Time budget and flock structure in spring staging Dark-bellied Brent Geese

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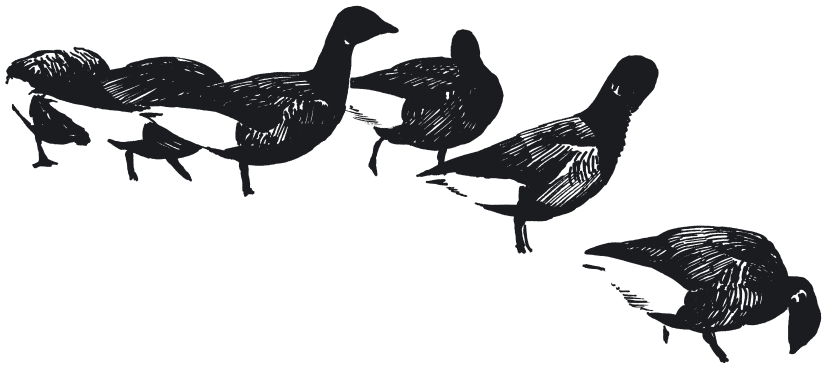

(Med et dansk resumé: Tidsbudget og flokstruktur hos forårsrastende Mørkbugede Knortegæs)

Introduction

There are advantages and disadvantages of group life to the individual. A main advantage is the possibility of benefitting from the "dilution effect" and thereby reduce risk of predation (Lazarus & Inglis 1978, Pulliam & Caraco 1984). Flocking animals take turns being vigilant and thus reduce the time each individual has to spend vigilant (Fox & Madsen 1981, Inglis & Lazarus 1981, White-Robinson 1982, Pulliam & Caraco 1984, Black et al. 1992). However, there are also costs involved, such as food competition (Wilson 1975, Pulliam & Caraco 1984, Teunissen et al. 1985, Prop & Loonen 1988, Black et al. 1992, Ebbinge & Spaans 1992).

This study describes costs and benefits of the behaviour of a group-living species, the Dark-bellied Brent Goose *Branta bernicla bernicla*, investigating differences in male and female behaviour, differences in behaviour of individuals positioned in the center, on the edge, or outside the flock, and changes in flock structure after upflights.

In early March, Dark-bellied Brent Geese migrate to spring staging areas in the Wadden Sea (Ebbinge et al. 1982, Madsen et al. 1990). Here they forage in the salt marshes, increasing their weight as a prelude to migration and breeding in northern Siberia (Prokosch 1984, Ebbinge 1989). Breeding success in Brent Geese follows a 3-year cycle: a good breeding year, a poor year and an unpredictable year (Summers & Underhill 1991). In addition to this, the breeding success is influenced by the ability of the Brent Geese to enhance food intake and weight gain during spring staging (Ebbinge et al. 1982, Ebbinge 1989, Ebbinge & Spaans 1992).

Material and methods

The study took place on the island Langli in the Danish part of the Wadden Sea. The size of the island is approximately 2.5×1 km and the tidal range is about 1 m. The island with surrounding tidal flats is a reserve with no human access in spring. It has served as a spring staging area for up to 1200 Dark-bellied Brent Geese since the early 1980s (Madsen et al. 1990). I selected the salt marsh at the southern end of the island including the surrounding tidal flats and shallow waters, approximately 5 km^2 in total, as my study area.

Observations were made on 62 days between 15 March and 31 May 1993 and covered all daylight hours. 1992 was a non-breeding year (Madsen 1994), and no juveniles were present in the flocks during the study period.

For recording observations I used a spotting scope, a stop watch, and an event recorder (Psion organiser). The observations were made from a hide placed at the edge of a range of dunes and overlooking the study area.

Procedure

The study was based on focal animal observations and scan sampling observations (Altmann 1974). For a focal animal observation sample, the sex of the selected individual as well as its position inside or outside the flock were recorded at the start of the focal sampling period. I sexed the geese in the field using morphological characteristics. This can be done accurately, as the male Brent Goose has a thicker neck and a larger head than the female (J. Madsen pers. comm.). In case of doubt, another goose was chosen for focal sampling. I recorded a Brent as being in the center of the flock when it was surrounded by other Brent on all four sides and as being on the edge of the flock when it was surrounded by other Brent on three sides or less (Inglis & Lazarus 1981, White-Robinson 1982, Black et al. 1992). When a Brent was at least 10 goose-lengths (from chest to tip of tail) away from the flock I termed it "outside".

I recorded the following behaviours:

Vigilance. Head raised above shoulder level and neck stretched (Inglis & Isaacson 1978, Inglis & Lazarus 1981, White-Robinson 1982, Black et al. 1992).

Foraging. Feeding on the vegetation in the salt marsh or on *Enteromorpha* sp. on mudflats or in shallow water (only few geese foraged on *Enteromorpha* during the study period). On the salt marsh, a Brent Goose would interrupt its foraging every two or three seconds to lift its head a few centimeters above the ground and look around for about half a second. These short watchful periods with the head kept below shoulder level were distinguished from vigilance and the time included in the time spent foraging.

Agonistic behaviour included **threatening** (stretching the neck parallel to the ground and hissing while running towards another Brent) and **fleeing** (running away from a threatening Brent).

Resting without foraging.

Walking, also without foraging.

Preening with beak or scratching with foot.

Running, when not part of agonistic behaviour.

Swimming. Active swimming and lying on water were not distinguishable in the field, and both were recorded as "swimming".

Flying. It was often impossible to register the duration of a flight as the Brent might leave the study area and disappear out of sight. Flying was therefore omitted from the record, and focal sampling was interrupted when the goose flew up.

During the focal sampling period, time of each shift in behaviour as well as the type of behaviour were recorded. A focal sampling period lasted until the individual could no longer be distinguished from other individuals in the flock, left the study area, or changed its position in the flock, e.g. moved from center to edge. 387 individuals were focal-animal sampled, and the total number of behavioural bouts recorded was 8441.

I used a scan sampling method to record how Brent Goose flocks dispersed during foraging. Flocks varied in size from 32 to about 1500 individuals. When a flock settled, the distance (in goose-lengths) between pairs in the flock was scan-sampled every ten minutes (inter-pair distance). I estimated inter-pair distance by single goose-lengths at distances below 10 goose-lengths and by 5 goose-lengths at longer distances (Bregnballe & Madsen 1990). In between these scan samplings, I sampled the sex and behaviour of both individuals in each pair along with the inter-pair distance to the nearest pair. This would continue until the dispersing flock could no longer be distinguished from the rest of the Brent on the salt marsh. For scan samplings 25 flocks were observed, 3472 inter-pair distances were recorded, and behaviour and distance to nearest pair was scan-sampled in 1421 pairs.

A test of normal distribution was performed on all data. None of the data could be assumed to be normally distributed, so nonparametric tests were used. SAS System, Release 6.04 (SAS Institute Inc., Cary, NC, USA) was used for calculations and tests.

Results

Time budget

The average percentage of time that the Brent Geese spent performing each behaviour did not vary with their position in the flock, except for the average time spent performing agonistic behaviour (Tab. 1) which was more than 3 times longer when the goose was in the flock (edge or center) than when it was outside it. The length of focal sample periods varied, however, as it depended on the position of the goose, and in longer sample periods the recorded individuals spent more time resting and less time foraging when outside the flock, and more time resting and less time vigilant when on the edge of the flock (Tab. 2). In general, when Brent Geese spent less time foraging they correspondingly spent more time resting and being vigilant, whether being outside or on the edge or in the center of the flock, while Brent Geese in the flock spent extra time performing agonistic be-

Tab. 1. The average percentage (SE) of time per individual spent performing each behaviour in relation to position in flock. Results from focal animal sampling.
Gennemsnitlig procentdel (standardafvigelse af gennemsnittet i parentes) af den samlede tid brugt pr individ på hver adfærdsform i relation til position i flokken.

Behaviour *Adfærd*	Outside (N=85) *Udenfor*		Edge (N=144) *Rand*		Center (N=158) *Midten*		p[a]
Vigilance *Vagtsomhed*	16.0	(13.9)	18.1	(19.7)	16.3	(15.7)	n.s.
Foraging *Fouragering*	76.2	(23.9)	73.9	(25.9)	76.2	(23.2)	n.s.
Agonistic *Agonistisk*	0.4	(1.4)	1.4	(5.0)	1.4	(4.0)	<0.05
Resting *Rasten*	1.9	(10.5)	3.1	(12.9)	2.1	(10.6)	n.s.
Walking *Gang*	1.9	(5.5)	1.3	(4.2)	2.1	(4.8)	n.s.
Preening *Fjerpleje*	3.4	(21.3)	2.0	(9.0)	1.3	(6.2)	n.s.
Swimming *Svømning*	0.0	(0.0)	0.0	(0.3)	0.6	(7.3)	n.s.
Running *Løb*	0.0	(0.1)	0.2	(1.1)	0.0	(0.2)	n.s.

a: Kruskal-Wallis one-factor analysis of variance (n.s.=not significant)

haviour as opposed to Brent outside the flock (Tab. 3).

On average, females spent more time foraging and walking than males, who on the other hand spent more time running, being vigilant, and performing agonistic behaviour (Tab. 4).

Flock structure

The average inter-pair distance in the flock differed significantly between scan samples ($p<0.0001$, Kruskal-Wallis one-factor analysis of variance). Immediately after settling, the average inter-pair distance was 1 goose-length, while after 1.5 hours the average distance was 5.5 goose-lengths and several pairs had left the flock.

For each inter-pair distance, the percentage was calculated of observations in which both geese in a pair, or the male or the female, performed each behaviour. This percentage was termed frequency of behaviour. Where only a single observation was made at a certain inter-pair distance this observation was omitted. A Spearman rank correlation coefficient between inter-pair distance and frequency of behaviour was calculated. The test showed that as inter-pair distance increased, the percentage of observations where both geese in a pair foraged increased, and the percentage of observations where the male foraged decreased (Fig. 1; $r_s=0.61$, $p<0.02$ and $r_s=-0.70$, $p<0.004$, respectively). Correspondingly, the frequency of both

Tab. 2. Spearman rank correlation coefficient between length of focal sampling period and mean percentage of time per individual spent performing each behaviour in relation to position in flock. Results from focal animal sampling.
Spearman rang korrelationskoefficient mellem længde af focal sampling-periode og gennemsnitlig procentdel af den samlede tid brugt pr individ på hver adfærdsform i relation til position i flokken.

Behaviour *Adfærd*	Outside (N=85) *Udenfor*		Edge (N=144) *Rand*		Center (N=158) *Midten*	
Vigilance *Vagtsomhed*	0.09	n.s.	-0.28	**	-0.15	n.s.
Foraging *Fouragering*	-0.28	*	0.038	n.s.	-0.012	n.s.
Resting *Rasten*	0.46	***	0.36	***	0.14	n.s.

n.s. not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Tab. 3. Spearman rank correlation coefficients between average percentage of time per individual spent performing each behaviour in relation to position in flock. Results from focal animal sampling.
Spearman korrelationskoefficienter mellem gennemsnitlig procentdel af den samlede tid brugt pr individ på hver adfærdsform i relation til position i flokken.

Position in flock *Position i flokken*	Behaviour *Adfærd*	Fouragering *Fouragering*		Agonistic *Agonistisk*		Resting *Rast*	
Outside (N=85) *Udenfor*	Vigilance *Vagtsomhed*	-0.63	***	-0.03	n.s.	0.02	n.s.
	Foraging *Fouragering*	–		0.01	n.s.	-0.53	***
	Agonistic *Agonistisk*	–		–		-0.05	n.s.
Edge (N=144) *Rand*	Vigilance *Vagtsomhed*	-0.71	***	0.04	n.s.	-0.08	n.s.
	Foraging *Fouragering*	–		-0.19	*	-0.50	**
	Agonistic *Agonistisk*	–		–		-0.05	n.s.
Center (N=158) *Midten*	Vigilance *Vagtsomhed*	-0.71	***	0.06	n.s.	0.08	n.s.
	Foraging *Fouragering*	–		-0.17	*	-0.54	***
	Agonistic *Agonistisk*	–		–		-0.04	n.s.

n.s.=not significant, * p<0.05, ** p<0.01, *** p<0.001

geese in a pair or the female being vigilant decreased (Fig. 2; r_s=-0.54, p<0.04 and r_S=-0.56, p<0.03, respectively), as did the frequency of resting by both geese in a pair or by the female (r_s=-0.63, p<0.02 and r_s=-0.61, p<0.02, respectively; not depicted). For 5 distances the sample size was only 1; these were omitted from the figures but not from correlation tests.

Tab. 4. Mean percentage of time per individual spent performing each behaviour in relation to sex. Results from focal animal sampling.
Gennemsnitlig procentdel af den samlede tid brugt pr individ på hver adfærdsform for hanner og hunner.

Behaviour *Adfærd*	Male (N=198) *Han*	SE	Female (N=189) *Hun*	SE	p[a]
Vigilance *Vagtsomhed*	19.9	18.1	13.8	15.1	<0.001
Foraging *Fouragering*	72.8	24.3	78.0	24.2	<0.01
Agonistic *Agonistisk*	1.9	5.3	0.5	1.8	<0.01
Resting *Rasten*	1.7	8.5	3.2	13.9	n.s.
Walking *Gang*	1.5	4.7	2.1	4.8	>0.001
Preening *Fjerpleje*	2.1	9.4	2.0	8.5	n.s.
Swimming *Svømning*	0.0	0.3	0.5	6.7	n.s.
Running *Løb*	0.1	0.9	0.0	0.0	<0.001

a: Kruskal-Wallis one-way analysis of variance (n.s.=not significant)

The frequency of agonistic behaviour by both geese in a pair, or by the male or the female, also decreased with increasing inter-pair distance (r_s=-0.69, p<0.005; r_s=-0.64, p<0.01; and r_s=0.54, p<0.04, respectively), as did the frequency of preening by the male or by the female (r_s=-0.58, p<0.03 and r_s=-0.64, p<0.02, respectively) (these relationships are not depicted).

All combinations of inter-pair distance and behaviour were tested, but only the here mentioned showed significant correlations.

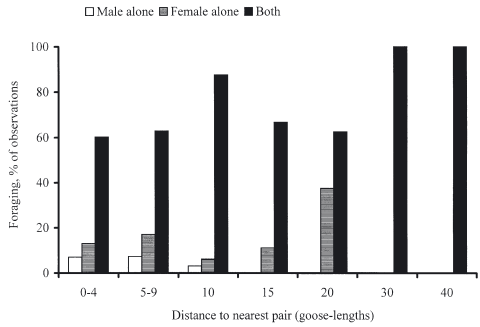

Fig. 1. Behaviour of paired Brent Geese as a function of inter-pair distance (goose-lengths). Percentage of observations at each distance where the male, the female, or both were foraging. Results from scan sampling (N=1416 pairs).

Adfærd hos udparrede Knortegæs som funktion af afstand til nærmeste par (gåselængder). Procentdel af observationerne hvor hannen, hunnen eller begge fouragerede. Resultater fra scan sampling (N=1416 par).

Discussion

Time budget

The study did not show any difference in the amount of time spent vigilant by Brent in the center, on the edge, or outside the flock. This is not consistent with the initial theory of shared vigilance in the flock.

However, when individuals on the edge or in the center of the flock were selected for focal sampling, those assuming the vigilance posture may unintentionally have been selected more often. Vigilance would then often be the first behavioural pattern to be registered and would become the prevailing behaviour in short sample periods. When Brent outside the flock were selected, a similar bias probably did not exist, since a solitary individual was conspicuous in itself. This could explain the increased vigilance during short sample periods (Tab. 2). If such a bias did indeed exist, the actual amount of time spent vigilant by geese in the flock (center or edge) might be less than indicated by the observations (Tab. 1).

The longest periods of unchanged behaviour (more than 10 min) were those spent resting. These could only be recorded in long sample periods, which explains why geese recorded for a longer time spent more time resting (Tab. 2). Brent outside the flock seemed to compensate for the increased time spent resting by spending less time foraging, while Brent on the edge of the flock reduced vigilance instead (Tab. 3).

Male and female behaviour

The data suggest that a division of labour exists between male and female in a pair of staging Brent (Tab. 4). The male spends more time watching for predators and keeping competing geese away, allowing the female to forage undisturbed and achieve a better condition (see also Fox & Madsen 1981, Ebbinge et al. 1982, Bregnballe & Madsen 1990, Black et al. 1992, Ebbinge & Spaans 1992).

Flock structure

The Brent Geese settled in a dense flock after a flight but soon dispersed, and some pairs separated themselves from the flock. As the Brent dispersed over the salt marsh, they foraged more frequently and reduced other kinds of behaviour (Fig. 1 and 2). When distance between pairs exceeded 15 goose-lengths, both Brent in a pair foraged at almost all observations. Owens (1977) likewise noticed that Brent dispersed over the salt marsh to

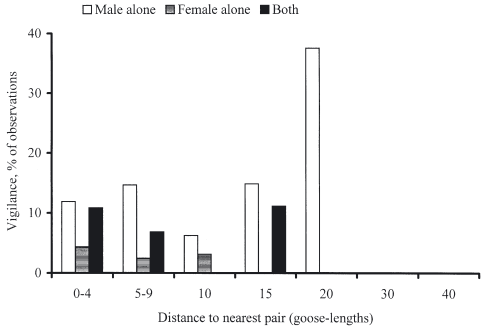

Fig. 2. Behaviour of paired Brent Geese as a function of inter-pair distance (goose-lengths). Percentage of observations at each distance where the male, the female, or both were vigilant. Results from scan sampling (N=1416 pairs).

Adfærd hos udparrede Knortegæs som funktion af afstand til nærmeste par (gåselængder). Procentdel af observationerne hvor hannen, hunnen eller begge stod i vagtsomhedspositur. Resultater fra scan sampling (N=1416 par).

Foto: Erik Thomsen, Biofoto.

graze, and Inglis & Lazarus (1981) stated that flocks of Brent Geese are roughly circular when they land but gradually turn more elliptical in shape.

The described flock structure suggests that every time the Brent Geese land they must go through a period with short inter-pair distances, leading to increased vigilance, more frequent agonistic behaviour, and less time for foraging. In case of disturbance this means that even if a flock of Brent seems to resume foraging immediately after resettling, disturbance may have long-term effects. Up to 1.5 hours can pass before the flock is dispersed over the salt marsh again and foraging intensity has achieved pre-flight level.

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Resumé

Tidsbudget og flokstruktur hos forårsrastende Mørkbugede Knortegæs

Adfærd hos forårsrastende Mørkbugede Knortegæs *Branta bernicla bernicla* observeredes for at undersøge fordele og ulemper ved floklevevis, forholdet mellem de to køn i et par samt gåseflokkenes struktur og ændringer i denne over tid. Ændringer i flokstrukturen samt hyppigheden af forskellige adfærdsformer blev registreret ved hjælp af *scan sampling* og *focal animal* observationer. De undersøgte adfærdsformer var fouragering, vagtsomhed, agonistisk adfærd, rast, gang, løb, fjerpleje og svømning. Desuden blev afstanden mellem parrene løbende registreret efter flokkens landing. Efter opflyvninger landede Knortegæssene i en tæt flok, men afstanden mellem parrene øgedes med tiden og nogle par forlod flokken. Gæssene brugte en større del af tiden på at fouragere og mindre tid på vagtsomhed når de gik i åbne flokke end når de gik tæt sammen, og det kunne vare op til 1.5 time efter en opflyvning før afstanden mellem parrene og dermed fourageringsintensiteten havde nået et niveau svarende til før opflyvningen.

Resultaterne tyder på, at vagtsomhedsniveauet var højere uden for flokken end inden i den, så gæssene især i åbne flokke havde en fordel i form af mindre tid brugt på vagtsomhed og mere tid brugt til fouragering. Generelt brugte hannen i et par mere tid på vagtsomhed og mindre tid til fouragering end hunnen, hvilket tyder på en arbejdsdeling mellem kønnene.

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