Parental behaviour in autumn-staging Pink-footed Geese *Anser brachyrhynchus*

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Abstract

Goose parental behaviour is costly and represents a compromise between an individual's need to spend time and resources maintaining its own body condition and survival with that required to successfully rear young. Geese are long-term monogamous species, with pair members cooperating to maximise their fitness outcomes by contributing differentially in time and function to the success of breeding attempts. For instance, enhanced male alertness during the reproductive season contributes to predator detection, whilst defending territories and broods from conspecifics also helps increase reproductive success. Such behaviour supports the female, which faces the high energy demands involved in producing and incubating eggs, by enabling her to spend more time foraging before, during and after the nesting period. Males also need to rebuild body stores after spending less time foraging during a period of heightened alertness, but this will be less marked than for the female following incubation. Hence, the time spent feeding and alert by parents would be expected to be more similar during autumn migration than during the breeding season, although both parents would be predicted to be more alert and to feed less than goslings, so that the still-growing young could maximise their food intake. To test these hypotheses, we observed the behaviour of individual Pink-footed Geese *Anser brachyrhynchus*, which were autumn-staging on spilt grain in stubble fields in central Norway. As predicted, there were no significant differences between female and male parents in the time spent foraging, alert or being aggressive towards conspecifics. Time spent by the parents on preening and sleeping were also similar for both sexes. Goslings and adult geese without young spent significantly more time foraging and less time alert than parental geese. On considering behaviour patterns in relation to the time of day, all geese were found to spend significantly more time foraging during the evening. We conclude that the behaviour of Pink-footed Geese at an autumn staging site, on their way to their wintering areas, reflects their age and breeding status, which may have positive fitness consequences.

Key words: *Anser brachyrhynchus*, autumn, effort, farmland, foraging, vigilance.

Geese are long-term monogamous species, which live in flocks at their moulting, staging and wintering sites. Although usually territorial during the breeding season, colonial nesting may also occur, and family cohesion is generally maintained within the large flocks at least through the goslings' first winter (Owen 1980). Flocking behaviour has costs and benefits (Amano *et al.* 2006). Whilst competition for food occurs within a flock, the cost of being alert for predators can be shared among individuals, resulting in increased foraging activity and thus energy intake rate *per capita* as flock size increases (Pulliam & Caraco 1984; Hupp *et al.* 1996). Flock membership remains a compromise, however, between the foraging benefits of sharing alertness (enabling individuals to reduce their vigilance levels) and the increase in foraging competition for shared resources (Amano *et al.* 2006). Maintaining family units within the flock therefore will be additionally beneficial, as common fitness interests lead to cooperation and costs can be divided among family members, both in the breeding and non-reproductive seasons (Raveling 1970; Black & Owen 1989a; Black *et al.* 1992; Ely 1993; Tinkler *et al.* 2007).

For herbivorous geese, parental vigilance behaviour represents a significant investment in their offspring, allowing young to forage undisturbed, at a cost to vigilant parents of lost feeding time (Amano *et al.* 2006). Alertness enables the geese to detect predators earlier, with parents in particular investing in vigilant behaviour to enhance protection from predators and to provide more foraging time with improved access to food resources for the young. Individual geese which are paired, or part of a family, are more dominant and gain more resources than single adults or young without parents (Boyd 1953; Raveling 1970; Lazarus & Inglis 1978; Black & Owen 1989a,b; Gregoire & Ankney 1990; Black *et al.* 1992; Poisbleau *et al.* 2006). The value of parental alertness is also indicated by the positive association between their vigilance activity and brood size, both after hatching (Forslund 1993) and also in winter, when pairs with large broods are more vigilant than those with smaller broods (Siriwardena & Black 1998; Tinkler *et al.* 2007). Whether young from the larger families had higher survival was however not known in these studies. Sub-adult Barnacle Geese *Branta leucopsis* associating with their parents during their second winter may also contribute, by being more vigilant and repelling neighbours, which enables the parents to increase their feeding time (Black & Owen 1989a).

Given that geese may remain with the same mate over many years, parental cooperation can be advantageous not only for raising goslings in a single season but for the overall fitness of paired adults, because the behaviour of one partner may affect both members of the pair (Black & Owen 1995; Black *et al.* 1996; Black 2001). For instance, this is reflected in differences in the feeding behaviour of the two sexes at different stages of the breeding season. Female geese rely on lipid and protein stores for egg production and incubation, so spend more time feeding during the pre-laying period (Ankney & MacInnes 1978; Tombre & Erikstad 1996; Tombre *et al.* 2012), whereas the males spend more time being alert, enabling the females to forage intensively not only on arrival in the breeding range but also on taking feeding recesses during incubation (Prop *et al.* 1984; Gauthier & Tardif 1991; Reed *et al.* 1995; Tombre *et al.* 2012). Females also need to replace depleted stores when the eggs hatch and the family leaves the nest; hence, females have longer foraging periods during the post-hatch brood-rearing period, whereas males feed less and continue to be more vigilant (Lazarus & Inglis 1978; Bregnballe & Madsen 1990; Sedinger & Raveling 1990; Fowler & Ely 1997). After the nesting period, moulting is an energy demanding period for both sexes (Van Dellen *et al.* 2020), and the timing of the moult is phased to reduce the period when both parents are flightless in some waterbird species (*e.g.* Mute Swans *Cygnus olor*; Coleman *et al.* 2002; Czapulak 2002). Autumn mortality is higher for geese of both sexes that did not develop sufficient stores before departure from the breeding grounds (Owen & Black 1989, 1991), illustrating the vital importance of body stores to both sexes for individual fitness during migration.

That differential parental investment between two members of a pair continues outside of the breeding season has been shown for Barnacle Geese on their wintering sites. At this time, males forage less and are vigilant for longer than females (Black & Owen 1989a,b; Black *et al.* 1992), although females may also display aggressive behaviour in winter, particularly those with larger brood sizes (Siriwardena & Black 1998). In terms of energy expenditure, females are less stressed in the non-breeding season and hence can contribute more to the defence of young than in the breeding season. After the post-breeding period, female energy stores are presumably more or less reconstituted following their depletion during egg-laying and incubation, and she can assist the male as he in turn rebuilds stores spent during the reproductive season. We therefore expect that effort in terms of vigilance would be more equally shared between the parents in the non-breeding season, and this is considered here in further detail for autumn-staging goose flocks.

In autumn, Svalbard-breeding Pink-footed Geese *Anser brachyrhynchus* make a stopover in mid-Norway, where they forage on farmland before departing for their wintering areas in Denmark, the Netherlands and Belgium. In general, there is little detailed information about the foraging behaviour of geese at their autumn staging sites, although a main reason for stopping on their way southwards is the need for families, and particularly the young, to stop to rest and replenish body stores (Gundersen *et al.* 2017). Despite there being relatively few studies, Sedinger and Bollinger (1987) have found that young Cackling Canada Geese *Branta canadensis minima* spend more time foraging than adult birds, whereas no behavioural differences were found between the foraging time for adult males and females, which suggests that parental effort in vigilance is shared more equally at this stage of the annual cycle.

The present study was conducted on farmland where Pink-footed Geese forage in large flocks on harvested stubble fields. Although the geese stop in the region during the hunting season, they may forage undisturbed for long periods because hunting is organised so that there are several consecutive days without hunting (Jensen *et al.* 2016a; Tombre *et al.* 2022). The non-hunting days therefore provide excellent conditions for observing individual sex- and age-specific behaviour. Given that the birds are *en route* to their wintering areas in continental Europe, we hypothesise that: (i) parents will be more vigilant than pairs without young (hereafter referred to as non-parents), (ii) female parents will contribute at least as much as male parents in alertness (in contrast to males being more vigilant on the breeding and wintering grounds, as mentioned above), and (iii) the young geese hatched in the summer (hereafter referred to as "young") will forage relatively more and engage less in vigilance than their parents. We anticipate that results at this autumn stopover site will correspond to previous studies on goose flocks at their wintering grounds, which found a more equal share of parental care among the sexes for geese bringing young to their winter sites.

Methods

Study area

The Svalbard-breeding Pink-footed Geese stop at the inner part of Trondheimsfjorden (63.7°N, 11.3°E) in Trøndelag, mid-Norway, each year during their autumn migration to wintering areas further south (Madsen *et al.* 1999). The first geese arrive mid-September and commonly stay in the region until late October. In some years, particularly when the snow comes late, flocks may be observed until December. Based on the large proportion of young birds recorded in age counts during field observations, as well as in the recreational hunters' bags, Trøndelag appears to be an important stopover site for families, although non-breeders and adults without young are also present in the flocks (Clausen *et al.* 2017; Gundersen *et al.* 2017). Adults without goslings are a mixture of breeders which failed to raise any young in the current season and sub-adult geese (aged 1–2 years) that have yet to reproduce. The study was conducted in the Levanger municipality, where arable land provides an important stopover area for geese in both spring and autumn (Tombre *et al.* 2008; Madsen *et al.* 2014; Jensen *et al.* 2016b). The main food resource in autumn is spilt grain on harvested cereal fields (Jensen *et al.* 2016a).

Behavioural observations

Geese were observed with a telescope (20 × 60 mm) from a car and, judging by their behaviour, did not seem to be disturbed by the observer. Data were recorded from 24 September–15 October in 2015. When a foraging flock was detected, family groups, pairs and individuals without any obvious family relations were identified. Families were usually found at the outer edges of flocks, as reported for other species of geese in winter (Black *et al.* 1992). Male and female Pink-footed Geese have similar plumage, but males are on average slightly larger (10%) and longer-billed than females (Cramp *et al.* 1977) and sex can therefore be determined on comparing adult birds in pairs, although this was not always easy to detect in the field. The sex of colour-marked individuals was known (having been assessed by cloacal examination when the birds were caught for ringing); otherwise, males were identified as being the largest individual of the pair and by having a thicker neck than the females. The sex for each of the unmarked birds included in the study was determined on members of a pair standing close to each other, when both were in an upright position.

On recording the birds' behaviour, pairs and young were observed continuously for up to 30 min and each bird's activity was recorded on each minute of the scan. At the end of each ≤ 30 min observation period, the edges of the flock were searched and another family or pair without young was selected randomly from those present, for monitoring over the next observation period. On some occasions, observations were of < 30 min because the goose either walked out of sight or flew away. The minimum observation period used in the analyses was of 9 min, following linear regression assessment of observation duration in relation to the percentage time spent on the different behaviours recorded. For observation periods of ≥ 9 min, there were no significant relationships between the length of the observation and the percentage time spent on the different behaviours, indicating that descriptions of each behaviour were not being influenced by the amount of time that the bird was observed. Each minute, the behaviour was recorded and categorised as either: (i) foraging, (ii) alert with head up, (iii) aggression (*i.e.* walking and calling loudly towards other individuals, with neck extended in a threat posture), (iv) resting/sitting/sleeping, (v) preening, or (vi) walking. Prolonged resting periods were not included in this analysis; the flocks observed were foraging in fields, whereas extended periods of rest occurred mainly at the roost. For the minute-by-minute records, walking, preening and resting were grouped into a single "other behaviour" category, giving a total of four behaviour categories ("foraging", "alert", "aggression" and "other behaviour") for the analyses. For each observation period, the number of minutes recorded for each of the four categories was summed and the percentage time spent on each was then calculated.

Aggression was rare and lasted only a few seconds. Hence, in addition to the minute-by-minute behavioural records, all aggressive behaviour was noted whenever it occurred and analysed separately. This was possible because each goose was observed continuously whilst being monitored. The average number of aggressive attacks was then calculated for each observation period; aggression received was not recorded. As there was a positive relationship between the length of the observation period and the total number of aggressive attacks (linear regression: $R^2 = 0.11$, $n = 80$, $P = 0.002$), only observations of > 22 min were used for this analysis (at which point the P value increased to 0.08, n.s.). This behaviour therefore could also be analysed and compared among goose categories for 44 geese, without being significantly influenced by the length of the observation period.

The time of day may affect goose behaviour, so the start times for all observation periods were grouped to the nearest half hour and these were then categorised according to three periods of the day. Autumn daylight in this region gives a time window for observing and identifying geese of between 08:30 h and 19:00 h. Based on this, observations were categorised as morning (09:00–12.00 h), afternoon (12:30–16:00 h) and evening (16:30–19:00 h).

Many flocks were observed during the study period, and data were collected from different areas and fields. Flock size varied from a single family to several thousand birds (Jensen *et al.* 2017). There is a turnover of geese in the region, and they arrive and depart at different dates during autumn migration (Jensen *et al.* 2016a). Although we cannot exclude the possibility that the same goose was observed multiple times, we find it unlikely and presumably it happened only rarely, in an area where several thousand geese foraged on the fields over several weeks. The small number of colour-marked individuals seen and identified by their collar codes were included only once in the study.

Data were sorted and analysed using SAS 9.4. ANOVAs were used to compare variation between the different goose categories (*i.e.* young, and adult geese with and without young) in the percentage time spent on each of the behaviour categories. Given that the percentages were not independent of each other, a separate model was run for each behaviour. When the ANOVA was statistically significant, Tukey's HSD (Honestly Significant Difference) was run as a *post hoc* test to identify which groups differed significantly. Variation in the aggression frequency data (*i.e.* of the number of aggressions recorded for each bird during the 23–30 min observations) were also analysed using ANOVAs, to test for differences in aggression levels among the age and breeding status categories. As behaviours may be affected by the time of day, a general linear model (GLM, Type III Sum of Squares) was carried out to test for the combined effects of goose category and time of day on the percentage time spent on foraging, being alert, and on the interaction of these two behaviour variables.

Results

We observed 256 geese categorised by sex and social group for an average of 21 min (range = 9–30 min; Table 1). The percentage of time that the geese spent on each behaviour, grouped by the different observation periods, is presented in Table 2. For all behaviours recorded, there were no significant differences between female and male parents in the percentage time spent on the different activities (Fig. 1). The parental birds spent significantly less time foraging and more time being alert than their young, and also in comparison with other paired females and males without young (alert: $F_{4,251} = 37.70$, $R^2 = 0.38$, $P < 0.001$; foraging: $F_{4,251} = 19.74$, $R^2 = 0.24$, $P < 0.001$). The time spent on "other behaviour" was similar for all groups ($F_{4,251} = 2.00$, $R^2 = 0.03$, $P > 0.095$, n.s.; Fig. 1). Aggressive behaviour constituted < 2% of the observation periods, and female parents spent significantly more time on this than the young geese ($F_{4,251} = 5.52$,

Table 1. Numbers of Pink-footed Geese observed and whose behaviours were recorded at an autumn stopover site in Trøndelag, mid-Norway. Sample sizes, average duration (± s.e.) and range (in minutes) of the observations are shown for the different categories of geese.

	Sample size	Observation length (average minutes ± s.e.)	Range (min–max)
Parent females	56	21.59 ± 1.0	9–30
Parent males	56	21.66 ± 1.0	9–30
Young	102	21.82 ± 0.8	9–30
Paired females, no young	21	21.38 ± 1.4	9–30
Paired males, no young	21	21.38 ± 1.4	9–30

Table 2. Percentage of time spent on different behaviours by Pink-footed Geese observed at their autumn stopover site in Trøndelag, mid-Norway, grouped according to the observation period for each individual goose. Numbers in parentheses are sample sizes.

Length of observation period (sample size)	Foraging (%)	Alert (%)	Aggression (%)	Other (%)
5–9 min (12)	57.5	21.9	0.0	20.6
10–14 min (60)	40.3	36.1	0.6	23.0
15–19 min (47)	62.1	23.1	0.8	14.1
20–24 min (41)	65.0	17.0	1.0	17.0
25–30 min (103)	61.6	24.3	1.0	13.0

$R^2 = 0.08$, $P < 0.001$; Fig. 1). When all aggressive attacks by individual geese were evaluated (*i.e.* not only those registered each minute), there were no differences between the categories in aggression frequency ($F_{4,43} = 1.06$, $R^2 = 0.10$, $P > 0.39$, n.s.; Fig. 2). Sample sizes were limited, however, so these results should be interpreted with caution.

In the GLM models where both the time of day and the goose category were included, goose category still had a significant effect on the percentage time spent foraging (goose category: $F_{4,8} = 18.63$, $R^2 = 0.28$, $P = 0.0001$; time of day: $F_{4,8} = 2.30$, $R^2 = 0.28$, $P = 0.10$, n.s.; Fig. 3A) and on being alert (goose category: $F_{4,8} = 33.05$, $R^2 = 0.39$, $P = 0.0001$; time of day;

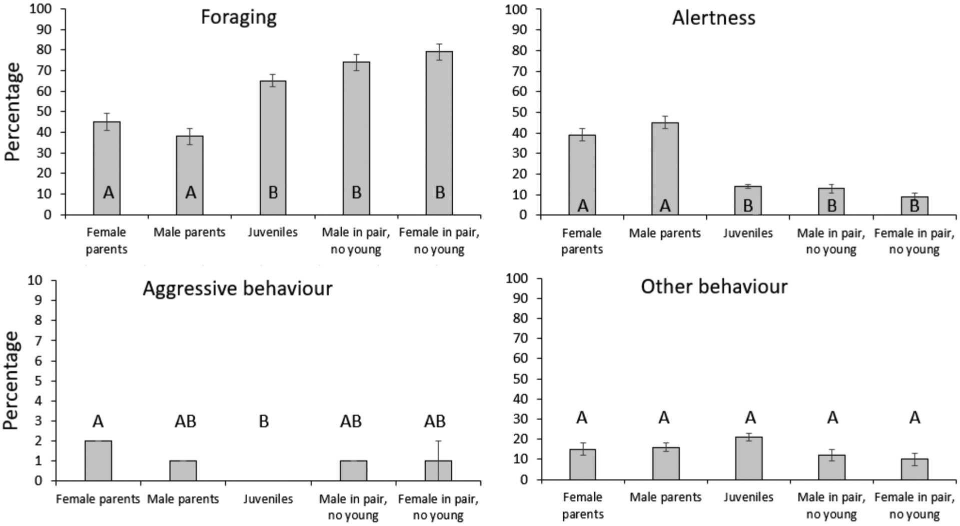

Figure 1. Percentage of time (± s.e. bars) spent by Pink-footed Geese on different behaviours during observations made of flocks on stubble fields at an autumn staging site in central Norway. Letters in/on top of columns are results of Tukey's HSD (Honestly Significant Difference) tests, with different letters illustrating significant differences ($P < 0.05$) between the goose categories for each behaviour. For sample sizes, see Table 1. Note the different scale on the y-axis for aggressive behaviour, and that no aggression by young geese was recorded during the observations.

$F_{4,8} = 0.63$, $R^2 = 0.39$, $P = 0.53$, n.s.; Fig. 3B). Interaction terms between the two factors were not significant (P values > 0.70, n.s.). Regardless of goose category, however, and on including only time of day as a factor, a higher percentage of time was found to be spent foraging in the evening, in comparison with the morning and afternoon (ANOVA: $F_{2,255} = 4.82$, $R^2 = 0.04$, $P = 0.009$; Fig. 3A).

Discussion

Our observations on the behaviour of Pink-footed Geese at Trøndelag in central Norway, an important staging site for the Svalbard-breeding population during both their spring and autumn migrations (Madsen *et al.* 2023), correspond with those reported for geese on their wintering grounds. At sites in Trøndelag the geese build up body stores by foraging on the crops available on farmland, either on pasture and new-sown fields (in spring) or on stubble fields and other harvest remains (in autumn). The region is commonly the birds' first stop on leaving Svalbard, where families with young need to refuel before the onward flight to their wintering areas (Clausen *et al.* 2017). Our study found that, in accordance with our first hypothesis, parent birds invested in their offspring by foraging less and being more alert than

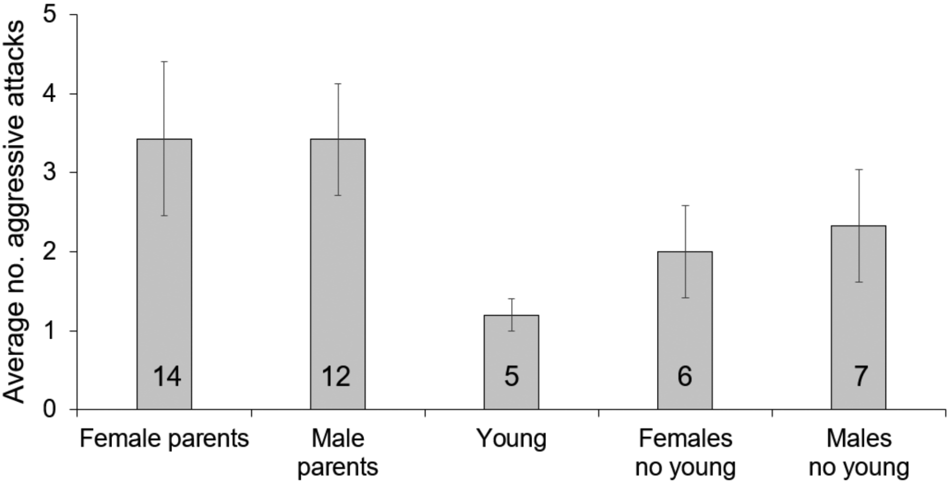

Figure 2. Average number of aggressive attacks observed for different categories of Pink-footed Geese at an autumn staging site in central Norway. Averages are calculated from the total number of aggressive attacks recorded during observations made of each goose observed for 23–30 min. Numbers in columns are sample sizes; vertical lines are ± 1 s.e. bars.

their young, which enabled the latter to feed. Paired adults without young were also found to forage more than parent birds, and this difference in adult behaviour illustrates the continued cost of reproduction (Williams 1966).

Whilst long-lived species such as Pink-footed Geese are expected to have lower investment in their offspring compared to their own survival and future reproduction, parents nonetheless need to balance these activities (Stearns 1992). Sharing the costs of parental care benefits both individuals and offspring in terms of individual body stores and survival. Among geese at Trøndelag, both parents not only showed higher alert behaviour than pairs without young (in support of our first hypothesis), but this effort was made equally by males and females (our second hypothesis). Young birds appeared to benefit, as they spent significantly less time alert as well as more time foraging (our third hypothesis). Prolonged parental care is evident in many waterbirds, and geese may operate as family units in different ways, not only in their foraging activities. For instance, a long-term study of Greater White-fronted Geese *Anser a. albifrons*, found that family size as well as social status (*i.e.* whether single, paired or in a family) affects the timing of migration, with larger families arriving later on the wintering grounds (Gupte *et al.* 2019). This could reflect either the need for longer stopovers *en route* for larger families compared to smaller families and non-breeders or, alternatively, that larger and more dominant families (see Boyd 1953), have a competitive advantage for relatively limited resources at the stopover sites. The family advantages of having a high dominance rank continues during the winter

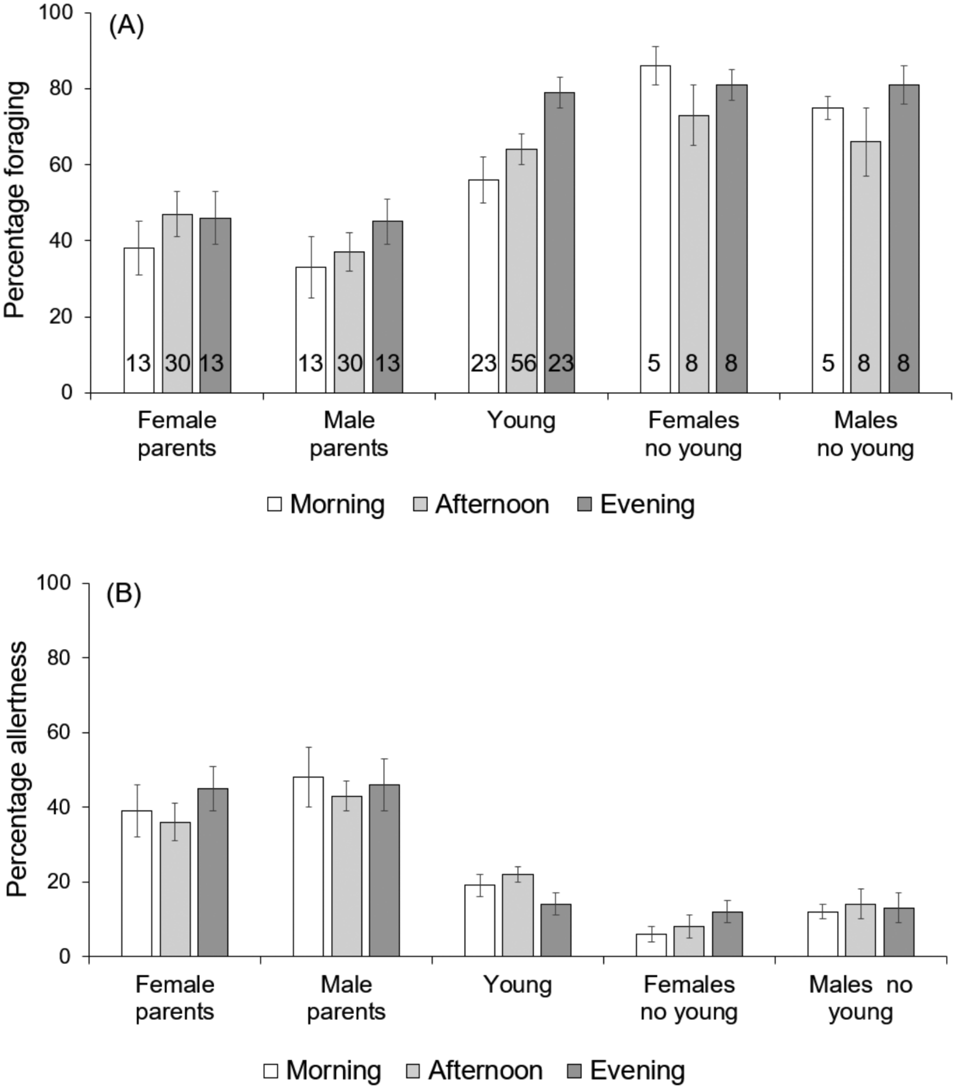

Figure 3. Percentage of time that the different categories of Pink-footed Geese spent on (A) foraging, and (B) alert behaviour, at different times of day. Numbers in the columns on Fig. 3A are sample sizes; vertical lines are ± 1 s.e. bars.

(Black & Owen 1989b) and may also be carried over to increased likelihood of breeding the next summer (Sedinger *et al.* 2011).

Resting could reflect digestive constraints, so more resting might also reflect better foraging conditions. Given the limited sample sizes, however, we were unable to assess whether there is a trade-off between walking, as a sign of poor foraging conditions, and resting, as a sign of good foraging conditions. Differences were found mainly in the time allocated to foraging and being alert. Additionally, parent females spent more time being aggressive than young geese at our study site, whereas aggression by male parents was similar to that recorded for paired birds without young. As such, the female appears to take on additional parental care responsibilities during autumn, as aggression is more usually led by the male on defending his mate and young on the wintering grounds (*e.g.* Black & Owen 1989a,b). This effort, regardless of sex and time of year, will probably pay off in terms of energy intake, with better food patches being secured when conspecifics are chased away, as demonstrated for wintering Barnacle Geese and Dark-bellied Brent Geese *Branta bernicla bernicla*, where families (being more aggressive than pairs and single individuals) gain better access to the food in terms of the best plants available (Black & Owen 1989b; Tinkler *et al.* 2007). On the breeding grounds, Barnacle Goose goslings in larger families have also been shown to grow faster as female parents, being dominant with larger broods, gained access to better foraging areas (Loonen *et al.* 1999).

The behavioural differences between the classes were the same regardless of the time of day. There was an increase in foraging activity in the evening compared to the morning, a typical risk-sensitive behaviour pattern where individuals are willing to take greater risks of predation to secure sufficient energy before a period without food (Stephens & Krebs 1986).

The importance of both members of a breeding pair contributing to vigilant behaviour may be vital, because losing a partner providing such protection may have serious fitness consequences in terms of reduced survival probabilities (Nicolai *et al.* 2012). This illustrates the importance of being alert and hence providing extra time for the partner or young to forage. Sharing costs equally between the sexes in a period where both can allocate time for this – *i.e.* outside the breeding season, when there are more sex-specific roles – will therefore be an advantageous strategy for the parents.

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Photograph: Pink-footed geese on a stubble field during autumn migration in Norway, by Kjell Heggelund.