second was slightly less significant than the correlations between other months.

### Adult dominance score preservation across winters

For adults, linear regressions on dominance score were not statistically significant for one of the three comparisons of consecutive winters, and of borderline significance for another (Table 2). Slopes were significantly different from one and intercepts were all significantly different from zero. Even when individual dominance status was

approximately maintained across winters, subordinate birds had increased and dominant birds had decreased their dominance score.

### Dominance score correlates for juveniles

Morphological size of juveniles did not significantly affect their dominance scores ($F_{1,9} = 0.143$, $P = 0.714$). Juvenile social dominance scores were mainly explained by social unit size ($F_{1,10} = 92.071$, $P < 0.001$; Fig. 1). Juveniles in larger families were dominant over others, and isolated juveniles were subordinate. Accounting for social unit size, sex tended to be significant, males being almost always dominant over females ($F_{1,10} = 3.934$, $P = 0.075$; Fig. 1). All interactions between age class, sex and morphological size were statistically non-significant (all $P > 0.500$).

### Relative contribution of fixed and fluctuating traits on dominance score for adults

Adult males had significantly higher social dominance scores than adult females ($F_{1,149} = 31.750$, $P < 0.001$; Fig. 2). Sex explained 18.5% of the variance. Morphological size was significantly correlated with dominance score ($F_{1,113} = 4.822$, $P = 0.030$) but explained only 4.1% of the variance. In both models, social unit size was positively correlated with the social dominance score and

**Table 1** Results of linear regressions and slope and intercept tests on arcsine transformed dominance scores of Dark-bellied Brent Geese *Branta bernicla bernicla* between each five consecutive monthly periods during winter 2003–2004

| Months | n | $R^2$ | P | a | b | t(a) | P(a) | t(b) | P(b) |
|---|---|---|---|---|---|---|---|---|---|
| 1 vs 2 | 13 | 0.646 | 0.001 | 0.948 | 2.401 | −0.246 | 0.810 | 0.216 | 0.833 |
| 2 vs 3 | 14 | 0.703 | <0.001 | 0.903 | 8.095 | −0.573 | 0.577 | 0.954 | 0.359 |
| 3 vs 4 | 21 | 0.702 | <0.001 | 0.866 | 9.580 | −1.035 | 0.314 | 1.579 | 0.131 |
| 4 vs 5 | 24 | 0.580 | <0.001 | 0.789 | 1.701 | −1.473 | 0.155 | 0.245 | 0.809 |

*n* Number of ringed Brent Geese recorded in both periods, $R^2$ and *P* results of the linear regression, *a* slope of the linear regression, *b* intercept of the linear regression, *t(a)* and *P(a)* results of the test of comparison of an estimated slope with a theoretical slope (here equal to 1), *t(b)* and *P(b)* results of the hypothesis test for intercept (here theoretically equal to 0)

**Table 2** Results of linear regressions and slope and intercept tests on arcsine transformed dominance scores across consecutive winters for adult Brent Geese

| Winters | n | $R^2$ | P | a | b | t(a) | P(a) | t(b) | P(b) |
|---|---|---|---|---|---|---|---|---|---|
| 2001–2002 vs 2002–2003 | 14 | 0.286 | 0.049 | 0.385 | 34.198 | −3.506 | 0.004 | 3.558 | 0.004 |
| 2002–2003 vs 2003–2004 | 24 | 0.011 | 0.624 | 0.093 | 35.822 | | | | |
| 2003–2004 vs 2004–2005 | 37 | 0.195 | 0.006 | 0.516 | 17.723 | −2.730 | 0.010 | 2.224 | 0.033 |

*n* Number of ringed Brent Geese recorded in both winters, $R^2$ and *P* results of the linear regression, *a* slope of the linear regression, *b* intercept of the linear regression, *t(a)* and *P(a)* results of the test of comparison of an estimated slope with a theoretical slope (here equal to 1), *t(b)* and *P(b)* results of the hypothesis test for intercept (here theoretically equal to 0)
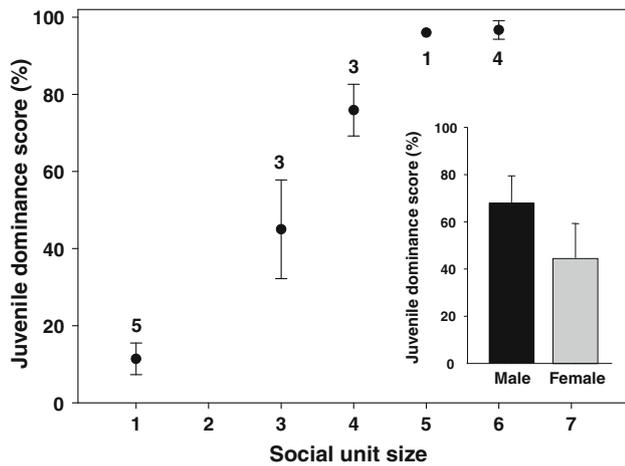
**Fig. 1** Mean (±standard error) of juvenile Dark-bellied Brent Goose *Branta bernicla bernicla* dominance scores (percentage) according to social unit size, from 1 for single juveniles to 7 for juveniles with their parents and four siblings. No juvenile was with only one parent or only with siblings. *Inset* mean (±standard error) of juvenile dominance scores according to sex. *Numbers above* and *below error bars* represent sample sizes
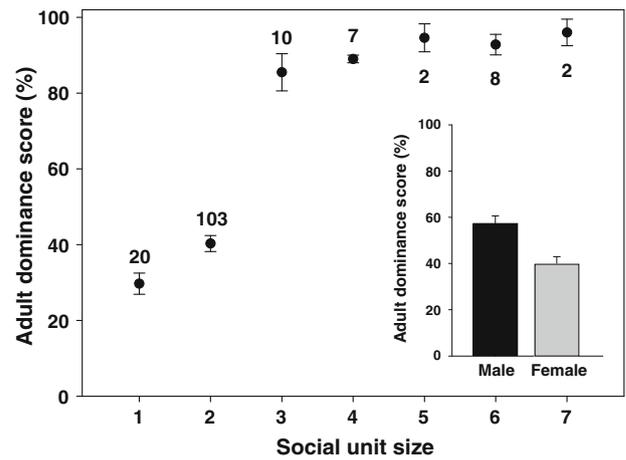


**Fig. 2** Mean (±standard error) of adult dominance scores (percentage) according to social unit size, from 1 for single adults to 7 for paired adults with five juveniles. No adults with juveniles were without a partner. *Inset* mean (±standard error) of adult dominance scores according to sex. *Numbers above* and *below error bars* represent sample sizes

explained most of the variance ($F_{6,144} = 36.894$, $P < 0.001$, 60.6% of the variance in the model with sex and $F_{5,113} = 28.629$, $P < 0.001$, and 55.9% of the variance in the model with morphological size; Fig. 2).

### Adult dominance score preservation across winters after controlling for social unit size

To test for the existence of a stable dominance hierarchy once social unit size was accounted for, we tested for the preservation of dominance score among individuals that had kept the same social unit size during two consecutive winters. The analysis was only possible for the most common social unit size: paired without juveniles (social unit size equal to 2). Between the first and second winter, only five birds met these criteria, preventing rigorous tests. Between the second and third winters, individual dominance scores for paired birds without juveniles were highly correlated, showing a preservation of dominance order ($F_{1,11} = 106.808$, $P < 0.001$), although the slope differed from one [$a = 0.563$, $t(a) = -8.035$, $P(a) < 0.001$] and the intercept differed from zero [$b = 15.332$, $t(b) = 6.709$, $P(b) < 0.001$]. This suggested that the score of more dominant birds tended to decrease slightly whereas those from subordinates increased. Between the last two winters, birds significantly conserved their dominance status as they rigorously conserved their dominance score [$F_{1,19} = 21.217$, $P < 0.001$, slope: $a = 0.779$, $t(a) = -1.308$, $P(a) = 0.206$, intercept: $b = 5.531$, $t(b) = 0.812$, $P(b) = 0.427$].

### Discussion

#### Dominance preservation within and across winters

According to both our predictions and Lamprecht's results (1986b), Brent Geese conserved their individual social dominance score within the same wintering period. Consequently, all observations made during winter could be summed to assess the overall winter dominance score. Nevertheless, because dominance scores for the first 2 months were more weakly related to each other than were those for subsequent pairs of months, dominance relationships seemed to be slightly less stable just after Brent Geese arrival in the wintering areas. Just after arrival on the wintering grounds, birds may encounter unfamiliar individuals for the first time and learn and/or test their respective dominance status. Perhaps it is also a period of intense migration, potentially increasing group instability (Summers et al. 1996), where interactions with transient birds could potentially influence the dominance score of residents.

Consistent with our predictions, the individual dominance scores fluctuated significantly between winters. Several factors may explain these results. The first is the major influence of social unit size, as it appears to drive individual dominance status in our studies, as in others. Reproductive success, however, seems to be partly disconnected from individual quality, probably through the major influence of environmental conditions in the breeding grounds (Ebbinge 1989; Sedinger and Flint 1995; Spaans et al. 1998; Sedinger et al. 2004). Similarly, some birds may have skipped breeding in a given year instead of

having a failed breeding attempt. Nevertheless, dominance order was preserved once the effect of social unit size was accounted for. This additionally suggests, as our results showed, that some fixed individual characteristics such as sex or morphological size may also contribute to the dominance status of a given bird. Some of the fluctuations in dominance status and score preservation may on the other hand come from the fact that Brent Geese group composition fluctuates considerably across winters, and individual recognition between two or more subsequent winters is complicated. In this context, geese need to establish new dominance relationships each winter according to individual fighting quality and status signalling.

### Dominance status as a by-product of breeding success in free-living goose populations

For both juveniles and adults, dominance score was mainly and positively correlated with social unit size. As parents and their offspring normally stay together until spring, with no or few temporary separations between family members (Lambeck 1990b), this result is coherent with the high dominance score preservation within winters. Indeed, like social unit size, dominance score is a fluctuating trait across winters but a stable trait within a winter. While the fixed traits tested in this study had a much lower contribution to dominance score, sex (and secondary morphological size) also had a significant impact on the individual dominance score with adult males being dominant over adult females (and larger birds dominating smaller). In Bar-headed and Barnacle Geese, male characteristics and behaviour mainly or entirely determine the dominance status of a pair or family, and the bigger the family, the more motivated is the male (Lamprecht 1986b; Black and Owen 1989a). The same mechanism seems to act in our Dark-bellied Brent Geese study population.

In stable flocks, the outcome of a fight between two ganders determines their future dominance relationships (Fischer 1965 and Scott 1978 cited in Lamprecht 1986b). Lamprecht (1986b) therefore suggested that birds in stable flocks know each other individually, and that the hierarchical order may also be partly stabilised by the birds' experiences obtained during earlier interactions. In our field conditions, with large and partially unstable group compositions, individual recognition (Halpin 1980; Dugatkin and Earley 2004) and thus preservation of dominance relationships by social inertia (Guhl 1968; Archawaranon et al. 1991; Wiley et al. 1999) are probably not sufficient for the establishment of a stable social relationship. Brent Geese therefore may use an alternative means of status signalling (Ketterson 1979; Brotons 1998) to reduce costs of interactions. As suggested in former studies (see also

Poisbleau et al. 2006a), social unit size may be the first indicator of pair quality and status in larger groups, dominant geese potentially having a higher reproductive success (Lamprecht 1986a, b), but also being more motivated in encounters. As paired birds had higher hierarchical positions than singletons in a flock of non-breeding moulting Barnacle Geese, Stahl et al. (2001) also advocated the hypothesis of mating status as a signal for dominance. The lack of a significant correlation between social unit size and dominance status in stable flocks (Lamprecht 1986b) may also support this hypothesis. The age effect on individual dominance scores in geese could thus be only an artefact of the age-related increase in the probability of being paired and having goslings. This probably explains why the dominance score of both sexes increased drastically between their second and third winter, the age when birds began to form pairs (Stahl et al. 2001). Indeed, age and breeding status were positively correlated (Stahl et al. 2001).

### Zusammenfassung

Stabilität im winterlichen sozialen Dominanzstatus von Ringelgelgänsen *Branta bernicla bernicla* innerhalb und zwischen Wintern

Dominante wie untergeordnete Individuen könnten von einer Stabilität der sozialen Dominanzstruktur profitieren, weil dadurch der hohe Zeit- und Energieaufwand aggressiver Interaktionen vermieden und das Verletzungsrisiko reduziert wird. Dennoch könnte der wahrscheinlich vorhandene Evolutionsdruck auf Individuen dominant zu werden und weiterhin zu bleiben, solche festen Dominanzhirarchien destabilisieren. In diesem Zusammenhang könnte der relativen Bedeutung der festen (z.B. Geschlecht, Körpergröße) und veränderlichen Merkmale (z.B. Körperkondition, Familienstand, Fortpflanzungserfolg, Größe der sozialen Einheit) auf die Etablierung und den Erhalt der Dominanzbeziehungen eine Schlüsselrolle in der Gruppenstruktur zukommen. Wir untersuchten die relative Rolle fester und veränderlicher Merkmale auf den sozialen Rang von Ringelgänsen *Branta bernicla bernicla*, die über und zwischen Wintern große, ziemlich unstabile Gruppen bilden. Wir verglichen die Dominanzwerte von beringten Ringelgänsen während vier auf einander folgenden Wintern. Ringelgänse behielten ihre Dominanzwerte während eines betrachteten Winters unabhängig von ihrem Alter, aber waren in der Regel nicht dazu in der Lage, sie über zwei aufeinander folgende Winter aufrecht zu erhalten. Da die Winterdominanzwerte am besten mit der Größe der sozialen Einheit korrelierten, erschien der Dominanzstatus überwiegend ein

Nebenprodukt eines veränderlichen Merkmals zu sein, nämlich des Bruterfolgs im vorherigen Sommer. Betrachteten wir nur Altvögel, deren soziale Gruppeneinheit in zwei aufeinander folgenden Wintern gleich groß war, beobachteten wir eine signifikante Aufrechterhaltung der Dominanzwerte. Dieses Ergebnis deutet darauf hin, dass auch ein festgelegtes Merkmal wie Geschlecht oder Körpergröße eine Rolle bei der Festlegung von Dominanzrängen spielt.

# References

Archawaranon M, Dove L, Wiley RH (1991) Social inertia and hormonal control of aggression and dominance in white-throated sparrows. Behaviour 118:42–65

Archer J (1988) The behavioural biology of aggression. Cambridge University Press, Cambridge

Bernstein IS (1981) Dominance: the baby and the bathwater. Behav Brain Sci 4:419–458

Bêty J, Gauthier G, Korpimäki E, Giroux J-F (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J Anim Ecol 71:88–98

Black JM, Owen M (1987) Determinants of social rank in goose flocks: acquisition of social rank in young geese. Behaviour 102:129–146

Black JM, Owen M (1989a) Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. Anim Behav 37:199–209

Black JM, Owen M (1989b) Parent-offspring relationships in wintering barnacle geese. Anim Behav 37:187–198

Bowler J (2003) Family cohesion in greylag goose *Anser anser* broods following catching and ringing. Ring Migr 21:181–182

Boyd H (1953) On encounters between wild white-fronted geese in winter-flocks. Behaviour 5:85–129

Brotons L (1998) Status signalling in the coal tit (*Parus ater*): the role of previous knowledge of individuals. Etología 6:49–52

Bub H (1991) Bird trapping and bird banding. A handbook for trapping methods all over the world. Cornell University Press, New York

Burley N (1986) Comparison of the band-colour preferences of two species of estrildid finches. Anim Behav 34:1732–1741

Cuthill IC, Hunt S, Cleary C, Clark C (1997) Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). Proc R Soc Lond B 264:1093–1099

Dugatkin LA, Earley RL (2004) Individual recognition, dominance hierarchies and winner and loser effects. Proc R Soc Lond B 271:1537–1540

Ebbinge BS (1989) A multifactorial explanation for variation in breeding performance of brent geese *Branta bernicla*. Ibis 131:196–204

Ens BJ, Goss-Custard JD (1984) Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. J Anim Ecol 53:217–231

Gregoire PE, Ankney CD (1990) Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. Auk 107:550–560

Guhl AM (1968) Social inertia and social stability in chickens. Anim Behav 16:219–232

Halpin ZT (1980) Individual odors and individual recognition: review and commentary. Biol Behav 5:233–248

Hochbaum HA (1942) Sex and age determination of waterfowl by cloacal examination. Trans N Am Wildl Conf 7:299–307

Ketterson ED (1979) Status signaling in dark-eyed juncos. Auk 96:94–99

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

Lambeck RHD (1990a) Differences in migratory pattern and habitat choice between social classes of the brent goose *Branta b. bernicla*. Ardea 78:426–440

Lambeck RHD (1990b) The applicability of age ratio and brood size counts in population dynamic studies of the brent goose *Branta b. bernicla*. Ardea 78:414–425

Lamprecht J (1986a) Social dominance and reproductive success in a goose flock (*Anser indicus*). Behaviour 97:50–65

Lamprecht J (1986b) Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). Behaviour 96:28–48

Loonen MJJE, Bruinzeel LW, Black JM, Drent RH (1999) The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. J Anim Ecol 68:753–768

Owen M, Black JM (1989) Factors affecting the survival of barnacle geese on migration from the breeding grounds. J Anim Ecol 58:603–617

Piper WH (1997) Social dominance in birds. Early findings and new horizons. In: Nolan V Jr, Ketterson ED, Thompson CF (eds) Current ornithology. Plenum, New York, pp 125–187

Poisbleau M, Fritz H, Valeix M, Perroi P-Y, Dalloyau S, Lambrechts MM (2006a) Social dominance correlates and family status in wintering dark-bellied brent geese, *Branta bernicla bernicla*. Anim Behav 71:1351–1358

Poisbleau M, Jenouvrier S, Fritz H (2006b) Assessing the reliability of dominance scores for assigning individual ranks in a hierarchy. Anim Behav 72:835–842

Poisbleau M, Desmonts D, Fritz H (2008) Dominance relationships in dark-bellied brent geese *Branta bernicla bernicla* at spring staging areas. Ardea 96:135–139

Rowell TE (1974) The concept of social dominance. Behav Biol 11:131–154

Scherrer B (1984) Biostatistique. Morin, Boucherville, Canada

Sedinger JS, Flint PL (1995) Environmental influence on life-history traits: growth, survival, and fecundity in black brant (*Branta bernicla*). Ecology 76:2404–2414

Sedinger JS, Herzog MP, Ward DH (2004) Early environment and recruitment of black brant (*Branta bernicla nigricans*) into the breeding population. Auk 121:68–73

Siriwardena GM, Black JM (1999) Parent and gosling strategies in wintering barnacle geese. Wildfowl 44:18–26

Sloman KA, Wilson L, Freel JA, Taylor AC, Metcalfe NB, Gilmour KM (2002) The effects of increased flow rates on linear dominance hierarchies and physiological function in brown trout, *Salmo trutta*. Can J Zool 80:1221–1227

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening dark-bellied brent geese *Branta bernicla*. Ardea 89: 427–440

Spaans B, Blijleven HJ, Popov IU, Rykhlikova ME, Ebbinge BS (1998) Dark-bellied brent geese *Branta bernicla bernicla* forego breeding when Artic foxes *Alopex lagopus* are present during nest initiation. Ardea 86:11–20

SPSS (1999) SPSS Base 10.0 user's guide. SPSS, Chicago

Stahl J, Tolsma PH, Loonen MJJE, Drent RH (2001) Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim Behav 61:257–264

Summers RW, Underhill LG, Howells RJ, Vickery JA, Prÿs-Jones RP (1996) Phenology of migration and use of wintering sites by the increasing population of dark-bellied brent geese *Branta bernicla bernicla*. J Zool Lond 239:197–208

Underhill LG, Prÿs-Jones RP, EE Syroechkovski Jr, Groen NM, Karpov V, Lappo HG, Van Roomen MWJ, Rybkin A, Schekkerman H, Spiekman H, Summers RW (1993) Breeding of waders (Charadrii) and Brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russian, in a peak and decreasing lemming year. Ibis 135:277–292

Weatherhead PJ, Ankney CD (1984) Comment: a critical assumption of band-recovery models may often be violated. Wildl Soc Bull 12:198–199

Wiley RH, Steadman L, Chadwick L, Wollerman L (1999) Social inertia in white-throated sparrows results from recognition of opponents. Anim Behav 57:453–463