

Time allocation in Canada Geese during the breeding season

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The effect of breeding status and sex on time allocation in Canada Geese *Branta canadensis* during the breeding season was studied in 1988 in central Sweden. Time budgets were established during four parts of the breeding season: on the breeding grounds before egg-laying, during incubation, when the goslings were newly hatched and when the goslings were fledged or nearly fledged. Most differences in time allocation between categories and sexes were due to differences in energetically costly processes and in the demands of other types of behaviour than foraging, mainly vigilance. Prior to nesting, there were indications that the use of reserves could be important, at least for breeding females. The allocation of time to foraging prior to and during the moult by non-breeding geese suggested that during the moult they relied on energy reserves gained in the preceding period. Vigilance was the most common behaviour for breeding geese after the goslings had hatched. During the early brood-rearing period, breeding females showed a weak tendency to be less vigilant and spend more time foraging than breeding males, though these differences were not statistically significant. When the goslings were fledged or nearly fledged, the time allocation of breeding females and males was almost identical. The proportion of time spent on vigilance by geese with goslings was not significantly correlated with the brood size.

1. Introduction

Most of the recent studies on the time budgets of different goose species have covered only a small portion of the breeding season, e.g. before or during spring migration (McLandsress & Raveling 1981a, Fox & Ridgill 1985, Madsen 1985, Gauthier et al. 1988), on breeding grounds before egg-laying (Fox & Madsen 1981), during incubation (Aldrich & Raveling 1983, Thompson & Raveling 1987), and during brood rearing (Lazarus & Inglis 1978, Giroux et al. 1986, Les-

sells 1987, Sedinger & Raveling 1988, 1990, Eberhardt et al. 1989). To my knowledge, time budgets covering the whole breeding season have not been reported, but see Harwood (1977) for figures on the feeding behaviour of Lesser Snow Geese (*Anser c. caerulescens*).

Time and energy allocation during the breeding season can in general be expected to greatly influence reproductive success (King 1974). Time allocation can thus be expected to reflect the energetic and behavioural needs and restrictions that an individual experiences in a given situation.

In geese, migration, egg formation, incubation, wing moult and growth are assumed to be energetically or nutritionally costly (Ankney 1979, Raveling 1979a, Owen 1980, Sedinger 1986) and therefore to require much foraging or use of body reserves. These demands show clear temporal patterns during the breeding season, but differ between the sexes in breeding geese and between breeding and non-breeding individuals.

In order to examine the variation of time allocation within a species and especially the effect of breeding status and sex on time allocation in Canada Geese *Branta canadensis* during the breeding season, I determined time budgets during four parts of the breeding season. Non-breeding geese were included to contrast the demands associated with breeding (cf. Lazarus & Inglis 1978). At the breeding grounds prior to nesting and during incubation, breeding female geese largely use reserves gained at the wintering or staging grounds (Newton 1977, McLandress & Raveling 1981b, Thomas 1983, Murphy & Boag 1989). This reliance on reserves is probably due to low food availability at the breeding grounds prior to nesting (cf. Newton 1977). During this period, breeding females can thus be expected only to allocate as much time to foraging as non-breeders. Breeding males can be expected to spend much time on vigilance in order to protect the females and nesting places. It is thus likely that breeding males spend less time foraging than any other category of geese at the breeding grounds prior to nesting (Fox & Madsen 1981, Gauthier & Tardif 1991).

During incubation, females spend very little time off the nest (Aldrich & Raveling 1983, Thompson & Raveling 1987). Breeding males of many goose species guard their females and can thus be expected to spend more time on the alert and less time foraging than non-breeders.

When the goslings are newly hatched, both parents can be expected to spend much time on vigilance (Harwood 1977). Breeding females, however, are probably forced to allocate more time to foraging than breeding males, to compensate for their weight loss during incubation (Harwood 1977, Raveling 1979a, b, Aldrich & Raveling 1983). This possibly also restricts the time available for vigilance for breeding females

(cf. Sedinger & Raveling 1990). Non-breeders moult during this period and can thus be expected to spend much time foraging, to fulfil their increased energy and nutrient demands.

As the goslings grow older, the parents can be expected to differ less in their time allocation, since their energetic and behavioural demands differ less (Sedinger & Raveling 1990). The vigilance of the parents may be supposed to be the unshared fixed-loss type of parental investment (Lazarus & Inglis 1986). The proportion of time spent on vigilance by the parents can thus be predicted not to vary with brood size. The goslings can be expected to spend most time foraging and little time on vigilance.

2. Methods

2.1. Study area and population

The data were collected in 1988 in an area of central Sweden (63°N, 18°E) consisting of about 40 lakes, varying in size from 0.05 to 5.0 km². The lakes are generally oligotrophic, with sparse stands of mainly *Phragmites*, *Carex* and *Equisetum* along the shores. Most lakes are partly surrounded by arable land or pastures. At least 46 pairs of Canada Geese were breeding in 1988, and the population consisted of approximately 250 individuals. A large part of the Canada Goose population was previously marked with neck bands with individual codes. Marking also took place in late July 1988.

The data were collected from four parts of the breeding season: before egg-laying (end of April), during incubation (mid-May), when the goslings were newly hatched (beginning of June) and when the goslings were fledged or nearly fledged (mid-August). The onset of the wing moult in breeding Canada geese occurs about 3–4 weeks after the goslings have hatched (Owen 1980). This means that for this population, the onset of wing moult occurs in the beginning of July and the adults reach the flying stage in the second half of August. The non-breeding geese start the wing moult 2–4 weeks before the breeders, i.e. in the beginning of June, and reach the flying stage at the end of July (Owen 1980). There were no indications of any moult migra-

tions by non-breeders, although during the moult they aggregated to some extent in the larger lakes within the area. The onset of the southward migration varies, but both breeders and non-breeders remain in the area at least until September.

2.2. Time-budgeting

Time-budget data were collected by instantaneous scan sampling (Altmann 1974). The behaviour of all observable individuals in a lake was scanned at a constant interval during a scanning period. Each individual goose observed in a scan, thus, gave one behavioural record. The interval used between each scan was as short as possible (1–6 minutes). Each scanning period used in the analysis consisted of a minimum of 10 scans and lasted for a maximum of 60 minutes. The scanning periods were evenly spread during daylight for each individual or group of individuals. The birds were observed at a distance with a spotting scope (20-60X), and the following types of behaviour were recorded; “foraging”, “alert” (also termed vigilant, equivalent to extreme head-up position), “resting” (not engaged in any other activity, i.e. sleeping, head up), “comfort” (preening, bathing and some social behaviour), “locomotion” (swimming, walking or flying), “incubating”, “aggression”, “honking” or “drinking”. Aggression, honking and drinking were all rare and were pooled in the further analysis as “other behaviour”.

During the three first parts of the breeding season, time budgets were established for both breeding and non-breeding adults. During the fourth part of the breeding season, adults with goslings and their goslings were the only categories included in the time budget sampling. A systematic search was made for nests and the designation of breeders and non-breeders for April and May was based on whether or not the female in a pair was observed incubating in May. In June, the classification was mainly based on whether or not the adults had any goslings. Marked individuals known to have failed in breeding were not included as non-breeders. As only a few (2) marked non-breeding males in May and non-breeding females in June (1) could be included in the time-budgeting, data from ob-

servations of non-breeding geese were not broken down by sex in May and June. Unmarked non-breeding geese were also included in the analyses for these parts of the season. It is thus possible that some failed breeders were included among the unmarked geese and wrongly labelled as non-breeders, especially in June. The time budget records from unmarked geese were, however, summed for each lake and thereafter treated as if they represented the proportion of time allocated to the different types of behaviour by one individual. The bias stemming from a failed breeder classified as non-breeder would thus be less severe. In April and August, only individually marked geese were included in the analysis. Determination of the sexes was done by cloacal examination during marking (cf. Owen 1980).

2.3. Statistical analyses

For the statistical analysis of differences in time allocation between goose categories and sexes, the behavioural records for each individual goose during all the scanning periods were summed for each part of the season. This gave a percentage value for each type of behaviour for each individual during each part of the season. These individually based percentage values form the base for the statistical analyses. The data from unmarked geese in May and June could not, however, be summed at the level of individuals, but were summed for each lake and then treated as if they were the proportional time allocation of one individual. The Student-Newman-Keuls test was used for multiple comparisons of the proportion of time allocated to each type of behaviour within each part of the season ($\alpha = 0.05$). For these analyses the proportion of time allocated to each type of behaviour by each individual (or lake) was arcsine-transformed (Zar 1984). The effect of brood size on the proportion of time spent on the alert, during early and late brood rearing, was tested with Spearman's rank correlation. The data for these analyses were summed for each breeding individual within the early and the late brood-rearing periods. In all pairs both parents were present. In the early brood-rearing period, the goslings were estimated to be approximately one

week old and during the late period they were between 8 and 10 weeks old. The effect of brood size was also analysed without dividing the brood-rearing season into two portions. As some pairs were observed during both brood-rearing periods and some of these pairs lost goslings during the season, only data from one of the periods were used in these correlation analyses. The period with the largest time-budget samples was chosen for each individual (i.e. the brood-rearing period with most scans). In all the statistical analyses each individual appears only once during each part of the season. All tests were performed using the SAS statistical package (SAS Institute Inc. 1985).

In total, 19 334 records (number of scans times the number of geese in each scan) were

used in the analysis, stemming from 398 goose hours (75 hours of observation). The distribution of the records over the parts of the season, categories and sexes is detailed in Table 1.

3. Results

During all periods, there were differences between goose categories and sexes in the amount of time allocated to different types of behaviour. The mean percentage (not arcsine-transformed) of time allocated to each type of behaviour by each category and sex is presented in Table 1. The three most common types of behaviour (foraging, on the alert and resting) exhibited the largest variation between categories and among seasons.

Table 1. Time budgets of Canada Geese during the breeding season. Mean percentage of time devoted to different behaviour. Means of behaviour types with the same letter are not significantly different ($P > 0.05$, Student-Newman-Keuls test). Bm = breeding males, Bf = breeding females, Nbm = non-breeding males, Nbf = non-breeding females, Nb = non-breeding (both sexes), Gosm = gosling males and Gosf = gosling females. Sample size (N = number of individuals in all situations except for non-breeders in May and June, where N stands for the number of marked individuals plus the number of lakes with pooled samples of unmarked individuals (see also main text)) and the number of records (number of scans times the number of geese in each scan) are provided for each row.

	Foraging	Alert	Resting	Comfort	Locomotion	Others	N	Records
April (pre-nesting)								
Bm	12.0 a	32.4 a	34.4 a	6.4 a	10.3 a	4.5 a	3	208
Bf	31.1 b	11.6 b	37.7 a	4.9 a	11.6 a	3.1 a	4	301
Nbm	39.2 b	18.8 b	18.3 a	6.5 a	15.9 a	1.4 a	15	701
Nbf	47.0 b	15.8 b	15.2 a	4.0 a	18.1 a	0.0 a	7	313
May (incubation)								
Bm	20.4 a	31.1 a	22.7 a	11.6 a	13.7 a	0.5 a	5	991
Bf*	0.1 b	0.0 b	0.0 b	0.4 b	0.0 b	0.0 a	5	991
Nb	52.7 c	20.4 a	4.7 c	6.7 a	12.3 a	3.3 b	8	2459
June (early brood rearing)								
Bm	21.5 a	58.3 a	1.9 a	6.8 a	8.9 a	2.7 a	6	1221
Bf	34.3 a	44.6 a	3.0 a	5.8 a	9.9 a	2.3 a	6	1211
Nb	30.2 a	24.3 b	7.7 a	23.3 b	13.5 a	1.0 a	9	3670
August (late brood rearing)								
Bm	13.6 a	51.3 a	3.8 a	12.6 a	18.1 a	0.6 a	8	1361
Bf	14.3 a	47.7 a	4.6 a	13.1 a	19.8 a	0.6 a	8	1354
Gosm	29.7 b	9.5 b	19.2 b	23.8 a	17.8 a	0.0 b	16	2859
Gosf	37.7 b	9.0 b	18.2 b	14.8 a	20.2 a	0.0 b	8	1694

*In May, breeding females spent 99.5% of their time incubating.

3.1. Pre-nesting period

Breeding females did not spend more time foraging than non-breeding geese. Breeding males spent significantly more time on vigilance than on all other categories and also spent least time foraging.

3.2. Incubation period

Only one very short recess was observed for one of the incubating females. Breeding males spent most of their time on vigilant behaviour in May and they spent less time foraging than non-breeders. Although they had not yet started their wing moult, non-breeders actually spent more than twice as much time foraging as breeding males.

3.3. Early brood-rearing period

In June, after incubation, both breeding sexes were significantly more vigilant than non-breeders. Breeding males were, however, not significantly more vigilant than breeding females and the proportion of time spent foraging did not differ between any category. The proportion of time spent on vigilance by breeding geese did not show any significant correlation with brood size (for breeding males $r_s = 0.03$ $P = 0.95$ $n = 6$ and for females $r_s = 0.46$ $P = 0.36$ $n = 6$, brood sizes ranged from 1 to 3).

3.4. Late brood-rearing period

In August, the time allocation did not differ between the sexes in the breeders. The breeders spent most time on vigilance. No significant correlation was found between the proportion of vigilance and brood size (for breeding males $r_s = 0.24$ $P = 0.56$ $n = 8$ and for breeding females $r_s = 0.09$ $P = 0.83$ $n = 8$, brood sizes ranged from 1 to 5). The goslings spent much time foraging and little time on vigilance.

The proportion of time spent on vigilance by breeding geese did not show any significant correlation with brood size even when the brood-

rearing periods were pooled (for breeding males $r_s = 0.08$ $P = 0.83$ $n = 10$ and for breeding females $r_s = 0.18$ $P = 0.62$ $n = 10$, brood sizes ranged from 1 to 5).

4. Discussion

Although egg-laying and incubation are energetically and nutritionally very costly (Ankney & MacInnes 1978, Raveling 1979a,b, Fox & Ridgill 1985), breeding females did not spend more time foraging than non-breeders. The storage of lipids and protein by Canada Geese at the wintering and spring staging areas has been found adequate to cover the energy and nutrient requirements (perhaps except for minerals) and egg formation (Ankney & MacInnes 1978, Raveling 1979a,b, McLandress & Raveling 1981b). In this study, the breeding geese in the pre-laying period probably relied on reserves gained at the wintering grounds (Southern Sweden, Denmark or Northern Germany) or the staging grounds. The large proportion of time allocated to resting, especially by the breeders, may also indicate that foraging was not very profitable during this period. Herbers (1981) actually suggested that when foraging is very unsuccessful and costly, a large amount of time should be spent resting rather than foraging (cf. Lundberg 1985).

Prior to nesting, breeding males were the most vigilant of all the categories. The vigilance of the males during this period is probably mostly devoted to guarding the females and nesting sites (Mineau & Cooke 1979, Fox & Madsen 1981). Guarding of females can help to prevent extra-pair copulations (Mineau & Cooke 1979, McKinney et al. 1983) and to enable the females to spend more time foraging (Harwood 1977, Fox & Madsen 1981, Gauthier & Tardif 1991). Guarding of nesting places may also prevent or diminish nest parasitism or safeguard food supplies (Inglis 1976, Mineau & Cooke 1979, Quinn et al. 1987).

During the incubation period, the non-breeders spent much time foraging. Their forthcoming moult, entailing high energetic and/or nutritional demands may explain this observation. Later in the season (in June), when the non-breeders were

moulting their remiges or just about to moult, the time spent foraging by them was similar to that spent by the breeders. Non-breeders thus appeared to gain much of the extra food needed for the moult before its onset. This might be a profitable strategy for lowering the risk of predation during a critical period of the year.

In June, both sexes in the breeders allocated more time to vigilance than non-breeders. This could be expected when the goslings are newly hatched and benefit from guarding against predation (Harwood 1977, Sedinger & Raveling 1990). Vigilance can thus be regarded as parental investment in the brood for Canada goose parents (Lazarus & Inglis 1986). There was no significant correlation between vigilance and brood size, as predicted if parental investment is of the unshared fixed-loss type (Lazarus & Inglis 1986). The sample size was rather small, however, and the probability of getting a significant correlation correspondingly low. Sedinger & Raveling (1990) recently found alertness in Cackling Canada Geese males to be positively related to brood size.

Breeding females did not spend significantly more time foraging and less time on the alert than breeding males. The sample sizes were probably too small, however, and the individual variation too large to allow us to draw any conclusions from this lack of significance.

During the late brood-rearing season, the breeders did not show any tendency to differ in their time allocation. By this time, breeding females seem to have compensated for their depleted body reserves. Both adults and juveniles spent more time moving in August than in the early brood-rearing period, perhaps searching for food of high quality. Eberhardt et al. (1989) found that broods that foraged on fertilized pastures spent less time moving and more time resting than did broods that used only native plant communities. Food quality has been found to decrease in the late breeding season for Lesser Snow geese (Harwood 1977) and for cackling Canada geese (Sedinger & Raveling 1986).

In conclusion, there were large differences in the time allocation of the different categories and sexes of Canada Geese during the breeding season. The time allocation of Canada Geese seems to reflect trade-offs between energetically costly

processes and the demands of other types of behaviour than foraging. Vigilance proved to play an important role in the time budgets of breeding geese. The use of nutrient reserves, though not measured, probably allowed allocation of time to other types of behaviour than foraging.

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Sammanfattning: Tidsallokeringen hos kanadagäss

Effekten av häckningsstatus och kön på tidsallokeringen hos kanadagäss studerades under häckningsäsongen 1988 i centrala Sverige. Tidsbudgetdata insamlades under fyra delar av häckningsäsongen; innan äggläggning, under ruggningen, då gässlingarna var nyckläckta och då de var flygga eller nästan flygga.

De flesta skillnaderna i tidsallokering mellan kategorier (häckande eller icke häckande aduler samt gässlingar) och kön kan sättas i samband med skillnader i energetiskt kostsamma processer samt kraven på andra beteenden än furagering, framförallt alerthet. Tidsallokeringen innan häckningen antyder att nyttjandet av energireserver kan vara viktigt för de häckande honorna under denna period. Andelen tid allokerad till furagering före och under ruggningen hos de icke häckande gässen antyder att de under ruggningen litar till reserver de lagrat under perioden innan.

Då gässlingarna kläckts fram ägnade de häckande gässen mesta tiden till alerthet. Under den första perioden av vallningen av gässlingarna visade de häckande honorna en svag tendens att vara något mindre alerta och furagera mer än hanarna, dessa skillnader var dock inte statistiskt signifikanta. När gässlingarna var flygga eller nästan flygga var tidsallokeringen hos de häckande honorna och hanarna näst intill identisk. Andel tid ägnad åt alerthet hos gäss med gässlingar var inte signifikant korrelerad med kullstorleken.

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