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BREEDING SUCCESS IN BRENT IN RELATION TO INDIVIDUAL FEEDING OPPORTUNITIES DURING SPRING STAGING IN THE WADDEN SEA

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1. INTRODUCTION

The nominate or dark-bellied form of the Brent Goose *Branta bernicla bernicla* has a high-arctic breeding range along the coastline of Siberia. In common with other arctic-nesting geese, the acquisition of sufficient body reserves on the spring staging grounds is a prerequisite to successful reproduction. Virtually the entire population gathers in the Wadden Sea region of Denmark, Germany and The Netherlands from the latter part of March through to the end of May (Ebbinge *et al.* 1981). During this period total body weight increases by one third and detailed work on individuals showed that females returning in the fall with young had achieved significantly heavier body weights in the previous spring than those failing to do so (Ebbinge *et al.* 1982). The question we pose here, is what factors might contribute to the differences in body condition accumulated by individuals using the same spring staging areas. Of primary importance at this time of year are the saltings or merselands of the Wadden Sea islands and coastline, tidal foreshore habitats where the spring growth of various grasses (in particular *Festuca rubra* and *Puccinellia maritima*) and other plants (*Plantago maritima* and *Triglochin maritima*) are the staple foods for Brent. In some years, Brent devote considerable time to

collecting algae on the mudflats at low water, but in 1982, the year in which most of our observations were done, geese spent little time in this habitat and we can ignore this complication.

Previous work on the merse during the spring staging period indicated that Brent select only the new growth and exert such heavy grazing pressures that regularly the entire harvestable portion is removed during a single flock visit (Prins *et al.* 1980) and measurements on the rate of movement of individuals filmed during a massive flock visit suggested that depletion occurs so rapidly that individuals differ in foraging opportunities according to their position in the flock (Drent & Van Eerden 1980). In recent years enough geese have been colour-ringed on the island to allow these points to be explored on an individual level, and we here ask 1) do individuals occur consistently in the same sector of the flock, *i.e.* are there early, modal, and late birds in relation to the total feeding pressure exerted by the flock, 2) do individuals in the same flock encounter differences in foraging opportunities as revealed by observational parameters of feeding behaviour or diet analysis from droppings of marked individuals, 3) can these differences be related to breeding performance.

2. STUDY AREA AND METHODS

The study was carried out on the Frisian island Schiermonnikoog in the northern Netherlands (for a description see Prins *et al.* 1980). Most observations were done in May 1982, when among the three thousand Brent staging on the island approximately 70 were individually recognizable. These birds had previously been provided with engraved DARVIC legrings bearing a code, which could be read by 30× telescope at distances up to 300 m. Most sightings were in fact done at close range (within 150 m) from permanent towers (4 m high) erected on the merse. The basic approach was to collect observations on the marked individuals in May, and to evaluate them with regard to the reproductive outcome, determined in autumn, when the Brent return from their breeding grounds. In the fall under the undisturbed conditions prevailing on Schiermonnikoog, repeated

sightings of the marked individuals made it possible to ascertain if they were accompanied by juveniles and if so how many. Juveniles can readily be distinguished from adults at this time of year on the basis of plumage characteristics (see for example Cramp *et al.* 1977) and according to our observations the family stays together as a unit throughout the winter period.

In order to determine how food supply influences foraging behaviour, selected plots on the lower merse, dominated by *Puccinellia maritima*, were treated with fertilizer on 4 May (25 g/m² using a commercial NPK mixture) and in some cases in addition movable hothouses were placed during one week. For each plot vegetation was sampled at the time the plot was made available to the geese, for subsequent analysis of protein content (6.25 × N according to Kjeldahl), and the biomass on offer measured as cumulative blade length per cm² (by clipping of five subplots each 200 cm²). Each plot was given a configuration (2 m × 13 m) with the long axis in the line of vision from the nearest tower to provide the observers with maximal discrimination and enable behaviour observations to be collected on individuals within the plots. Next to each plot a matching control plot was staked out, and after a visit by a group of Brent the droppings in the manipulated plot and the adjacent reference plot were all counted and removed. The ratio of droppings accumulated on the test plot divided by the number in the reference plot will be used as a measure of the preference

exerted by the geese. During a goose visit the number of birds within the plot was counted every fifteen seconds, and for each interval the total number of agonistic interactions was scored. The frequency of agonistic interaction is thus known for each plot in relation to the density of geese present at that moment. A second observer determined pecking and pacing rates (recording time required for fifty pecks, and steps per minute, using a stopwatch) and other behavioural measures not further treated here.

A second series of unmanipulated plots, 2 × 15 m, marked with low wooden pegs, were arranged radially around the main observation tower located on the transition between the higher *Festuca rubra* dominated bench and the lower lying *Puccinellia maritima*, in an opening of the *Juncus gerardii* belt that marks this transition (Fig. 1). Since the Brent often started their feeding day by landing on the *Festuca*, later grazing in the direction of the *Puccinellia*, observations in this natural opening allowed the marked individuals to be arranged in the grazing sequence adopted by the group. As the flock streamed past the tower, one observer counted the individuals every 15 sec within the radial sector best situated to intercept the flock, while a second kept a watch out for the marked individuals, and scored the exact moment a bird with given ring code was seen to traverse the plot. Following the goose passage, the counts were tallied to provide an index of feeding minutes exerted by the flock on its first visit to that vegetation sector that day, and the figures converted to a cumulative percentage (100% = total minutes accumulated during flock passage). Finally, the sightings of the ringed individuals were plotted along this percentage scale, and hence in relation to the cross-section of feeding by the flock, which we have termed the "group profile".

Aside from these plot-oriented observations, whenever opportunity offered marked individuals were kept in view for an uninterrupted span of 10 min. During this time a complete record of all agonistic interactions (for a good description in a related species see Raveling 1970) was maintained, and the outcome noted (win, lose, draw), the direction of travel noted every 15 sec (in relation to the grazing path of majority of geese in that group), and all steps taken in the period counted. Actual foraging time (head down to sward) was timed with a summing stopwatch, and before and after each 10-min protocol the peck rate was timed (sec to fifty pecks). Ideally, the mates of a pair were recorded simultaneously, two observers working together, otherwise the mates were observed one after another. In order to avoid misinterpretations of the agonistic interactions, each observer strove to keep both members of the pair within his telescope field at all times. Data on length of feeding bouts, frequency of head up and extreme alert were also collected but will not be considered here. In all cases the vegetation type and where possible the plant species fed on were noted.

Since marked birds were kept under telescope surveillance for protracted periods, it was sometimes possible to record the time interval between successive droppings and under ideal conditions the droppings in question could subsequently be recovered. A system of small stakes assisted in plotting the locations of droppings on field sketches, and generally one observer retrieved the dropping while the other supervised the operation from the tower. These droppings provide information on diet (see Owen 1975 for technique; for descriptions of epidermis characters see Metcalfe 1960) of known individuals.

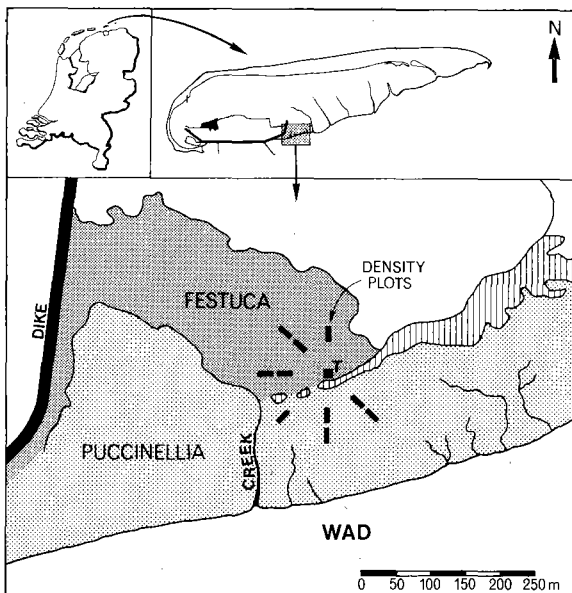


Fig. 1. Situation of the intensive study area on the island Schiermonnikoog (see inset). The observation tower commanding the transition between the *Festuca*-dominated upper merse and *Puccinellia*-dominated lower merse was employed for the group profile measurements (note radial arrangement of counting plots). In winter the geese utilized primarily the enclosed pasturelands (polder). Vertical hatching indicates *Juncus* belt; WAD = mudflat.

3. BEHAVIOURAL REACTIONS TO ENHANCED VEGETATION

The vegetation of the saltmarsh was locally enhanced by fertilization and the use of removable hothouses, providing differences between treatments in biomass (mm leaf material/cm²) and food quality (protein content). Preference exerted by the geese has been quantified by a comparison of the density of droppings accumulated on the manipulated plots in relation to the density on adjacent areas of non-manipulated vegetation. Fig. 2 shows that the index of preference (droppings on manipulated plot/droppings on adjacent control) is clearly related to both biomass (left) and protein content (centre) but as these measures are themselves closely correlated (Fig. 2C) we cannot tease these factors apart. For the sake of the present argument it is sufficient to accept that the index of preference is a reasonable expression of the relative ranking of the vegetation manipulations by the geese themselves, and we will use the index as a means of exploring how observational parameters tend to vary with food supply. We note that both goose density (Fig. 3A) and the rate of agonistic encounters when corrected for density (Fig. 3B) increase with enhanced feeding conditions as revealed by the dropping index. Furthermore, geese tend to decrease pace rate when entering the enhanced areas (Fig. 3C). In our interpretation of the observations on marked individuals, we will assume that a high

rate of agonistic encounters and a low rate of walking are indicative of feeding sites preferred by the geese.

4. INDIVIDUAL POSITION IN THE GRAZING SEQUENCE: GROUP PROFILES

As explained earlier, the marked individuals can be plotted in what we have termed the group profile, providing a measure of their position in the grazing sequence as the flock passed by the observation tower. In all, 45 group passages were recorded, and when the data on the marked individuals are assembled it is clear that the pairs concerned tend to occur consistently in a certain segment of the flock (Fig. 4). For analysis of the observational parameters we have divided the marked birds into three groups, early (occurring within approximately the first 25% of the cumulative foraging time of the flock at that site) mid (occurring between 25% and 50% of the foraging time) and late (beyond 50% of the foraging time). It will be noticed that none of the ringed birds consistently occurred at the tail-end of the flock, so we are in fact dealing with successive segments of approximately equivalent total flock foraging time (0–25, 25–50, and 50–75% respectively).

Reproductive outcome of these pairs is indicated in the figure, as determined when the birds returned in the autumn from their Siberian breeding grounds. Pairs in the leading sector did reasonably well, but highest success, both in

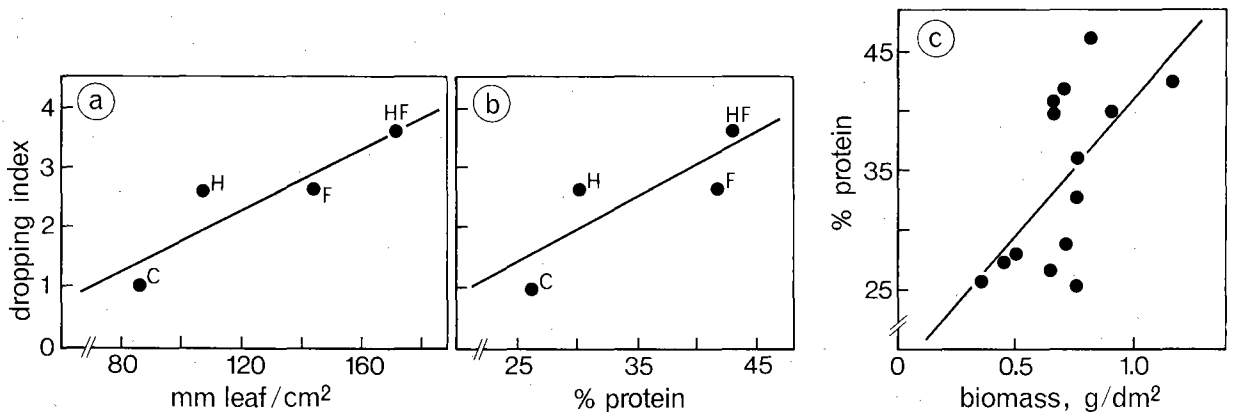


Fig. 2. Calibrating the experimental plots: goose preference as measured by the quotient of droppings inside the plot to those on the adjacent control (dropping index) in relation to biomass (mm grassblades per cm², left) and protein content (centre) on the hothouse (H), fertilizer (F), hothouse + fertilizer (HF) and untreated plots (C). At right, interrelation between protein and biomass.

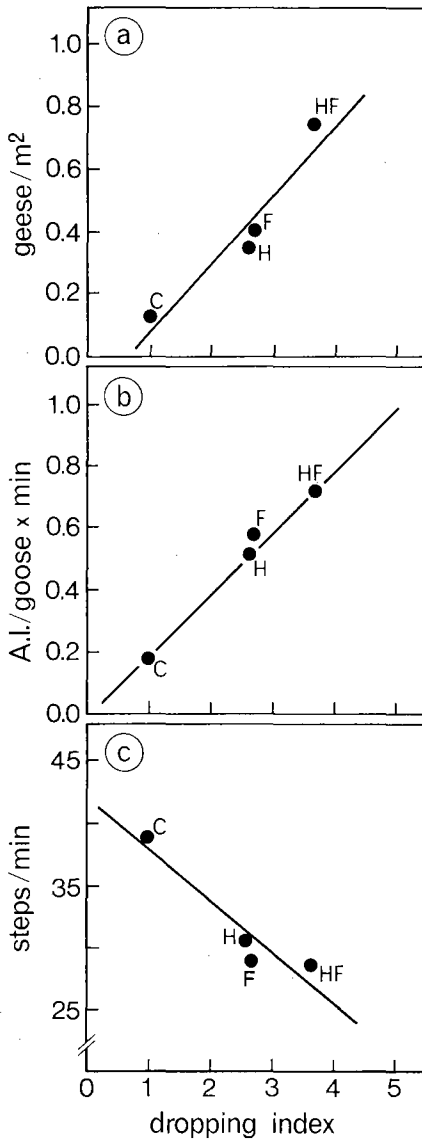


Fig. 3. Goose density (A), rate of agonistic interaction (B) and pace rate (C) in relation to the dropping index as measure of goose preference on the plots (see Fig. 2, where code is explained). All relations are statistically significant ($p < 0.05$).

terms of young per pair and in proportion of pairs with young, was achieved by pairs in the second quarter, whereas pairs in the third of late quarter did very poorly indeed, only one of the five returning with young.

When the observational data for the three groups obtained in May are compared (Table 1) the least successful group (group III, "late") is

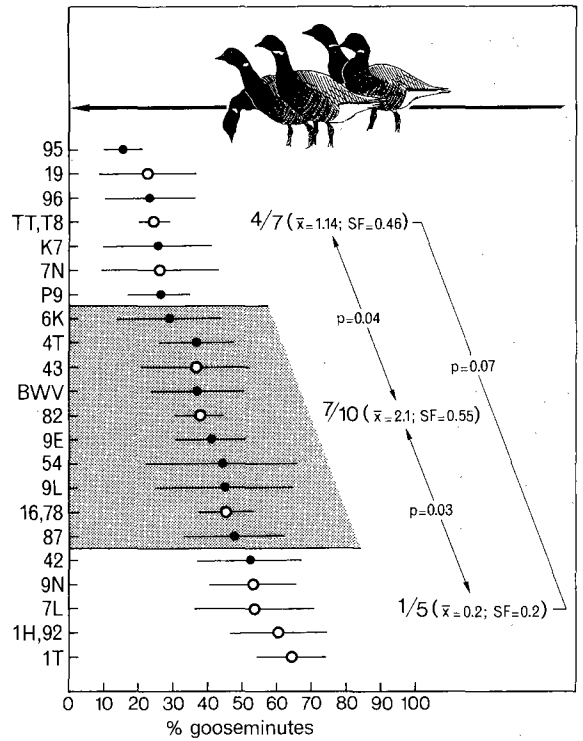


Fig. 4. Ringed individuals (code at left margin) plotted in relation to the grazing sequence of the group expressed as cumulative foraging time of the entire flock (horizontal axis). Individuals subsequently returning with young in the fall shown by filled circles, those without by open circles. Birds early in the grazing sequence tend to be more successful than those at the rear (see text). Means and standard error (S.E.) are given.

clearly distinct in showing a lower rate of agonistic interaction and a shorter defeacation interval, both of which can be taken as indicating less favourable feeding conditions (see section 6). The group scoring highest in breeding performance (group II, "mid") is characterized by the highest rate of agonistic interactions, lowest pace rate, and longest defeacation interval. Our interpretation of these data is that pairs subsequently successful in breeding preempted the most favourable feeding sites, and most likely depleted them before the second half of the total feeding time commenced. The data do not allow a distinction to be made between the feeding conditions encountered by pairs in group I and group II, although the lower step rate experienced by the second group hints at better opportunities for birds somewhat behind the leading edge of the flock. Particularly revealing is

Table 1. Differences in dropping interval, step frequency, AIF (Aggressive Interaction Frequency) and status (= % won) between the three groups. The differences are tested with the Mann-Whitney U test

	Group I	Group II	Group III	Level of significance			
				I II	I III	II III	
Dropping interval (sec)	291.3 (\pm 13.6) (n = 48)	294.6 (\pm 20.1) (n = 19)	237.8 (\pm 14.2) (n = 29)	NS	*	*	
Step frequency (steps/min)	35.2 (\pm 2.6) (n = 23)	28.9 (\pm 3.1) (n = 13)	35.0 (\pm 4.3) (n = 10)	**	NS	NS	
AIF/10 min	4.86 (\pm 0.9) (n = 24)	5.25 (\pm 1.0) (n = 13)	3.73 (\pm 1.0) (n = 9)	NS	NS	*	
Status δ (= % won)	46.3 (\pm 9.0) (n = 10)	72.6 (\pm 10.4) (n = 9)	6.1 (\pm 6.1) (n = 4)	**	*	*	

NS = Not Significant, * = $p < 0.05$, ** = $p < 0.10$.

the measure of success of the male partner in agonistic interactions, the only measure for which each group differs significantly from every other group. The suggestion to be made, is that the leading birds, although encountering favourable feeding opportunities, risk being supplanted by the pairs following behind them.

Third sector birds are clearly subordinate, as the males lose almost all encounters they are involved in. The identity of birds at the rear of the flock remains somewhat of a mystery. Perhaps unpaired individuals and members of the sub-adult non-breeding cohorts tend to accumulate here, but as we had no marked birds in these categories this is no more than conjecture.

5. FEMALE FORAGING OPPORTUNITY IN RELATION TO STATUS OF HER MATE

The classical approach to defining status is to arrange the individuals in a linear sequence on the basis of observations on the outcome of contests between them. In our case, the ringed birds are diluted by vast numbers of unmarked individuals and the observation of a conflict between two marked geese is a rare event. We therefore must use an alternative ranking method, and calculated dominance score as the percentage of interactions with any other bird marked or not, which the focal animal won. This method has been found to correctly predict the outcome of contests between marked individuals (Patterson 1982, Ens & Goss-Custard 1984) and the proportions of agonistic encounters in which the marked male was scored as winner can thus be taken to reflect competitive ability. We can now arrange the marked individuals along this scale and investigate whether male

status has effects for female foraging opportunity. As we have seen, the observations on the fertilized plots provide evidence that a lowered stepping rate is indicative of a better food supply. Plotting the season means, Fig. 5 shows that indeed the mates of high status males enjoy a lowered step rate. Another difference is that high mate status tends to minimize the risk that

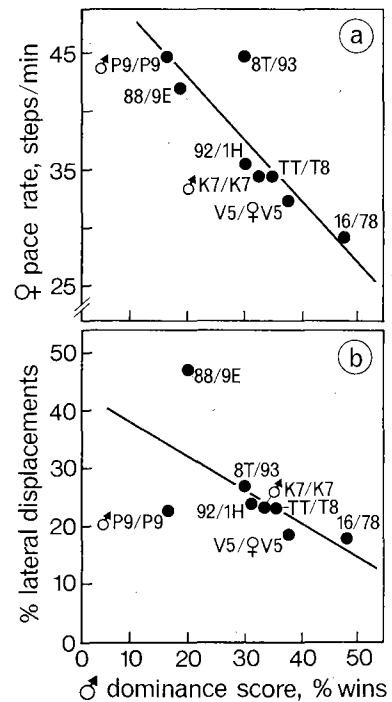


Fig. 5. Partners of the most dominant males (dominance score = % of all interactions won by the male in question) have the lowest pace rate (above $p < 0.01$) and lowest rate of lateral displacement (below $p < 0.05$). Individuals identified by ring code, each symbol referring to season mean for 1982.

the female will be supplanted during foraging, and forced to turn from her path of travel (Fig. 5, bottom). In a subsample of the data it is possible to examine the measure of pecks per step, another indicator of food supply, in relation to the fighting proficiency of the male during the same period (Fig. 6) and again the most favourable conditions are experienced by the females whose mates have the highest success rate.

Taken together with the analysis of relative position in the flock (section 4) we conclude that high competitive status of the male provides enhanced feeding conditions for his mate, mainly because the pair (feeding together in close association at all times) can gain access to the food resource before it has been heavily depleted by other flock members.

There is further evidence of the impact of male status on female feeding opportunity from observations in May 1981, when a positive relationship between the rate of agonistic encounters by the male and female foraging time emerged (Fig. 7) albeit based on but a small sample of marked pairs. The data derived from the same individuals watched in May 1982, when no effect on female feeding time could be detected. The vegetation in the immediate surroundings of the tower was much more patchy in 1981 due to an abortive fertilizer experiment in that year (the merse was unexpectedly immersed after fertilizer application and the vege-

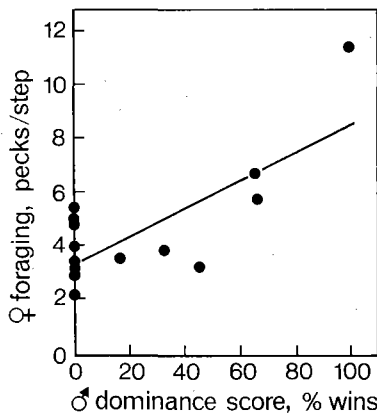


Fig. 6. Partners of the most dominant males (scale as in Fig. 5) show the highest number of pecks per step during foraging ($p < 0.05$ each point represents one 10-min simultaneous protocol of the pair members).

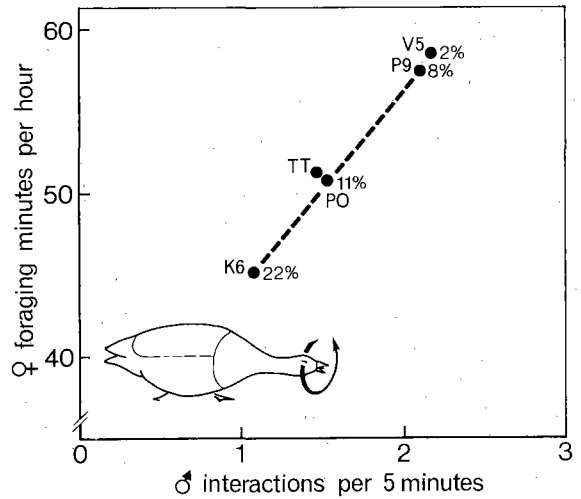


Fig. 7. Female feeding time (ordinate, min per h) in relation to male dominance (measured by rate of interactions). Each point (ringcodes shown) is a season mean for 1981, (minimum sample observation 140 min) and the percentage figure indicates the rate of interactions lost when the male in question was attacked.

tation severely burned as a result).

How consistent is male status from year to year? If we arrange the marked males in order of highest proportion of interactions won or down, we obtain the following:

1980	1981	1982	1983
V5	V5	V5	V5
TT	P9	TT	TT
K6	TT	P9	P9
P9	K6	(K6 dead)	

The disappearance of K6 coincided with an increasing disability: this male had developed a slight limp in 1980 (he had been ringed together with his mate the previous year at the site of observation), walked with difficulty in 1981 and was not seen when the geese returned from the breeding quarters in the fall and his mate K7 was remated to an unringed male in the following spring (1982). We have no ready explanation for the relative changes between TT and P9, but as the partner of P9 was unmarked we cannot be sure of identity (TT was mated to T8 throughout).

We assume that the position taken up by the pair within the flock is the net outcome of a continuing contest of agonistic skirmishes and as such reflects the social status of the pair. Al-

Table 2a. Number of juveniles observed with parents in fall

Ring code	Season						
	1976	1977	1978	1979	1980	1981	1982
V5♂	2	—	3	6	0	3	3
TT/T8	—	—	—	0	0	0	0
K7♀	—	—	—	0	0	0	3
P9♀	—	—	—	6	0	0	1
Mean performance of population	0.4	0.08	1.1	1.3	0	0.05	1.5

Table 2b. Dominance score (% of all agonistic interactions won) of selected males

	Ring code				
	V5	TT	♂ of P9	K6	♂ of K7
1980	46	26	—	21	—
1981	49	54	21	23	—
1982	38	38	19	—	36
Mean % (± S.E.)	44.3 (± 3.3)			29.25 (± 4.3)	
Total observation minutes	329	482	102	306	110

Difference between V5 and rest significant at 0.05 level, Mann-Whitney U test.

though the pair should be considered as a unit, our data are too limited at present to do more than consider the status of the male in relation to other males. In a small sample of only four pairs that we were able to follow over several seasons, the top male contributed to raising by far the most young in a four-years span (and indeed raised at least seventeen altogether in the period 1976—1983). This individual contributed to raising more young than could be expected from the performance of the population as a whole, the others were “average” (Table 2). The data on agonistic interactions in 1982 show a stepwise difference between the top male and the others, and we interpret this as indicative of intrinsic differences (such as experience, see Raveling 1981) between these birds, since none was accompanied by young at the time of observations (status in waterfowl is known to shift upward with an increase in family size, see Boyd 1953, Raveling 1970, Scott 1980).

6. DIET DIFFERENCES BETWEEN BIRDS IN THE SAME FLOCK

Under favourable conditions it was possible to retrieve droppings from marked individuals, and a sample originating from a varied segment of the merse is analyzed in Fig. 8. The sample concerns females only and has been divided

according to whether the individuals concerned subsequently proved to return accompanied by young (successful) or not (unsuccessful) when sighted again in the fall. Although the sample is small, the difference in diet is statistically significant (Mann-Whitney U test, $p < 0.02$), successful birds including far more *Triglochlin maritima* in the diet. Unfortunately we do not have sufficient material from their mates and do not know if a similar trend occurs in the male. In our ex-

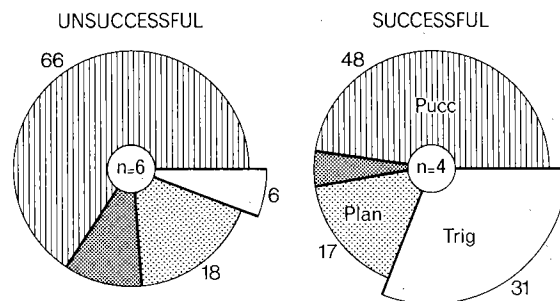


Fig. 8. Diet in female Brent in the second half of May 1982 according to subsequent breeding success (Faecal analysis for six unsuccessful and four successful individuals, Pucc = *Puccinellia maritima*, Trig = *Triglochlin maritima*, Plan = *Plantago maritima*, crosshatched other species, mainly *Festuca rubra* and *Juncus gerardii*). Diagrams depict percentages occurrence (shown along perimeter) based on counts of epidermis fragments when viewed microscopically (sample per individual 300 fragments). Data provided by J. van Nugteren.

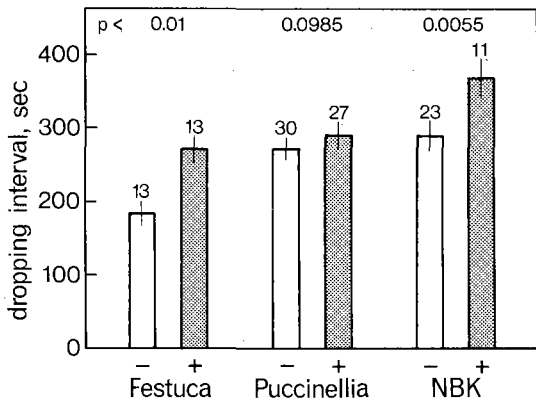


Fig. 9. Dropping intervals (in sec ordinate) in relation to subsequent breeding success for individuals observed in three vegetations. Statistical significance of means indicated (Mann-Whitney U test), the vertical line showing ± 1 S.E., and sample size indicated above. NBK = mixed vegetation.

perience the *Triglochin* clumps are patchy in distribution, and there is more fighting over this food than any other plant. Interestingly, the seed capsules of *Triglochin maritima* are also a highly preferred food item for geese (Thomas & Prevet 1980).

Less direct evidence of differences in type of food ingested is forthcoming when the dropping intervals are compared (Fig. 9). It will be noted that in all sites successful birds (*i.e.* those subsequently returning with young) have longer intervals than unsuccessful ones, in two areas significantly so (in these figures data from males and females have been combined as no consistent differences were found). Unfortunately we do not have enough weights of droppings from known individuals, and cannot extend this approach to an analysis of presumed throughout times. Judging from the digestibility trials carried out by T. Boudewijn using captive Brent on these same vegetations in 1978 (see for methods Boudewijn 1984, Prins *et al.* 1981) there is a tendency for dropping intervals to increase as digestibility improves. Our data thus hint at a difference in the digestibility of the ration collected by the geese even when moving together through the vegetation, birds proving successful apparently achieving a better selection.

7. DISCUSSION

We have shown that on the spring staging grounds individual Brent tend to be restricted to

a certain segment of the flock. Behavioural measures, calibrated by means of the fertilizer experiments, indicate that birds in the various segments of the flock do not have equal access to the most favourable feeding sites. Finally, the proportion of marked individuals returning with young in the fall identified the birds just behind the leading edge of the flock in the spring as being the most successful in breeding.

Working with Canada Geese *Branta canadensis* at a spring staging area some 900 km south of the Manitoba breeding grounds, McLandress & Raveling (1981a) documented an increase in body weight by about one-third, coinciding with a dietary shift from waste maize to the new growth of *Poa pratensis* pastures. Relying on observations of neck-collared individuals, McLandress & Raveling (1981b) found that the paired birds were the first to shift to the grass sites, and the paired females at all sites spent more time feeding than any other category (paired males or unpaired birds of either sex). Adult geese without mate weighed less before the period of weight gain, and accumulated less weight than the paired birds. From previous work (Raveling 1970) it was known that paired geese are higher in the dominance hierarchy than non-paired birds, and the spring observations were interpreted to reflect the benefits in terms of space and food acquisition of the higher status. We would argue that even within the category of mated birds, the scale of social status is wide enough to contribute to differences in performance. The search for the determinants of social status has only just begun (Raveling 1981) but geese offer exceptional opportunities for long-term ontogenetic studies.

There are a number of striking parallels between our goose observations and the extensive investigation of winter flocking in the Wood Pigeon *Columba palumbus* carried out by Murton and his coworkers, who concluded that individuals on the leading edge were at a disadvantage in feeding. Marked individuals seen consistently on the front edge included adults, and these were considerably lighter than adults feeding elsewhere in the flock (431 g versus 506 g), and edge individuals caught later in the winter had lost more weight than those from the main body of the flock. Edge birds walked faster and

pecked less, and when birds were shot examination of the crop contents revealed that these edge birds had collected fewer new growth clover leaves (the main food at the time) compared to the average birds sampled (summarized in Murton *et al.* 1971). Diet differences between these categories of birds in the flock were confirmed in later work when stupefying baits were applied in the fields and individuals subsequently picked up for examination (Murton 1971). Taken together, these observations point to differences in feeding opportunity in the different parts of the flock, differences that have repercussions for maintaining body weight and by inference repercussions on survival. Murton viewed the front edge birds as subordinates that were continually being displaced by the more dominant birds moving up behind them, although systematic data on rate of supplanting were not presented.

The question immediately arising from these observations, is why the disadvantaged individuals do not simply go off on their own. Murton *et al.* (1971) were able to show that Wood Pigeons feeding solitarily performed less well than even the edge birds in the flock, the heavy cost of vigilant behaviour being one of the contributory causes (*cf.* Inglis & Lazarus 1981). Solitary feeding is thus not an alternative, and the choice facing the individual is thus which flock should it join? This question is a critical one, as it can be supposed that the quality of the feeding grounds exploited by a given flock may well differ from that available to another flock. Although our own work on the Brent has not yet yielded unequivocal data on this point, there are suggestive data from other goose populations.

Concomitant with a sharp rise in the total population, the Greater Snow Goose *Anser c. caerulescens* has extended its range on the spring staging grounds in the St Lawrence estuary of eastern Canada, spilling over from the traditional marshes where *Scirpus* is the staple food to the more seaward *Spartina* marshes. Gauthier *et al.* (1984) were able to show that individuals using the recently invaded *Spartina* habitat were unable to accumulate as much depot fat during the six-week spring staging period as were the birds using the traditional *Scirpus* belt. Although this comparison is complicated

by the role of supplementary feeding on agricultural fields in the two areas, it is clear that site choice on this level affects the ability of individuals to accumulate the body reserves needed for reproduction in the arctic. Whether the flocks utilizing the two areas differ in composition with regard to social status as has been suggested for the Gadwell *Anas strepera*, when exploiting a feeding gradient (Paulus 1983) is not yet known. Observation on the integrity of the flock and confirming flockwise differences in reproductive output are obviously the next steps in understanding how social factors bring about inequality between individuals. The actual process of the amalgamation of subordinate birds in the flock has been rarely observed, and for waterfowl the only data we have found refer to the Shelduck *Tadorna tadorna*. In a large-scale experiment, Patterson (1982) was able to influence the retention of young, subordinate birds by supplementary feeding in May, and it seems that recruitment to the local population at this time depends on the balance between the aggressive hostility of the established birds in relation to the feeding opportunities.

Paradoxically, all these studies of group living tend to emphasize the differences in access to resources between individuals, rather than the advantages enjoyed by all group members (Ydenburg & Prins 1981). Foraging socially, whether it entails herbivores (Red Deer *Cervus elaphus*, Appleby 1980) seed-eating Juncos *Juncos hyemalis* (Baker *et al.* 1981) or mussel-eating Oystercatchers *Haematopus ostralegus* (Goss-Custard 1980, Ens & Goss-Custard 1984) leads unavoidably to the dominant individuals gaining priority.

Attempting to forge a causal chain from correlative links is a hazardous undertaking and we must take care that interpretation does not outpace the facts. Having demonstrated an inequality in feeding opportunity between members of a flock when observed together during spring staging does not mean that differences in breeding performance are due solely to events in spring. Rather, what we have shown is that in a competitive situation when high quality food is scarce, individuals can be sorted in a dominance ranking, and it is the ranking that yields the relationship with subsequent performance. We

would expect the high-ranking pairs to have priority at all stages of the annual cycle and a great deal of work remains to be done to quantify the contribution of each phase towards successful parenthood. To start with, in the spring situation a number of points need following up. We have not yet demonstrated that high status Brent in fact accumulate body reserves at a faster rate than low ranking birds. Much more work must be done to investigate diet in relation to status. Finally, far more detail is needed on how individual geese use the staging area. Although the marked birds were together in one flock for part of each day, they spent at least one-third of their feeding time dispersed over the merge in much smaller groupings. We suspect that preferential site use at this level will also prove to be under the influence of social status, and that individual differences in food selection and intake rate at this time are not less than when all geese are together. The fact that as the total population has increased, total Brent numbers on the Schiermonnikoog spring staging area have been virtually constant over the past ten years must mean that an active process of exclusion is at work. Intensive observation of marked individuals on a wider scale than reported here is bound to be rewarding.

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9. SUMMARY

Brent Geese *Branta bernicla* individually marked with inscribed leg-rings were intensively watched from permanent towers on the saltings of the island Schiermonnikoog in the Dutch Wadden Sea during the spring staging period April—May 1982 when 3000 used the area. By observing geese on plots with enhanced vegetation (biomass, protein content)

as a result of fertilizer treatment, it was found that individuals on the improved sites fought more and walked more slowly. The position of the marked individuals in relation to the total feeding minutes accumulated by the flock as the group grazed past the tower was determined by making use of a radial system of counting plots. Individuals tended to be consistent in their relative timing in the grazing sequence, and the highest rate of interaction and lowest pacing rate was found just behind the leading edge of the flock, in the second quartile of feeding minutes, and by inference birds in this sector experienced the best feeding conditions. Status of the males (proportion of interactions won) was highest for individuals habitually in this sector, and observation of the same birds in the fall revealed the highest incidence of breeding success (pairs accompanied by young) for this group. A number of measures reflecting a good food supply (low pace rate, highest percentage feeding times, highest number of bites per step) were found to correlate positively with male status supporting the conclusions from the grouped data presented in relation to the grazing sequence. Though a causal relation cannot be proved from such correlations, we interpret these findings to indicate that males of high status can provide their mates with enhanced feeding opportunities, resulting in accumulation of more body reserves in the spring, and a heightened probability of successful breeding. Females subsequently found to prove successful had a larger proportion of *Triglochin maritima* in their spring diet but a larger sample of droppings will be needed to substantiate this hint of a difference of diet in birds of the same flock.

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11. SAMENVATTING

Rotganzen *Branta bernicla* werden intensief waargenomen vanuit hoge schuilhutten op de kwelders van Schiermonnikoog. Tijdens het voorjaar van 1982 (april—mei) pleisterden ruim 3000 ganzen op het eiland, waarvan ca. 70 individueel herkenbaar waren door middel van gecodeerde ringen (afleesbaar tot 200 m). Veel van deze dieren werden in het najaar opnieuw opgespoord, waarbij kon worden bepaald of het individu wel of niet werd vergezeld van jongen. Om door middel van waarnemingen een idee te krijgen of het betreffende individu op een gunstige plek foerageerde, werden op kleine schaal door toedienen van kunstmest vakken met verbeterd voedselaanbod gecreëerd. Waarnemingen leerden dat op deze gunstige plekken de ganzen langzamer liepen en vaker agressieve interacties vertoonden. In ongestoorde situaties werd vanuit de toren de plaats van het individu in de groep bepaald. Door gebruik te maken van tellingen in een radiaal uitgezet vakkenpatroon, kon voor ieder individu het moment van passeren ten opzichte van de hele groep worden berekend. Veel interacties en een lage stapfrequentie (uitgaande van waarnemingen in de bemeste vakken: de meest gunstige foerageeromstandigheden) kwam niet voor onder de randdieren, maar werd bereikt in de daaropvolgende sector van de groep. Wij interpreteren deze gedragsverschillen als aanwijzing dat de dieren die direct achter de koplopers komen gunstige foerageeromstandigheden het best kunnen uitbuiten. Mannetjes van de paartjes die gewoonlijk in deze "top sector" verbleven bleken het vaakst te winnen in agressieve interacties en werden ook het vaakst met jongen aangetroffen in de herfst. Analyse van een groot aantal gedragsprotocollen liet ook zien dat deze dominante mannetjes klaarblijkelijk in staat zijn de meest gunstige foerageeromstandigheden voor de partner te garanderen, althans de vrouwtjes van zulke mannetjes hadden de laagste stapnelheid, langste eettijden, en meeste happen per stap, alles maten indicatief voor een gunstige voedselopname. Analyse van keutels van bekende individuen gaf bovendien aanwijzingen voor een dieetverschil in het voorjaar: de vrouwtjes die in het najaar met jongen werden aangetroffen hadden veel meer *Triglochin* (Zoutgras) in het dieet opgenomen dan kinderloze vrouwtjes. Veel onderzoek zal nodig zijn voor wij zeker kunnen zijn hoe deze feiten in een causale keten passen. De suggestie is wel dat omstandigheden op de voorjaarspleisterplaatsen in het Waddengebied, en vooral de toegang tot de meest gunstige plekken (die beïnvloed wordt door de sociale rangorde), mede bepalend zijn voor het hebben van succes op de Sibेरische broedplaatsen.