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Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks

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Social dominance plays an important role in assessing and obtaining access to patchy or scarce food sources in group-foraging herbivores. We investigated the foraging strategies of individuals with respect to their social position in the group in a flock of nonbreeding, moulting barnacle geese, *Branta leucopsis*, on high Arctic Spitsbergen. We first determined the dominance rank of individually marked birds. The dominance of an individual was best described by its age and its sex-specific body mass. Mating status explained the large variation in dominance among younger birds, as unpaired yearlings ranked lowest. In an artificially created, competitive situation, subordinate individuals occupied explorative front positions in the flock and were the first to find sites with experimentally enriched vegetation. Nevertheless, they were displaced quickly from these favourable sites by more dominant geese which were able to monopolize them. The enhanced sites were subsequently visited preferentially by individuals that succeeded in feeding there when the exclosures were first opened. Data on walking speed of foraging individuals and nearest-neighbour distances in the group suggest that subordinates try to compensate for a lower energy intake by exploring and by lengthening the foraging bout. Observations of our focal birds during the following breeding season revealed that females that returned to the study area were significantly more dominant in the previous year than those not seen in the area again.

Social dominance is a common feature of many animal societies (for review see Gauthreaux 1978; Piper 1997). It is viewed as a means of reducing costly intraspecific competition whereby a group of individuals coexists with minimal interactions permitting the most efficient use of resources (Piper 1997). The creation of a dominance hierarchy suppresses fighting in the group as the individual learns to evaluate its chances of winning conflicts. Threats by the initiator suffice to maintain the benefits of being superior and the relative position of individuals in the group will be constantly reinforced (Raveling 1970).

The majority of goose species live in large flocks and dominance hierarchies can play an important role in foraging (Boyd 1953; Raveling 1970; Black & Owen 1989a, b; Mulder et al. 1995). Within the groups, flock members, even at the gosling stage, can identify large numbers of groupmates individually (Fischer 1965). Studies on various species of geese and swans show that families dominate pairs without goslings in aggressive encounters and that pairs tend to win over single birds (Lazarus & Inglis 1978; Scott 1980; Lamprecht 1986a; Black & Owen 1989a). Lamprecht (1986a) showed that pairs of bar-headed geese, *Anser indicus*, improved their dominance rank after successfully completing the breeding season. In white-fronted geese, *Anser albifrons*, dominant individuals lost their ranking position when they lost their partner, decreasing in dominance to the level of unpaired individuals (Boyd 1953). Moreover, families of barnacle geese, *Branta leucopsis*, also increased in dominance when family size was experimentally enlarged (Loonen et al. 1999).

The size of the social unit predicts dominance in geese well, whereas the effects of parameters such as age or body size on dominance are less apparent (Boyd 1953; Hanson 1953; Raveling 1970; Lamprecht 1986a). The question remains how a goose might assess the dominance rank of an unknown opponent in a situation where family size cannot be used as a signal. We examined the dominance structure of a wild flock of barnacle geese in the moulting areas on Spitsbergen. The flock studied consisted of nonbreeders and failed breeding pairs only, providing a situation that allowed us to investigate correlates of dominance in bird assemblages irrespective of family size as a status badge.

In terms of foraging opportunities in a large flock of potential competitors, dominance is an important attribute. The rank an animal occupies will determine its

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share of resources, which suggests that the trade-off between costs and benefits of group foraging is related to the dominance position of the individual group member and the size of the group. In social groups, dominant individuals have prior access to food (e.g. herbivorous red deer, *Cervus elaphus*: Appleby 1980; seed-eating juncos, *Junco hyemalis*: Baker et al. 1981; mussel-eating oystercatchers, *Haematopus ostralegus*: Goss-Custard 1980). Various studies show that plots with high-quality plants are exploited by the dominant geese in the flock (Prop et al. 1984; Teunissen et al. 1985; Prop & Deerenberg 1991). Spring foraging opportunities, mediated by individual dominance, translate into improved body condition of female geese and subsequently into successful reproduction at the Arctic breeding grounds (Teunissen et al. 1985; Ebbinge & Spaans 1995).

The shepherd hypothesis, posed by Rohwer & Ewald (1981) and reviewed by Piper (1997), tackles the question why subordinate flock members remain in the group despite their low status. Rohwer & Ewald (1981) argued that dominance and subordination can be equally advantageous strategies, as long as dominants protect familiar subordinates from attacks by other dominant flock members and in turn profit from food exploration by their established underlings. Alternatively, the ‘hopeful dominants’ hypothesis (e.g. Ens & Cayford 1996) links dominance rank with age for long-lived species in stable aggregations and suggests that subordinate young birds queue for higher status which they eventually achieve when they get older.

Foraging in a large flock, which depletes resources rapidly, results in different foraging opportunities for individuals according to their position in the flock (Drent & van Eerden 1980). In an experimental study on brent geese foraging on fertilized plots of salt marsh vegetation (Teunissen et al. 1985), the rate of agonistic encounters on favourable plots was positively correlated with the quality of, and therefore preference for, a plot. Teunissen et al. (1985) showed that individual birds tend to occur consistently in a certain segment of the flock and hypothesized from the outcome of agonistic encounters that birds in the leading segment of a foraging group run the risk of being supplanted by more aggressive birds following them. From the correlation between walking speed of individual geese and grazing pressure, Prop & Loonen (1988) suggested that unpaired and, therefore, lower-ranking birds try to improve their positions in the group by walking faster.

We addressed the individual costs and benefits of foraging in a flock in relation to the prevailing dominance hierarchy. In a field experiment we confronted wild barnacle geese of known dominance status with plots of enhanced vegetation and we investigated the effects of dominance on foraging success in relation to future fitness.

METHODS

The Study Area

During July and August 1998, we studied a flock of moulting barnacle geese of the Ny-Ålesund breeding colony in Kongsfjorden, Spitsbergen. The first breeding pair in this colony was recorded in 1980 (Tombre et al. 1998). During their flightless period, nonbreeders and failed breeders use distinct sites near the small research village Ny-Ålesund as a predator-safe foraging site (Stahl & Loonen 1998). From the middle of June to the middle of August, 100–140 nonfamily birds visit meadows close to a shallow lake, where sprouts of mainly *Poa arctica* protrude through the thick cover of wet moss. About 75% of the birds are marked individually with coded Darvic rings which can be read from a distance of up to 250 m with a 20–60 × telescope. During the 24-h daylight period of the Arctic summer, observations were mainly carried out in the night hours when disturbance caused by other research activities was low.

Dominance Hierarchy

We determined the dominance hierarchy of the flock by observing interactions between marked individuals and between marked and unmarked individuals. 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. We observed the flock from a hide and noted any participant in an interaction as well as the outcome, while the geese were foraging on unmanipulated vegetation. We considered an agonistic interaction as being won by an individual when the opponent turned and walked or ran away. Conflicts were resolved within seconds. The dominance score is 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 & Goss-Custard 1984; Lamprecht 1986a). We calculated a dominance score for each marked individual with a minimum total number of three interactions (involving at least two different opponents). Paired birds were assigned a dominance score based on interactions of both partners. The score was chosen in preference to a dominance hierarchy as a linear sequence for the whole flock (Henderson & Hart 1991) as our moulting group included unmarked birds whose interactions with marked birds contributed to the score of the marked focal bird.

Size and Age

During the last week of July, the moulting flock was caught by a rounding-up technique, unmarked birds were ringed and all individuals were sexed, measured and weighed. Body mass was measured with an electronic balance to the nearest 5 g. Tarsus length was measured to the nearest 0.1 mm as the distance between the extreme bending points when the foot was bent at the intertarsal joint and the ‘ankle’. Head size was assessed to the nearest 0.1 mm as the distance between the back of the head and the tip of the bill (for measuring techniques see Dzubin & Cooch 1992). Mating status, classified as paired or unpaired, was determined from direct observations of ringed birds. Exact age was known only for individuals that were ringed as goslings or yearlings in former years.

Minimum age is indicated by the year previous to which a bird was ringed as an adult. Permission to ring the geese was granted to M. Loonen by the Governor of Svalbard. During ringing and measuring, groups of 50–100 geese were kept in movable enclosures of nylon netting on the tundra for about 4 h and released as a group afterwards. We detected no adverse effects on the birds. Foraging flocks returned to the catching areas within a few hours of their release.

Experimentally Enriched Vegetation

To determine the ability of an individual to monopolize favourable foraging sites in relation to its dominance rank, we selected four plots of 2 × 2 m on a moss meadow dominated by *P. arctica*. We excluded grazing animals by placing small fences of chicken wire around each plot from the end of June to the last week of July. The fences prevented grazing by geese as well as reindeer, *Rangifer tarandus*, which were the only herbivores in this area. In the last week of June, all plots were fertilized with a nitrogen-based commercial fertilizer ($CaCO_3$ NH_4NO_3, 23% N, concentration 125 kg/ha), dissolved in 2 litres of water/m^2. After 1 month, we opened the enriched exclosures to grazing. During each observation period, only one plot was offered to the geese at a time. The time each individual goose spent on the plot was recorded to the nearest second. All social interactions that occurred either in the plot or within 3 m of it were noted. The dominance status of individuals calculated from their interactions within the experimental set-up correlated well with dominance values of the same individual obtained from observations on unmanipulated vegetation as described above ($F_{1,15}=21.02$, $P<0.001$). We used individual dominance ranks determined previously and independently from the experimental set-up throughout our analyses.

A foraging period during which birds of the flock passed or entered the enriched plot was defined as a flock passage. These flock passages were terminated when the flock either retreated to the safety of the lake shore as a reaction to disturbance or moved to a different foraging site. During one flock passage, each individual entering a plot was given an ordinal number representing its position within the sequence of visitors. Each ringed visitor could be characterized by its previously determined dominance score. We recorded the foraging time of each bird on the enriched plot to the nearest second with a stopwatch and calculated the relative foraging time for each visitor within one flock passage. For pairs of geese visiting the same plot, only data on the female contributed to the analysis to avoid pseudoreplication. We excluded cases from the analysis where flock densities were so low that no interactions occurred at the enhanced plots. Preceding visitors were actively chased from the plot by their successors in all cases presented here.

From multiple sightings of ringed individuals on one plot, we calculated the return rate of individuals in relation to their dominance rank and to their previous foraging experience on the plot.

Behavioural Parameters

We observed individuals of known dominance status within the group while the geese were foraging on unmanipulated vegetation. In periods of 1 min, we noted vigilance as the number of head-up movements, step rate as number of steps/min foraging and the total time (s) spent foraging. Periods with bouts of comfort or resting behaviour were excluded. We tried to observe every marked individual in a flock, changing focal birds every minute, and conducted the observations during several nights within a 3-week period in July. For these analyses only, focal birds were grouped into two categories: birds with a dominance score of 50% or more (referred to as dominant) and birds with a dominance score of less than 50% (referred to as subordinate). Observed flock sizes were either small (up to eight birds) or large (16–32 birds).

Walking speed and distances to the nearest neighbour were quantified with a high precision optical range finder (Leica Vector 1000, 7 × 42) which measured the distance and the compass angle of a goose in relation to the observer. Focal birds were followed for 10 min and repeated measurements were taken for the focal individual, its partner and the nearest neighbour at 1-min intervals. We determined walking speed and neighbour distances from each pair of consecutive measurements, and assessed arithmetic mean values for the 10-min observation period. The variation of neighbour distances was calculated as the standard deviation of measured distances within each 10-min period, giving an indication of the mobility of an individual in the group. Focal birds were categorized as paired or single.

Over 10 days, we observed the main nonbreeder group for at least 2 h and determined the percentage of unpaired birds in the flock. Foraging events were followed by resting bouts lasting 120–150 min. During the subsequent resting bout of the group, we observed small subgroups that foraged while the other members of the flock rested. We recorded the percentage of unpaired birds within these subgroups and in the whole flock. With this method, differences in the activity patterns between single and paired individuals were detected.

Return Rates

From ring readings carried out in Kongsfjorden during the 1999 breeding season, we determined the number of the 1998 focal birds that were observed breeding, observed as nonbreeders and not observed at all and classed the birds according to their 1998 dominance score. We compared the mean dominance score for these three return categories.

Statistical Analysis

All percentage values underwent arcsine transformation before entering statistical tests as a dependent variable to satisfy underlying assumptions of the tests used. The relation of the transformed dominance score with mating status, age and body parameters was

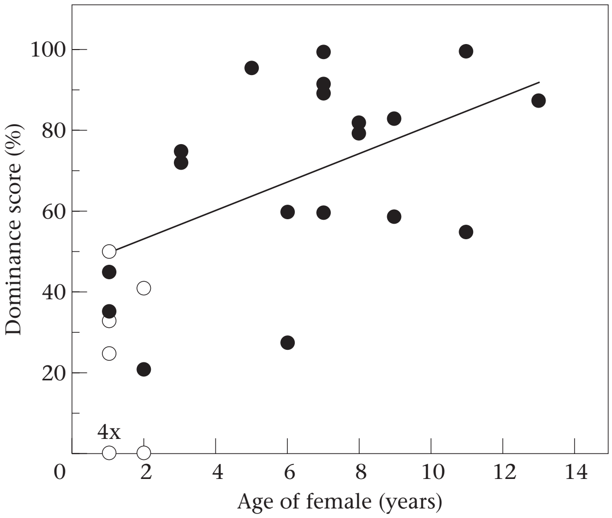

Figure 1. Effects of age and mating status on dominance in female barnacle geese. ●: Paired birds, ○: unpaired birds. Regression line shown for paired birds only.

analysed with a general linear model. Both continuous variables (covariates) and categorical variables (factors) can be entered as explanatory variables in these models. Categorical variables were transformed to dummy variables with the values 0 and 1, the number of cases for the dummy variables being 1 minus the number of classes for each categorical variable. All interactions between explanatory variables were also tested. The procedure is analogous to a stepwise multiple regression using dummy variables and a forward selection of explanatory variables. Data on individuals of both sexes were analysed separately. A Spearman rank correlation was carried out to test for correlations among independent variables.

We used (paired, two-tailed) *t* tests on transformed data to compare the dominance and foraging performance of birds using the experimental plots and χ^2 statistics to compare return rates. We used two-tailed *t* tests to test for differences in behavioural parameters between the two dominance categories and between single and paired birds. Transformed data on dominance values of ringed females entered a one-way ANOVA (post hoc Tukey test) to test for long-term consequences of dominance. Statistical testing was done with the software package SPSS for Windows, release 8.0.

Table 1. Linear regression of dominance score (after arcsine transformation) on mating status, age and body size parameters

Independent variable	*df*	*F*	*P*
Females			
Mating status	1, 27	37.28	<0.001
Minimum age	1, 27	27.40	<0.001
Exact age	1, 12	8.76	0.012
Body mass	1, 27	13.04	0.001
Tarsus length	1, 27	2.22	0.148
Head size	1, 27	0.80	0.379
Males			
Mating status	1, 31	9.61	0.004
Minimum age	1, 31	4.88	0.035
Exact age	1, 6	0.07	0.439
Body mass	1, 31	6.09	0.019
Tarsus length	1, 31	4.16	0.050
Head size	1, 31	1.10	0.302

RESULTS

Correlates of Dominance

For both male and female barnacle geese mating status was the most significant explanatory variable entered in the general linear model. Paired birds had a significantly higher dominance score than single birds. Dominance increased significantly with age in females (ANCOVA: age: $F_{1,27}$=4.90, P=0.036; mating status: $F_{1,27}$=10.51, P=0.003; interaction: $F_{1,26}$=0.06, NS; Fig. 1). None of the other explanatory variables had a significant effect on dominance when mating status was included in the model. In Table 1, the various explanatory variables are compared in linear regression models for each sex. The dominance rank of an individual was correlated with its mating status, that is, paired or unpaired, minimum age (and for females also exact age), body mass and, for males, tarsus length. Dominance was not correlated with head size for either of the two sexes. Summarizing these positive correlations, paired, old or large individuals ranked highest. In our study population however, effects of age and body size were correlated (Table 2) because of density-dependent processes constraining gosling growth and adult size (Loonen et al. 1997). Therefore, any influence of body size on the observed dominance pattern is difficult to detect. Our analysis rendered mating status

Table 2. Spearman rank correlations for independent variables used in the linear regression (Table 1)

	Mating status	Minimum age	Body mass	Tarsus length	Head size
Mating status	—	0.728**	0.633**	0.052	0.000
Minimum age	0.602**	—	0.810**	0.372*	0.080
Body mass	0.563**	0.643**	—	0.514**	0.331
Tarsus length	0.399*	0.409*	0.571**	—	0.491**
Head size	0.335	0.392*	0.469**	0.577**	—

The results in the top right half of the table are based on data of 29 female barnacle geese, those in the bottom left half of the table are based on 33 male barnacle geese.
**P*<0.5; ***P*<0.01.

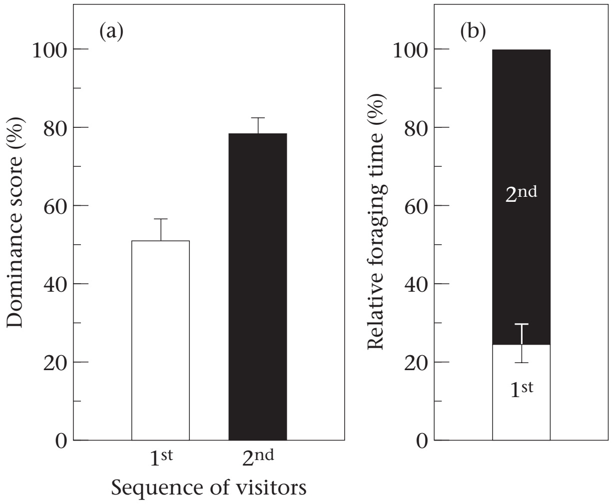

Figure 2. (a) Comparison between the position of an individual in a series of visitors to an enriched plot and its dominance score ($\bar{X}$+SE). (b) Foraging time of subsequent visitors on an enriched plot in relation to the total foraging time of both individuals.

Table 3. Return rate (*N*, %) of marked geese to enriched plots, and their dominance rank ($\bar{X}$±SE), in relation to where they foraged during their first visit

	During first visit	
	Foraging on plot	Foraging in vicinity of plot only
Return rates		
Return to plot	19 (59)	7 (18)
Fail to return	13 (41)	32 (82)
N	32	39
Dominance scores (%)		
Return to plot	73.4±5.9	62.1±9.6
Fail to return	62.1±7.2	36.0±5.2
Mean dominance score	68.8±4.6	40.7±4.8

and age as likely explanatory parameters for social dominance.

Competition for Enriched Vegetation

Figure 2a shows that the order in which birds entered favourable patches was strongly related to dominance, a bird that discovered a rich patch being less dominant than its successor (paired *t* test: $t_{11}=-3.55$, $P=0.005$). Nevertheless, the dominant birds entering later spent more time foraging on the enriched plots than subordinate predecessors (*t* test testing for deviation from 50%: $t_{11}=4.84$, $P=0.001$; Fig. 2b).

Of 32 individuals that managed to forage on an enriched plot during a first flock passage, 59% returned to the plot during a second passage (Table 3). In contrast, only 18% of the 39 geese that foraged in the vicinity of the plot during a first visit returned (Table 3). Differences between these experience categories were statistically significant ($\chi^2_1=11.3$, Yates correction, $P<0.01$). Mean dominance scores of birds that foraged on the plot during a first visit were significantly higher than those of birds that foraged only in the vicinity of the plots (*t* test: $t_{69}=-4.07$, $P<0.001$; Table 3). Dominance scores of birds that were not able to enter the plot during the first visit and did not return with the second flock passage were lowest whereas dominance scores of all other categories did not differ significantly (one-way ANOVA with post hoc Tukey test: $F_{3,67}=8.41$, $P<0.001$).

Behavioural Parameters Related to Dominance

Under unmanipulated foraging conditions, vigilance behaviour of flock members was related to group size and dominance. Vigilance was higher among members of small foraging groups and dominant birds showed more vigilant behaviour than subordinates (group size: $F_{1,170}=15.16$, $P<0.001$; dominance: $F_{1,170}=9.48$, $P=0.002$). This finding is confounded by the fact that there were more dominant than subordinate birds in small groups (interaction of group size and dominance rank: $F_{1,169}=6.22$, $P=0.014$). However, dominant birds showed significantly more vigilant behaviour if we control for the group size effect and analyse data of large flocks only ($F_{1,140}=14.61$, $P<0.001$).

Lower foraging time was expected for dominant birds, but the two variables foraging time and step rate while foraging were explained by group size only. Birds that were foraging in large groups took more steps while foraging ($F_{1,170}=9.61$, $P=0.002$) and showed a nonsignificant tendency to spend more time foraging ($F_{1,170}=3.34$, $P=0.06$).

Unpaired birds tended to walk faster than paired birds although differences were not significant, probably because walking speed varied widely between individuals (paired birds: $\bar{X}\pm\mathrm{SE}=3.8\pm0.2$ m/min; unpaired birds: 4.7 ± 0.5 m/min; $N_{\mathrm{unpaired}}=78$, $N_{\mathrm{paired}}=92$; $t_{168}=-1.79$, $P=0.07$). Foraging distances to nearest flock neighbours were similar for paired and unpaired birds (paired birds: $\bar{X}\pm\mathrm{SE}=7.8\pm0.8$ m; unpaired birds: 7.3 ± 0.7 m; $N_{\mathrm{unpaired}}=78$, $N_{\mathrm{paired}}=92$; $t_{168}=0.508$, NS). However, unpaired birds showed a significantly higher variability in their distances to the nearest neighbour (paired birds: mean standard deviation ± SE=1.49 ± 0.04 m; unpaired birds: 2.08 ± 0.09 m; $N_{\mathrm{unpaired}}=76$, $N_{\mathrm{paired}}=92$, $t_{166}=6.64$, $P<0.001$) meaning that they continuously changed their position in the group.

While the mean percentage of unpaired birds in a foraging flock ± SE was 39 ± 5%, their share in subgroups that foraged while the main flock was resting rose to 50 ± 4%. These differences in the patterns of activity were significant ($t_{12}=1.85$, $P=0.04$).

Long-term Consequences of Dominance

Figure 3 shows the relation between dominance rank of individuals in one year and their performance in the next breeding season. Females that failed to return in the following season ($N=12$) had a significantly lower dominance rank than those that returned as nonbreeders

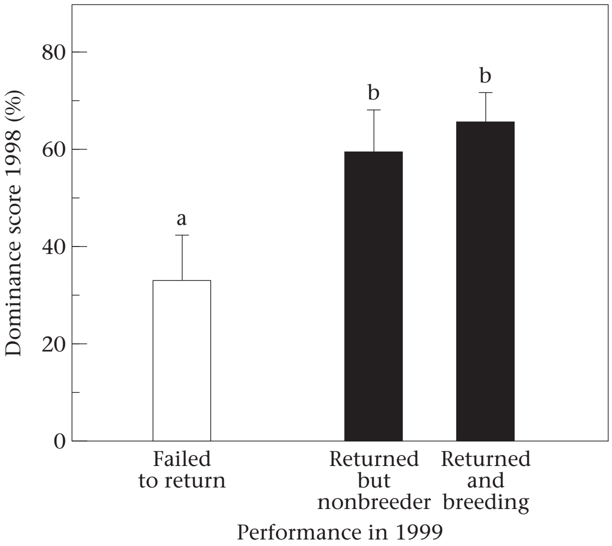

Figure 3. Dominance of females in 1998 in relation to performance during the subsequent breeding season (1999). Females were classed as failing to return (N=12), returning as nonbreeders (N=14) and producing a clutch (N=20). Letters a and b indicate significant differences between categories.

(N=14) and females that returned and produced a clutch (N=20; one-way ANOVA with post hoc Tukey test: $F_{2,43}$=5.83, P=0.006). There was no significant difference in dominance ranks between the latter two groups.

DISCUSSION

The Concept of Dominance in Goose Flocks

Studies on flock structure in geese mainly focus on the size of social units as the most important predictor of dominance. Families dominate pairs in aggressive encounters and pairs win interactions with singletons (Jenkins 1944; Boyd 1953; Hanson 1953; Raveling 1970; Lazarus & Inglis 1978). Parental birds raising goslings are not only more aggressive but also more successful in encounters with flock neighbours (Lamprecht 1986a; Black & Owen 1989b).

In our study, dominance was positively correlated with age, body weight and body measures (Table 1). But even in this group without parents and goslings, mating status could not be excluded as a signal for dominance. Paired birds ranked higher than singletons (Fig. 1). In line with our own findings, age is a fair predictor for dominance in studies on other bird species as well (e.g. great tit, *Parus major*: Lemel 1989; willow tit, *Parus montanus*: Koivula et al. 1993; Mexican jay, *Aphelocoma ultramarina*: Brown et al. 1997). Older birds are more experienced and therefore probably more successful in encounters with flockmates. Family size is a good predictor for dominance structure in mixed groups of breeding and nonbreeding geese (e.g. in wintering flocks). Our data suggest that in female geese mating status and age determine the dominance rank of a nonbreeding individual. In our study population, there was a complex interaction between age and conditions limiting growth during the gosling stage. These limiting conditions have been attributed to density-dependent effects in several goose populations (e.g. Spitsbergen barnacle geese: Loonen et al. 1997) but consequences for the dominance structure in the flocks remained unstudied.

Consequences of Dominance for the Individual

Our results from the experiment with enriched vegetation plots showed that favourable foraging sites were mainly detected by subordinate birds which were then quickly displaced from the plot by dominant flockmates (Fig. 2). This is in line with findings on wintering flocks of brent geese (Teunissen et al. 1985) where birds behind the leading edge of the group had the highest dominance rank. Prop & Deerenberg (1991) showed by faecal analysis that dominant birds in this species obtain more high-quality plants. The foraging situation was simpler in our experimental plots which consisted of homogeneous swards of only one grass species. In this situation, dominant second visitors were able to oust the geese discovering the favourable plots. The second visitor was responsible for 75% of the total foraging time on these high-quality plots. Moreover, a high percentage of successful foragers on enriched plots returned to the same place with a second foraging wave whereas unrewarded neighbourhood foragers tended to disappear from the area (Table 3). We suggest that dominant geese used their explorative but less high-ranking flockmates to detect patches of high-quality food which they monopolized easily afterwards. This idea of subordinate explorers and dominant profiteers is not new within the concepts of flock functioning. Nevertheless, our study on wild barnacle geese is one among few experimental approaches (white-throated sparrows, *Zonotrichia albicollis*: Wiley 1991; hummingbirds: Tiebout 1996; great tits: Verbeek et al. 1999) which reveal clearly the important role of dominance patterns for food finding. Classifying flock members as either producers or scroungers, Barnard & Sibly (1981) developed a model for different foraging strategies based on their findings in a captive flock of house sparrows, *Passer domesticus*. In their study, scroungers relied on interactions with explorative flockmates to obtain food whereas producers actively searched for food items themselves. Rita et al. (1997) developed this idea, showing that optimal patch exploitation times are shorter for individuals of the patch-finding phenotype (producers) than for scroungers, especially if the former are more severely affected by competitive interactions at the plot. Our investigations support these theoretical predictions, as in all cases subordinate ‘finders’ were actively chased out of the plot by more dominant ‘scroungers’.

Although an important issue for concepts of flock dynamics, the mechanisms of information transfer in foraging groups are still poorly understood (Prins & Ydenberg 1985). The high level of explorative behaviour of subordinate individuals in our study will increase their chances of finding high-quality food patches (see also Ward 1965; Murton et al. 1966) and their high walking speeds may improve their foraging position in the flock (Prop & Loonen 1988). The idea of a larger explorative zone of subordinates is also supported by our finding that lower-ranking single birds showed a higher variation in distance to their nearest flock neighbour than higher-ranking paired birds. This means that they are constantly shifting their relative position in the flock.

In our behavioural data of geese feeding on unmanipulated vegetation, we detected differences in vigilance for subordinate and dominant birds in large flocks. Even though their total foraging time did not differ, dominant birds showed more vigilant behaviour than subordinates. Kramps (1998) showed that dominant great tits scanned the surroundings more often than subordinates and suggested that birds benefit directly from their vigilance by reducing their predation risk as, within his wild population, dominant birds had higher survival. The maintenance of a certain level of vigilance is thought to be beneficial for the detection of profitable food patches in addition to predator detection (e.g. Drent & Swierstra 1977; Pöysä 1987). Especially within the 'producer–scrounger' situation in our study, vigilance may serve to maintain contact with subordinates to locate newly discovered patches quickly.

The question remains whether it is purely the relative safety of the group that is the incentive for subordinate individuals to stay in their flock. We hypothesize that subordinates compensate for the disadvantages of being forced to forage on patches of minor quality to some degree by changing their foraging patterns over the day. Unpaired, subordinate geese in our focal flocks prolonged their foraging bouts when the main part of the flock started to rest nearby. These data suggest that subordinate birds balance the benefits of safety and food finding against the cost of restricted food intake. Clearly, differences in time budgets and in actual food intake between social groups deserve further study.

For group-living animals such as geese, the theoretical framework of 'queuing for dominance' (Ens & Cayford 1996) argues that subordinate group members in reality should be characterized as 'hopeful dominants'. The long-term benefit of remaining in the group through the years is thus to enhance their dominance rank (involving both age and experience). Observations on Bewick's swans, *Cygnus columbianus bewickii* (Scott 1988) and data from our own study show a clear correlation between dominance rank and age and support this hypothesis. A fascinating aspect for further analyses are alliances between dominant and subordinate individuals within a flock, as suggested by the shepherd hypothesis of Rohwer & Ewald (1981). Such processes might be driven by subtle and long-lasting family bonds within those flocks in the breeding grounds, for example long-term mother–daughter cooperation (in barnacle geese, associations between mothers and daughters extend over several years; personal observations on ringed individuals in the winter quarters). If dominant and old birds support offspring from former years within the group and protect them from attacks by unfamiliar dominant flock neighbours, they may increase the benefits of flock foraging for subordinates.

Our findings suggest the main consequences of dominance concern access to favourable foraging patches and the ability to monopolize them over time; both are favourable traits in the poor and patchy Arctic environment. Cause and effect are difficult to disentangle, however, if we do not know how the positive correlation of dominance with body mass and size of the individual changes during ontogeny. In addition, foraging efficiency can increase with age, for example in captive barnacle geese (J. Black, personal communication) and in rooks, *Corvus frugilegus* (Henderson & Hart 1991).

Questions concerning the implications of dominance for life history traits are challenging although evidence is still fragmentary (see Piper 1997). With their studies on Spitsbergen barnacle geese in winter, Black & Owen (1989a) supported the hypothesis of a positive feedback between age, dominance and reproductive success first formulated by Lamprecht (1986b) for his captive flock of bar-headed geese. Our own data on dominance-related return rates (Fig. 3) provide strong evidence for the mechanism behind differences in performance of individuals on the breeding grounds.

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