

Time budgets of Snow Geese *Chen caerulescens* and Ross's Geese *Chen rossii* in mixed flocks: implications of body size, ambient temperature and family associations

JÓN EINAR JÓNSSON^{1,2*} & ALAN D. AFTON³

¹*School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA*

²*Present address: University of Iceland, Snæfellsnes Research Centre, Hafnargata 3, 340 Stykkishólmur, Iceland*

³*United States Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, LA 70803, USA*

Body size affects foraging and forage intake rates directly via energetic processes and indirectly through interactions with social status and social behaviour. Ambient temperature has a relatively greater effect on the energetics of smaller species, which also generally are more vulnerable to predator attacks than are larger species. We examined variability in an index of intake rates and an index of alertness in Lesser Snow Geese *Chen caerulescens caerulescens* and Ross's Geese *Chen rossii* wintering in southwest Louisiana. Specifically we examined variation in these response variables that could be attributed to species, age, family size and ambient temperature. We hypothesized that the smaller Ross's Geese would spend relatively more time feeding, exhibit relatively higher peck rates, spend more time alert or raise their heads up from feeding more frequently, and would respond to declining temperatures by increasing their proportion of time spent feeding. As predicted, we found that Ross's Geese spent more time feeding than did Snow Geese and had slightly higher peck rates than Snow Geese in one of two winters. Ross's Geese spent more time alert than did Snow Geese in one winter, but alert rates differed by family size, independent of species, in contrast to our prediction. In one winter, time spent foraging and walking was inversely related to average daily temperature, but both varied independently of species. Effects of age and family size on time budgets were generally independent of species and in accordance with previous studies. We conclude that body size is a key variable influencing time spent feeding in Ross's Geese, which may require a high time spent feeding at the expense of other activities.

Keywords: alertness, peck rates, energetics, foraging, predation, social behaviour, waterfowl.

Time budgets often vary among and within species (Guillemain *et al.* 2002, Jeschke & Tollrian 2005). Proportion of time spent feeding is generally inversely related to time spent resting, whereas time spent in other activities is usually similar among waterfowl species (Paulus 1988). Alert behaviour and time spent feeding are often considered mutually exclusive activities (Öst *et al.* 2002). Most animals forage until they experience satiation and spend less time handling than digesting a food item (Jeschke *et al.* 2002). In

contrast to feeding, digestion is a passive process that does not prevent animals from pursuing other activities, such as searching for food (Jeschke & Tollrian 2005).

Small body size places important physiological limitations on birds, all of which potentially influence time budgets. The rate of heat loss increases with decreasing body size because of increasing surface-to-volume ratio (Goudie & Ankney 1986, Calder 1996), and mass-specific metabolic rate is inversely related to body mass (Kendeigh 1970, Calder 1996). Gut size scales linearly with body size and partly determines the rate of energy extraction from food (Demment &

*Corresponding author.
Email: joneinar@hi.is

Van Soest 1985), and larger species generally have greater fasting endurance than do smaller species (Goudie & Ankney 1986, Calder 1996). These relationships form the basis of the body-size hypothesis, which has been proposed to explain interspecific relationships between body size and behaviour, such as incubation constancy in birds (Skutch 1962, Afton 1980, Afton & Paulus 1992, Jónsson *et al.* 2007). This hypothesis predicts that body size directly affects time spent feeding or forage intake rates via these energetic processes (Calder 1996, Gloutney *et al.* 2001).

Body size also interacts with social status and social behaviour, both of which directly influence foraging effort and intake rates (cf. Jarman's hypothesis; Jarman 1974). Moreover, smaller species generally are more vulnerable to predator attacks than are larger species (Krause & Ruxton 2002). However, smaller species may respond to predation pressure by forming mixed flocks with larger species, which reduces the success of predator attacks (Kristiansen *et al.* 2000, Randler 2004). Multi-species associations may be costly to smaller species if larger species are socially dominant and expel small species from foraging patches (Kristiansen & Jarrett 2002, Jónsson & Afton 2008).

The closely related Ross's Goose *Chen rossii* and Lesser Snow Goose *Chen caerulescens caerulescens* (hereafter Snow Geese) commonly nest together and form mixed flocks on wintering areas (Weckstein *et al.* 2002, Jónsson & Afton 2008). Ross's Geese are approximately two-thirds the size of Snow Geese and thus have higher mass-specific metabolic rates (expressed as kJ/day/kg; Calder 1996). Because of this size difference and sympatry throughout their life cycles, the two species have been the focus of comparative studies on the effects of body size on behaviour and physiology (see Jónsson *et al.* 2007, Jónsson & Afton 2008 and citations therein).

Spacing behaviour (i.e. territoriality, resource defence or aggressive behaviour) during the non-breeding season can vary with species, habitat, social status and predation pressure (Newton 2004). Most geese have a family social system in which family units are maintained from the end of one breeding system to the start of the next (Boyd 1953, Raveling 1970, Pevett & MacInnes 1980, Gregoire & Ankney 1990). Social status generally correlates with family size in geese (Loonen *et al.* 1999, Stahl *et al.* 2001, Kalmbach 2006), and family size generally affects time budgets (Austin 1990, Bélanger & Bédard 1992, Loonen *et al.* 1999). Snow Geese generally maintain families throughout winter (Pevett & MacInnes 1980, Williams *et al.* 1994), whereas Ross's Geese are unusual

among geese in that they rarely maintain families after autumn migration (dense-flock type social system; Johnson & Raveling 1988, Jónsson & Afton 2008).

Periods of cold temperatures impose energetic demands on birds (Bennet & Bolen 1978, Newton 1998, 2007). Larger birds have relatively more reserves and thus devote a smaller proportion of their daily energy intake to maintaining their basal metabolic rate (BMR) during cold periods (Aschoff & Pohl 1970; see also Newton 1998). Birds often increase time spent feeding with declining ambient temperatures until temperatures drop below 0 °C, at which point the costs of foraging may outweigh the benefits (Goudie & Ankney 1986, Newton 1998). In harsh environments, smaller species generally feed for greater portions of the day ($\geq 80\%$) to maintain their BMR and thus may be relatively less able to adjust their feeding budgets in response to declining temperatures (Goudie & Ankney 1986; see also Systad *et al.* 2000, Systad & Bustnes 2001). However, because of the mild winter conditions on our study site in southwest Louisiana and the low proportion of time spent feeding by wintering geese (often 13–40%; Paulus 1988, Davis *et al.* 1989), we expected that both species would increase time spent feeding with declining ambient temperatures. However, we predicted that Ross's Geese would alter their behaviour at higher temperatures than would Snow Geese, because of their higher lower critical temperature (LCT; the lowest ambient temperature at which a thermoregulatory animal maintains basal metabolism while at rest; Aschoff & Pohl 1970). Ross's Geese have an average LCT of around 6 °C whereas Snow Geese have an average LCT of around 2 °C.

Alert behaviour may be selfish or directed towards benefits for social allies (Squires *et al.* 2007). Time spent in alert behaviour is positively correlated with brood size in waterfowl (Forslund 1993, Williams *et al.* 1994), presumably because larger broods are more attractive targets for predator attacks. McWilliams *et al.* (1994) suggested that their smaller size made Ross's Geese more vulnerable to avian predation than are Snow Geese. In mixed flocks we assumed that both species were subject to an unknown but similar amount of predation pressure.

Although many investigators have analysed animal time budgets, relatively few have made interspecific comparisons (Jeschke & Tollrian 2005). We estimated time budgets of Snow Geese and Ross's Geese wintering in Louisiana and tested predictions based on the body-size hypothesis. We assessed whether Ross's Geese spent relatively more time feeding, had relatively

higher peck rates, spent more time in predator detection or responded to declining temperatures earlier than do larger Snow Geese.

METHODS

We collected data on Snow Geese and Ross's Geese wintering in the rice-prairies of southwest Louisiana from 10 November to 20 February of winters 2002–03 and 2003–04 (see also Jónsson & Afton 2006, 2008). We observed mixed flocks of these geese using non-flooded rice-fields (see also Alisauskas *et al.* 1988) adjacent to and directly north of Lacassine National Wildlife Refuge (NWR; 29°55'N, 92°50'W) and Cameron Prairie NWR (29°57'N, 93°04'W). The study area has been described in detail elsewhere (Alisauskas *et al.* 1988, Jónsson 2005). We obtained daily minimum, average, and maximum temperatures for November to February 2002–03 and 2003–04, from Lake Charles, Louisiana (Louisiana Office of State Climatology 2005).

Behavioural observations

Three observers and J.E.J. collected time budget data; J.E.J. trained and tested all observers prior to data collection to minimize observer variation (Jónsson & Afton 2006). Observers used spotting scopes with 20× magnification and collected 5- to 10-min focal sampling observations, alternating between species. Duration of observations varied because focal birds walked behind levees, other birds or vegetation or moved into holes or tractor tracks and, thus, were lost from sight. Lehner (1996; pp. 192–194) discussed out-of-sight time in focal sampling. We opted for a minimum 5-min sampling period (50% of the designated 10-min observation period) following Afton (1993). Our sampling periods were the experimental units. We believe that relatively short observations did not bias our findings, and their distribution did not differ much between species. For Snow Geese, 64% of all observations were for the full 10 min, and an additional 20% were between 7 and 10 min. For Ross's Geese, 52% of all observations were for the full 10 min, and an additional 30% were between 7 and 10 min. Time spent in each activity was expressed as proportions and the duration of the observations was therefore not a factor in the analyses.

Sequences of 20 random numbers were used to select focal geese within a field of vision, counting from left or right until a goose was located that corresponded to each random number. Observations

were made during daylight hours, between 8:00 h and 17:00 h. We attempted *a priori* to control for variation due to time of day via even sampling across time to ensure that comparisons between species were unbiased (Jónsson & Afton 2006); both species were sampled equally during mid-day hours (11:00–13:00 h), when geese tended to cease activities and rest (Paulus 1988).

Prior to each observation, we assigned age classes (adult or juvenile) to birds based on plumage colour (Ryder & Alisauskas 1996, Mowbray *et al.* 2000). Pairs and families were identified by mutual participation in social encounters, mutual chasing or avoiding other geese, and coordinated directions of locomotion (Raveling 1970, Stahl *et al.* 2001). We grouped focal individuals into five groups of social status (Boyd 1953): lone adults, parents, paired non-parents, juveniles in families, and lone juveniles (see Jónsson & Afton 2008 for detailed descriptions of social classes).

Behaviour was recorded continuously during focal sampling periods (Altmann 1974, Jónsson & Afton 2006), noting all changes in individual behaviour, using an Apple Newton Messagepad 2000 (Apple Computer Inc., Cupertino, California) equipped with ETHOSCRIBE software (Tima Scientific, Sackville, New Brunswick, CA, USA). When flocks under observation flushed (either leaving the site or landing again after a few minutes), observers did not resume sampling for at least 10 min (Jónsson 2005). During the two winters, we sampled time budgets of 707 Snow Geese (546 adults and 161 juveniles) and 624 Ross's Geese (554 adults and 70 juveniles) (see also Jónsson & Afton 2008).

Time budgets

Behavioural activities were recorded as feeding, resting, locomotion (walking or swimming), alert, social interactions and other activities (Table 1). We chose this classification to test our predictions based on the body-size hypothesis. Studies of foraging geese often select flocks that are foraging and ignore flocks that are mostly sleeping or preening (Gregoire & Ankney 1990, Stahl *et al.* 2001). However, such studies usually focus on a single species with a view to comparing behaviour among different habitats or parts of the annual cycle. We occasionally observed Ross's Geese foraging actively among sleeping Snow Geese (J.E. Jónsson & A.D. Afton pers. obs.); thus, time spent feeding would have been underestimated for Ross's Geese if only foraging flocks had been sampled.

Table 1. Classification and definitions of behavioural activities (Black & Owen 1989b, cf. Gauthier *et al.* 1984, Ganter & Cooke 1996) for Snow Geese and Ross's Geese observed in southwest Louisiana.

Feeding was a combination of three types of foraging activities:

Grubbing: goose dug for below-ground plant parts, removed mud with bill, softened mud with feet, and ingested bulbs and rhizomes. Food was ingested; thus, time spent grubbing was included in calculations of peck rates.

Grazing: goose picked up and ingested above-ground plant material, treaded to break water surface with bill, or washed a plant part. Food was ingested; thus, time spent grazing was included in calculations of peck rates.

Searching: displacements with head lowered and bill pointed toward the ground, looking for digging sites or food. No food was ingested; thus, time spent searching was not included in calculations of peck rates (see Methods).

Alert: goose was standing upright with head raised high.

Locomotion was a combination of two activities:

Walking: goose changed locations on foot with head raised.

Swimming: goose moved on water surface.

Inactive (reference activity in generalized linear models):

Social interactions: goose directed social displays at other geese.

Resting: goose sat or stood, with bill tucked under wing, or completely still with head upright, not moving, either awake or sleeping (eyes closed).

Other: activities that were not described above, including drinking, preening, and comfort activities.

Observations of marked individuals may be logistically possible when working with populations with restricted distributions, such as Barnacle Goose *Branta leucopsis*, where up to 70% of all individuals are individually marked (Stahl *et al.* 2001, Black *et al.* 2007). However, a large-scale banding and marking approach was unrealistic for our behavioural study because of the large number (250 000–400 000) of lightweight geese wintering in southwest Louisiana (Mowbray *et al.* 2000); thus, we could not readily find and observe marked pairs or families. Moreover, Ross's Geese were difficult to capture in southwest Louisiana; we caught 1134 Snow Geese but only 5 Ross's Geese for a banding study in the same study area (Jónsson 2005). Unfortunately, capturing large portions of the entire population of Snow and Ross's Geese (comprising 6 million birds; Abraham *et al.* 2005) is logistically difficult and therefore, we could not restrict our observations of social behaviour to marked families.

Peck rates and alert rates

Grazing geese can compensate for reduced foraging time by increasing intake rates (also termed peck rates; Owen 1972). It is therefore useful to compare intake rates between groups when studying time spent feeding (see Gloutney *et al.* 2001). We tested our predictions about intake rates by recording peck rates and assumed that this response variable was an appropriate index of actual forage intake rates (Quinn *et al.* 2006, see also Sol *et al.* 1998). Peck rate is a useful variable for measuring intake rate

because when peck quality and quantity are constant, peck rate correlates positively with intake rate (Prop & Deerenberg 1991, Fox *et al.* 1998, Sol *et al.* 1998). Peck rates were calculated as the number of pecks per minute of observation.

We tested our predictions about alertness by recording the number of times focal birds assumed an alert position per minute (hereafter alert rates). We compared alert rates to determine whether the two species differed in vigilance, as it was assumed that alert rate was directly proportional to general wariness.

Statistical analyses

Other observations indicated that Snow Geese were relatively more likely to maintain families than were Ross's Geese (Jónsson & Afton 2008). For analysis, we ranked lone adults, parents, paired non-parents, juveniles in families, and lone juveniles in the analysis as follows: 1 = lone bird, 2 = pair, 3 = parents + 1 juvenile, 4 = parents plus ≥ 2 juveniles. The number of juveniles in a family ranged from one to four in Snow Geese and one to three in Ross's Geese. Ross's Geese in families were categorized as one group (family size ≥ 3) and Snow Geese as two groups (family size = 3, and family size ≥ 4) (see Jónsson 2005 for details). Thus, we modelled family size as a nested effect in all analyses because the number of groups differed between species. Specifically, we nested family size within the species*age interaction to test the hypothesis that family size acted differentially within age groups and/or within each species; if this term was significant, it was kept in the model

for interpretation. Otherwise, the analysis was repeated twice, nesting family size within species, to test the hypothesis that family size differentially affected time budgets of the two species, independent of age, and then nesting within age group, to test the hypothesis that family size differentially affected time budgets of age groups, independent of species.

Generalized linear models (PROC GENMOD; SAS Institute 1999) were used to examine variation in time budgets, peck rates and alert rates between (1) Snow Geese and Ross's Geese, (2) adults and juveniles, and (3) lone birds, pairs, and birds in families. Separate models were constructed for each winter because we knew *a priori* that family units were more common in winter 2003–04 than in winter 2002–03 (Jónsson & Afton 2008) and that winter 2002–03 was cooler than winter 2003–04 (Louisiana Office of State Climatology 2005). Generalized linear models were chosen because they allow comparisons of goodness of fit (GOF tests) between models based on several distributions, rather than using non-parametric tests. The structural form of the best fitting model describes associations and interactions, as well as estimating means of the response distribution (Agresti 1996). Generalized linear models were based on normal and Poisson distributions; in this case, the Poisson log-linear model is equivalent to running a logistic regression based on the multinomial distribution (Agresti 1996). Goodness of fit was evaluated for these models by comparing ratios between degrees of freedom (df) and deviance of the models; a ratio of deviance to degrees of freedom close to 1.0 indicates a good model fit (Agresti 1996). Generally, models using a normal distribution with an identity link fitted reasonably well (deviance/df \leq 1.10), whereas multinomial models with a Poisson distribution and log link fitted poorly in all analyses and exhibited signs of overdispersion (deviance/df \geq 100). Thus, we subsequently used models based on the normal distribution for all analyses. Because the data on time budgets and peck rates contained some zero values, we added 0.05 to all data points prior to analysis (cf. Hosmer & Lemeshow 1989). For all analyses, we started with the saturated model and removed variables one at a time (Agresti 1996). A hypothesis testing approach with backwards model selection was chosen because we wanted to test a limited number of specific explanatory factors that, based on our hypotheses, were predicted to affect behaviours of interest. All terms in the models have well documented relevance to goose biology, i.e. family size and age, in addition to hypotheses about interspecific

differences. Least-square means are given for all explanatory variables reported as significant by PROC GENMOD.

Time budgets were estimated by dividing the time spent on each activity by the total time each focal goose was observed during a sampling period, to obtain proportions (Jónsson & Afton 2006). Social status and number of family members were combined into one variable, family size, as follows: (1) for adults, family size of three and higher indicated parents, two indicated pairs without juveniles, and one indicated lone birds; (2) for juveniles, three or higher indicated juveniles accompanied by parents and one indicated lone juveniles. For analysis, all initial models included species, age, and family size as explanatory variables, average daily temperature as a covariate, and all interactions of these variables.

Time budgets were analysed using generalized linear models with a multcategory (polytomous) response (Agresti 1996, Stokes *et al.* 2000), in which significance is tested by examining second-order interactions between activity and explanatory variables (see also Stokes *et al.* 2000). One activity was required to be the reference activity (Agresti 1996), so time spent on resting, social interactions, and other activities were summed into one reference activity, termed 'inactive' (Table 1), because we were most interested in time spent feeding, alert, and in locomotion. Response variables, for the time budget analysis, were proportions of time spent alert, feeding, in locomotion, and inactive. Arcsine transformations were not used because GOF statistics indicated a good model fit.

Peck rates were compared between species, using the number of pecks per minute by each focal bird as the response variable. For analysis, all initial models included species, age, and family size as explanatory variables, average daily temperature as a covariate, and all interactions of these variables. Alert rates also were compared between species, using the number of times the alert position was assumed per minute by each focal bird as the response variable. For analysis, all initial models included species, age, and family size as explanatory variables, average daily temperature as a covariate and all interactions of these variables.

RESULTS

Overall time budgets differed between species and age groups in both winters (Table 2). Time budgets varied significantly with average daily temperature and family size in winter 2002–03 but not in winter 2003–04 (Table 2).

Table 2. Summary of significant explanatory variables from generalized linear models comparing overall time budgets of Snow Geese and Ross's Geese in southwestern Louisiana during winters 2002–03 and 2003–04. Note that $df = 3$ (rather than $df = 1$) for testing age group and species because, in generalized multicategory models, significance is tested on the interaction of these terms with activity ($df = 3$).

Explanatory variables	winter 2002–03			winter 2003–04		
	df	χ^2	<i>P</i>	df	χ^2	<i>P</i>
Species ^a	3	11.96	0.0075	3	14.92	< 0.002
Age group ^a	3	30.68	< 0.0001	3	11.38	< 0.01
Average Daily Temperature (°C) ^b	3	49.84	< 0.0001	3	4.80	ns
Family size nested in age group ^a	20	48.10	0.0004	20	25.50	ns

^aCategorical variable (see Methods).

^bContinuous covariate (see Methods).

Table 3. Least-square mean percentages of time spent alert, feeding, in locomotion and other activities, by Snow Geese and Ross's Geese in southwestern Louisiana during winters 2002–03 and 2003–04. Inactive activities were resting, social interactions, preening, and activities classified as 'other'.

Winter	Species, age or family size	Alert	Feeding	Locomotion	Inactive	ASE	
2002–03	Ross's Geese	23.9	53.3	2.9	19.5	4.3	
	Snow Geese	20.8	45.4	3.6	30.1	2.1	
2003–04	Ross's Geese	20.0	57.1	7.2	16.0	3.5	
	Snow Geese	21.5	46.3	5.6	27.2	2.4	
2002–03	Adult	28.3	41.1	2.8	27.8	2.9	
	Juveniles	16.4	58.1	3.8	21.3	3.8	
2003–04	Adult	26.3	47.5	6.3	20.5	2.4	
	Juveniles	15.2	55.9	6.5	22.7	3.6	
2002–03	Adult lone	1	21.9	50.9	5.1	21.2	3.3
	Adult pair	2	21.9	49.8	2.1	26.4	3.7
	Adult parents	3	25.5	34.7	1.3	38.3	6.6
	Adult parents	4+	43.4	28.9	2.1	25.5	6.5
	Juvenile lone	1	17.5	52.3	5.7	23.9	4.3
	Juvenile family	3	19.9	51.4	1.5	26.8	6.2
	Juvenile family	4+	11.7	72.2	5.1	10.5	5.1

ASE, asymptotic standard error.

Comparison of time budgets between species and ages

Time budgets differed between species for three activities (Table 3). Ross's Geese spent more time feeding than did Snow Geese in 2002–03 ($\chi^2 = 11.30$, $df = 1$, $P < 0.001$) and in 2003–04 ($\chi^2 = 14.72$, $df = 1$, $P = 0.0001$). In 2002–03, Ross's Geese spent more time alert than did Snow Geese ($\chi^2 = 5.86$, $df = 1$, $P < 0.02$). In 2003–04, Ross's Geese spent more time in locomotion than did Snow Geese ($\chi^2 = 5.00$, $df = 1$, $P < 0.05$).

In 2002–03, overall time budgets of age groups varied with family size nested within age group. In

winter 2003–04, overall time budgets differed between adults and juveniles, independent of species or family size (Table 3). In winter 2003–04, adults spent more time alert than did juveniles ($\chi^2 = 5.14$, $df = 1$, $P < 0.05$); other activities were similar ($P > 0.05$) between age classes.

Effects of family size on time budgets

Overall time budgets differed by family size in winter 2002–03, independent of species, for two behaviours (Table 3). Adults in families with two or more juveniles spent more time alert than did lone adults ($\chi^2 = 9.27$, $df = 1$, $P < 0.005$). Adults in families with one or two

Table 4. Least-square mean peck rates (bouts/min) and alert rates (bouts/min) of Snow Geese and Ross's Geese in southwest Louisiana during winters 2002–03 and 2003–04.

Explanatory variable	Species	Age	Family size	Peck rates		Alert rates	
				Mean	SE	Mean	SE
Species	Snow Goose	Combined	All	1.00	0.09	1.12	0.08
	Ross's Goose	Combined	All	1.37	0.11	1.27	0.10
Age	Combined	Adults	All	1.09	0.06	1.33	0.05
		Juveniles	All	1.08	0.13	1.06	0.11
Family size	Snow Goose	Adults	1	0.80	0.11	0.95	0.10
			2	0.76	0.12	1.05	0.11
			3	1.21	0.20	1.25	0.17
			4	1.12	0.19	1.42	0.16
		Juveniles	1	1.12	0.26	0.89	0.23
			3	0.92	0.34	1.17	0.30
	Ross's Goose	Adults	1	0.90	0.10	1.28	0.08
			2	1.14	0.10	1.70	0.09
			3	1.60	0.23	1.50	0.20
		Juveniles	1	1.20	0.21	0.91	0.18
			3	1.06	0.34	1.17	0.30

juveniles spent less time feeding than did lone adults ($\chi^2 = 5.02$, $df = 1$, $P < 0.05$ and $\chi^2 = 9.45$, $df = 1$, $P < 0.005$ respectively). Juveniles in families with two or more juveniles spent more time feeding than did lone juveniles ($\chi^2 = 7.92$, $df = 1$, $P < 0.005$).

Ambient temperature and time budgets

In 2002–03, time spent feeding was inversely correlated with average daily temperature ($\chi^2 = 47.36$, $df = 1$, $P < 0.0001$); on average, a 1 °C increase in average daily temperature resulted in a 3.8% decrease in time spent feeding. In winter 2002–03, time spent in locomotion also had an inverse relationship with average daily temperature ($\chi^2 = 47.36$, $df = 1$, $P < 0.0023$); on average, a 1 °C increase in average daily temperature resulted in a decrease of 1.7% in time spent in locomotion. These effects did not differ between species.

Peck rates and alert rates

We detected no significant explanatory variables for peck rates during winter 2002–03, whereas the final model in 2003–04 included species ($\chi^2 = 5.70$, $df = 1$, $P < 0.02$). In 2003–04, peck rates were 1.4 feeding bouts per minute for Ross's Geese compared to 1.0 per minute for Snow Geese (Table 4).

The final model for alert rates included family size nested within the species*age interaction. Alert rates did not differ by family size in 2002–03, but in 2003–04 they differed by family size within adults of each species ($\chi^2 = 25.28$, $df = 12$, $P < 0.02$). In Snow Geese, alert rates differed between adults in families of four and lone adults ($\chi^2 = 5.95$, $P < 0.02$); adults in families of four or larger assumed the alert position on average 1.4 times per minute compared with 0.9 times per minute in lone adults (Table 4). In Ross's Geese, alert rates differed between pairs and lone adults ($\chi^2 = 5.39$, $P = 0.02$). Ross's Goose pairs, on average, assumed the alert position 1.7 times per minute as compared to 1.3 times per minute in lone adults (Table 4).

DISCUSSION

Interspecific differences in time budgets

Our findings generally are consistent with the body-size hypothesis, although fasting endurance may be less important during winter than during breeding (Gloutney *et al.* 2001). Snow Geese do not gain weight during winter (Ankney 1982), but rather do so later on spring migration stopover areas, where they deposit enough reserves to sustain them throughout incubation (Alisauskas 2002); a similar nutrient storage pattern was observed in Ross's Geese in California (Bob McLandress unpubl. data).

Our results did not support the prediction that Ross's Geese are more sensitive to ambient temperatures than are Snow Geese. However, the main effect of average daily temperature was significant and independent of species in winter 2002–03. Both species responded similarly to temperature changes in the cooler winter, but apparently neither species was influenced by ambient temperatures in the warmer winter. In Louisiana, changes in ambient temperature may affect these species similarly because the interspecific difference in lower critical temperature, estimated at 4 °C by the Aschoff-Pohl equation, is relatively small compared to within-day fluctuations in ambient temperatures during winter in southwest Louisiana. Also, once declining temperatures facilitate Ross's Geese to increase time spent feeding, some Snow Geese might also increase the proportion of time spent feeding. Snow Geese do not seem particularly sensitive to cool weather, for example temperatures above –6.7 °C had 'no observable effect' on Snow Geese in the Missouri River Valley (Davis *et al.* 1989). Furthermore, temperatures in Louisiana rarely declined below this value in winter 2002–03 or winter 2003–04. When wintering temperatures approached –20 °C, Snow Geese in Mississippi River Valley ceased activities and rested (Frederick & Klaas 1982).

Ross's Geese spent slightly more time alert than did Snow Geese in winter 2002–03, and alert rates within each species varied with family size. Two possible, non-exclusive explanations are that (1) Ross's Geese are more receptive to potential predation threats than are Snow Geese, as suggested by McWilliams *et al.* (1994), or (2) Ross's Geese remain alert towards Snow Geese to avoid forceful expulsion from feeding patches. Snow Geese generally are socially dominant over Ross's Geese (Jónsson & Afton 2008). By remaining alert, Ross's Geese may detect the approach of aggressive Snow Geese and vacate foraging patches prior to physical contact. Ross's Geese also may compete intraspecifically for patches where they can forage without Snow Goose harassment and thus remain alert against each other. As a result, the relatively higher alertness by Ross's Geese also may render them less vulnerable to predators than Snow Geese.

Ross's Geese spent more time in locomotion than did Snow Geese in winter 2003–04; this difference also may reflect avoidance of the larger Snow Geese by Ross's Geese. Ross's Geese feed more by scrambling (competition for a limited resource that is partitioned somewhat unequally among competitors), in contrast to the resource-defence foraging employed by Snow Geese (Jónsson & Afton 2008), and this difference

may result in greater time spent in locomotion by Ross's Geese, observed in 2003–04.

Ross's Geese spent more time feeding and alert than did Snow Geese and accordingly spent relatively less time resting. Resting is a common activity for wintering waterfowl (Paulus 1988) and may be an optimal strategy for minimizing energy expenditure when geese are not actively depositing fat. Resting is conducive to food digestion (Burton & Hudson 1978), particularly if the gut is full. Ross's Geese may be relatively more efficient at freeing up gut volume following satiation because smaller herbivorous waterfowl generally have faster defecation rates than do larger species (Mayhew & Houston 1993). Increased time spent feeding probably is beneficial during periods of reserve accumulation (for adults) or growth (juveniles). Increased time spent feeding is needed when eating less digestible or less nutritious diets (Jónsson & Afton 2006). Decreasing time spent feeding frees up time for other activities, such as social interactions and alertness. Thus, minimizing foraging time, to allow participation for social activities, may be essential, especially for 2–3-year-old birds reaching sexual maturity or widowed birds looking for new partners, as pair formation takes place during winter (Ganter *et al.* 2005).

Effects of age and family size

Age and family size effects on time budgets were independent of species. Thus, age and family size and the associated social status may be equally important determinants of time budgets as are interspecific differences in body size (Tchabovsky *et al.* 2001). Geese in families generally feed longer and are able to access better feeding patches than are lone geese (Black & Owen 1989a). When feeding, lone geese spend more time searching, whereas geese in families spend more time ingesting food by grazing or grubbing (Bélanger & Bédard 1992).

Juvenile geese generally spend more time feeding than do adults (Austin 1990, Bélanger & Bédard 1992). Juvenile waterfowl are less efficient foragers and also have less ability to avoid interference competition than do adults, and thus are more prone to starvation, which may lead to poorer body condition (Jamieson *et al.* 2006). Snow Geese do not reach full growth until they are 1 year old (Cooch *et al.* 1991). Thus, juveniles have relatively higher energy requirements than do adults, which must be satisfied with increased time spent feeding. Our findings indicate that juveniles in families spend more time feeding undisturbed, relative to that of lone birds.

Conversely, parents spend less time feeding but more time alert than do juveniles, which may represent parental expenditure (use of parental resources, including energy and time) in vigilance (Clutton-Brock 1991). The higher alertness by adults probably confers an advantage on juveniles (Davis *et al.* 1989), allowing them to devote more time to activities such as feeding or resting. For Snow Geese, parents spent more time alert than did other adults. Increased alertness of parents may function to protect offspring from predators and also from harassment by competitors.

The interaction between body size and social behaviour

Interspecific variation in time budgets may be partially due to the different family maintenance in the two species. Among focal Snow Geese, paired parents constituted 10% and 22% of all Snow Geese in winter 2002–03 and winter 2003–04, respectively and juveniles in families constituted 12% and 15% of all Snow Geese in winter 2002–03 and winter 2003–04, respectively (Jónsson & Afton 2008). In contrast, among focal Ross's Geese, paired parents constituted 0.1% and 6.9% of all Ross's Geese in winter 2002–03 and winter 2003–04, respectively and juveniles in families constituted 0.3% and 3.6% of all Ross's Geese in winter 2002–03 and winter 2003–04, respectively (Jónsson & Afton 2008). These differences are consistent with the hypothesis that smaller species are less likely to form family social groups than are larger species; small species also select more sheltered habitats and consume more specialized diets (Jarman's hypothesis; Jarman 1974). McWilliams *et al.* (1994) suggested that Ross's Geese were more vulnerable to predators than are larger goose species, and that predation pressure was a major evolutionary constraint selecting against maintenance of families in this species. We found that Ross's Geese were relatively more vigilant than were Snow Geese, consistent with McWilliams *et al.* (1994).

Smaller species also are more likely to be displaced in competition with larger species regardless of numbers present (Shelley *et al.* 2004). The observed species differences in family maintenance may have resulted from patterns of interspecific social dominance; Snow Geese won 70% of all interspecific social encounters (Jónsson & Afton 2008). The historical association and subordination of Ross's Geese to Snow Geese may have selected against family maintenance in Ross's Geese.

Our data indicate that Ross's Geese spend more time feeding and alert than do larger Snow Geese. The difference in time budgets may be explained partially by the ability of larger species to carry fat reserves (Goudie & Ankney 1986, Calder 1996). Although the difference in time budgets may partially be attributable to differences in family maintenance, Gloutney *et al.* (2001) found similar results for time spent feeding during nesting and incubation at Karrak Lake, a period during which families are not maintained (Prevett & MacInness 1980). Thus, small body size appears to be a key variable influencing time spent feeding in Ross's Geese, both during breeding and during winter. This constraint may limit time spent in other activities, such as resting, family maintenance and other social behaviours.

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REFERENCES

- Abraham, K.F., Jefferies, R.L. & Alisauskas, R.T. 2005. The dynamics of landscape change and Snow Geese in mid-continent North America. *Global Change Biol.* **11**: 845–855.
- Afton, A.D. & Paulus, S.L. 1992. Incubation and brood care. In Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) *Ecology and Management of Breeding Waterfowl*: 62–108. Minneapolis: University of Minnesota Press.
- Afton, A.D. 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* **82**: 132–137.
- Afton, A.D. 1993. Post-hatch brood amalgamation in Lesser Scaup: female behavior and return rates, and duckling survival. *Prairie Nat.* **25**: 227–235.
- Agresti, A. 1996. *An Introduction to Categorical Data Analysis*. New York: John Wiley.
- Alisauskas, R.T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent Lesser Snow Geese. *J. Wildl. Manage.* **66**: 181–193.

- Alisauskas R.T., Ankney, C.D. & Klaas, E.E.** 1988. Winter diets and nutrition of midcontinental Lesser Snow Geese. *J. Wildl. Manage.* **52**: 403–414.
- Altmann, J.** 1974. Observational study of behaviour: sampling methods. *Behaviour* **49**: 227–267.
- Ankney, C.D.** 1982. Annual cycle of body weight in Lesser Snow Geese. *Wildl. Soc. B.* **10**: 60–64.
- Aschoff, J. & Pohl, H.** 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* **29**: 1541–1552.
- Austin, J.** 1990. Comparison of activities within families and pairs of wintering Canada Geese. *Wilson Bull.* **102**: 536–542.
- Bélanger, L. & Bédard, J.** 1992. Flock composition and foraging behaviour of Greater Snow Geese (*Chen caerulescens atlantica*). *Can. J. Zool.* **70**: 2410–2415.
- Bennet, J.W. & Bolen E.G.** 1978. Stress response in wintering Green-winged Teal. *J. Wildl. Manage.* **42**: 81–86.
- Black, J.M. & Owen, M.** 1989a. Parent-offspring relationships in wintering Barnacle Geese. *Anim. Behav.* **37**: 187–198.
- Black, J.M. & Owen, M.** 1989b. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Anim. Behav.* **37**: 199–209.
- Black, J.M., Prop, J. & Larsson, K.** 2007. *Wild Goose Dilemmas*. Groningen: Branta Press.
- Boyd, H.** 1953. On encounters between wild White-fronted Geese in winter flocks. *Behaviour* **5**: 85–129.
- Burton, B.A. & Hudson, R.J.** 1978. Activity budgets of Lesser Snow Geese wintering on the Fraser River Estuary, British Columbia. *Wildfowl* **29**: 111–117.
- Calder, W.A. III** 1996. *Size, Function and Life History*. 2nd edn. Mineola, NY: Dover Publications.
- Clutton-Brock, T.H.** 1991. *The Evolution of Parental Care*. Princeton: Princeton University Press.
- Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F.** 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. *Ecology* **72**: 503–512.
- Davis, S.E., Klaas, E.E. & Koehler, K.J.** 1989. Diurnal time activity budgets and habitat use of Lesser Snow Geese in the middle Missouri River Valley during winter and spring. *Wildfowl* **40**: 45–54.
- Demment, M.W. & Van Soest, P.J.** 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* **125**: 641–672.
- Forslund, P.** 1993. Vigilance in relation to brood size and predator abundance in the Barnacle Goose, *Branta leucopsis*. *Anim. Behav.* **45**: 965–973.
- Fox, A.D., Kahlert, J. & Ettrup, H.** 1998. Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis* **140**: 676–683.
- Frederick, R.B. & Klaas, E.E.** 1982. Resource use and behavior of migrating Snow Geese. *J. Wildl. Manage.* **46**: 601–614.
- Ganter, B. & Cooke, F.** 1996. Pre-incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity? *Oecologia* **106**: 153–165.
- Ganter, B., Boyd, W.S., Baranyuk, V.V. & Cooke, F.** 2005. First pairing in Snow Geese *Anser caerulescens*: at what age and at what time of year does it occur? *Ibis* **147**: 57–66.
- Gauthier, G., Bédard, J. & Bédard, Y.** 1984. Comparison of daily energy expenditure of Greater Snow Geese between two habitats. *Can. J. Zool.* **62**: 1304–1307.
- Gloutney, M.L., Alisauskas, R.T., Afton, A.D. & Slattery, S.M.** 2001. Foraging time and dietary intake by breeding Ross's and Lesser Snow Geese. *Oecologia* **127**: 78–86.
- Goudie, R.I. & Ankney, C.D.** 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* **67**: 1475–1482.
- Gregoire, P.E. & Ankney, C.D.** 1990. Agonistic behavior and dominance relationships among Lesser Snow Geese during winter and spring migration. *Auk* **107**: 550–560.
- Guillemain, M., Fritz, H. & Duncan, P.** 2002. Foraging strategies of granivorous dabbling ducks wintering in protected areas of the French Atlantic Coast. *Biodiv. Conserv.* **11**: 1721–1372.
- Hosmer, D.W. & Lemeshow, S.** 1989. *Applied Logistic Regression*. New York: Wiley.
- Jamieson, S.E., Gilchrist, H.G., Merkel, F.R., Diamond, A.W. & Falk, K.** 2006. Endogenous reserve dynamics of northern Common Eiders wintering in Greenland. *Polar Biol.* **29**: 585–594.
- Jarman, P.J.** 1974. The social organization of antelope in relation to their ecology. *Behaviour* **48**: 215–267.
- Jeschke, J.M. & Tollrian, R.** 2005. Predicting herbivore feeding times. *Ethology* **111**: 187–6.
- Jeschke, J.M., Kopp, M. & Tollrian, R.** 2002. The evolution of the control of food intake. *Ecol. Monogr.* **72**: 95–112.
- Johnson, J.C. & Raveling, D.G.** 1988. Weak family associations in Cackling Geese during winter: effects of body size and food resources on goose social organization. In Weller, M.W. (ed.) *Waterfowl in Winter*: 71–89. Minneapolis: University of Minnesota Press.
- Jónsson, J.E.** 2005. *Effects of Body Size on Goose Behaviour: Lesser Snow Geese and Ross's Geese*. PhD Dissertation, Baton Rouge: Louisiana State University.
- Jónsson, J.E. & Afton, A.D.** 2006. Different time and energy budgets of Lesser Snow Geese in rice-prairies and coastal marshes in southwest Louisiana. *Waterbirds* **29**: 451–458.
- Jónsson, J.E. & Afton, A.D.** 2008. Body size relationships: why do Snow Geese and Ross's Geese form mixed flocks on wintering areas? *Wilson J. Ornithol.* **120**: 725–731.
- Jónsson, J.E., Afton, A.D. & Alisauskas, R.T.** 2007. Does body size influence nest attendance? A comparison of Ross's Geese (*Chen rossii*) and the larger, sympatric Lesser Snow Geese (*C. caerulescens caerulescens*). *J. Ornithol.* **148**: 549–555.
- Kalmbach, E.** 2006. Why do goose parents adopt unrelated goslings? A review of hypotheses and empirical evidence, and new research questions. *Ibis* **148**: 66–78.
- Kendeigh, S.C.** 1970. Energy requirements for existence in relation to size of a bird. *Condor* **72**: 60–65.
- Krause, J. & Ruxton, G.D.** 2002. *Living in Groups*. New York: Oxford University Press.
- Kristiansen J.N. & Jarrett, N.S.** 2002. Inter-specific competition between Greenland White-fronted Geese *Anser albifrons flavirostris* and Canada Geese *Branta canadensis interior* moulting in West Greenland: mechanisms and consequences. *Ardea* **90**: 1–13.
- Kristiansen, J.N., Fox, A.D., Boyd, H. & Stroud, D.A.** 2000. Greenland White-fronted Geese *Anser albifrons flavirostris* benefit from feeding in mixed-species flocks. *Ibis* **142**: 139–158.
- Lehner, P.N.** 1996. *Handbook of Ethological Methods*. Cambridge: Cambridge University Press.
- Loonen, M.J.J.E., Bruinzeel, L.W., Black, J.M. & Drent, R.H.** 1999. The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. *J. Anim. Ecol.* **68**: 753–768.

- Louisiana Office of State Climatology.** 2005. *Preliminary Daily summary: Southern Regional Climate Centre. Station: Lake Charles.* URL http://www.losc.lsu.edu/products/climate/lch/oct_2002.txt [accessed 1 August 2007].
- Mayhew, P.W. & Houston, D.C.** 1993. Food throughput time in European Wigeon *Anas penelope* and other grazing waterfowl. *Wildfowl* **44**: 174–177.
- McWilliams, S.R., Dunn, J.P. & Raveling, D.G.** 1994. Predator-prey interactions between eagles and Cackling Canada and Ross' Geese during winter in California. *Wilson Bull.* **106**: 272–288.
- Mowbray, T.B., Cooke, F. & Ganter, B.** 2000. Snow Goose (*Chen caerulescens*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 514. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.
- Newton, I.** 1998. *Population Limitation in Birds*. San Diego: Academic Press.
- Newton, I.** 2004. Population limitation in migrants. *Ibis* **146**: 197–384.
- Newton, I.** 2007. Weather-related mass-mortality events in migrants. *Ibis* **149**: 453–467.
- Öst, M., Mantila, L. & Kilpi, M.** 2002. Shared care provides time budgeting advantages for female Eiders. *Anim. Behav.* **64**: 223–231.
- Owen, M.** 1972. Some factors affecting food intake and selection in White-fronted Geese. *J. Anim. Ecol.* **41**: 79–92.
- Paulus, S.L.** 1988. Time activity budgets of nonbreeding Anatidae: a review. In Weller, M.W. (ed.) *Waterfowl in Winter*: 135–152. Minneapolis: University of Minnesota Press.
- Prevett, J.P. & MacInnes, C.D.** 1980. Family and other social groups in Snow Geese. *Wildl. Monogr.* **71**: 6–46.
- Prop, J. & Deerenberg, C.** 1991. Spring staging of Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* **87**: 23–29.
- Quinn, J.L., Whittingham, M.J., Butler, S.J. & Cresswell, W.** 2006. Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. *J. Avian Biol.* **37**: 601–608.
- Randler, C.** 2004. Coot benefit from feeding in close proximity to geese. *Waterbirds* **27**: 240–244.
- Raveling, D.G.** 1970. Dominance relationships of agonistic Canada Geese in winter. *Behaviour* **37**: 291–319.
- Ryder, J.P. & Alisauskas, R.T.** 1996. Ross's Goose (*Chen rossii*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 162. Philadelphia, PA: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.
- SAS Institute.** 1999. *SAS/SYSTAT User's Guide*. Version 8. Cary: SAS Institute.
- Shelley, E.L., Tanaka, M.Y.U., Ratnathicam, A.R. & Blumstein, D.T.** 2004. Can Lanchester's laws help explain interspecific dominance in birds? *Condor* **106**: 395–400.
- Skutch, A.F.** 1962. The constancy of incubation. *Wilson Bull.* **74**: 115–152.
- Sol, D., Santos, D.M., Garcia, J. & Cuadrado, M.** 1998. Competition for food in urban pigeons: the cost of being juvenile. *Condor* **100**: 298–304.
- Squires, K.A., Martyn, K. & Goudie, R.I.** 2007. Vigilance behavior in the Harlequin Duck (*Histrionicus histrionicus*) during the preincubation period in Labrador: are males vigilant for self or social partners? *Auk* **124**: 241–252.
- Stahl J., Tolsma, P.H., Loonen, M.J.J.E. & Drent, R.H.** 2001. Subordinates explore but dominants profit: resource competition in high Arctic Barnacle Goose flocks. *Anim. Behav.* **61**: 257–264.
- Stokes, M.E., Davis, C.S. & Koch, G.G.** 2000. *Categorical Data Analysis Using the SAS System*. 2nd edn. Cary: SAS Institute.
- Systad, G.H. & Bustnes, J.O.** 2001. Coping with darkness and low temperatures: foraging strategies in Steller's Eiders, *Polysticta stelleri*, wintering at high latitudes. *Can. J. Zool.* **79**: 402–406.
- Systad, G.H., Bustnes, J.O. & Erikstad, K.E.** 2000. Behavioral responses to decreasing day length in wintering sea ducks. *Auk* **117**: 33–40.
- Tchabovsky, A.V., Popov, S.V. & Krasnov, B.R.** 2001. Intra- and interspecific variation in vigilance and foraging of two gerbillid rodents, *Rhombomys optimus* and *Psammomys obsesus*: the effect of social environment. *Anim. Behav.* **62**: 965–972.
- Weckstein, J.D., Afton, A.D., Zink, R.M. & Alisauskas, R.T.** 2002. Hybridization and population subdivision within and between Ross's Geese and Lesser Snow Geese: a molecular perspective. *Condor* **104**: 432–436.
- Williams, T.D., Loonen, M.J.J.E. & Cooke, F.** 1994. Fitness consequences of parental behavior in relation to offspring number in a precocial species – the Lesser Snow Goose. *Auk* **111**: 563–572.

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