NOTE / NOTE

Surviving on cached foods — the energetics of egg-caching by arctic foxes

V. Careau, J.-F. Giroux, G. Gauthier, and D. Berteaux

Abstract: Food-caching by arctic foxes (*Vulpes lagopus* (L., 1758)) is a behavioural adaptation thought to increase winter survival, especially in bird colonies where a large number of eggs can be cached during a short nesting season. In this paper, we measured the energy content of greater snow goose (*Chen caerulescens atlantica* Kennard, 1927) eggs and evaluated their perishability when cached in tundra soil for a whole summer. We estimated that eggs lost only ~8% of their dry mass over 60 days of storage in the ground. We used published estimates on digestibility of nutrients by arctic foxes to estimate that fresh and stored goose eggs contained 816 and 730 kJ of metabolizable energy, respectively, a difference of 11%. Using information on arctic fox energetics, we evaluated that 145 stored eggs were required to sustain the growth of one pup from the age of 1 to 3 months (nutritional independence). Moreover, 23 stored eggs were energetically equivalent to the average fat deposit of an arctic fox during winter. Finally, we calculated that an adult arctic fox would need to recover 160–220 stored eggs to survive 6 months in resting conditions during cold winter temperatures. This value increased to 480 when considering activity cost. Based on egg acquisition and caching rates observed in many goose colonies, we conclude that cached eggs represent an important source of energy relative to the needs of an arctic fox during winter, and have thus a high fitness value.

Résumé : La mise en réserve de nourriture chez le renard arctique (*Vulpes lagopus* (L., 1758)) est une adaptation comportementale largement soupçonnée d'augmenter la survie durant l'hiver, plus particulièrement dans les colonies d'oiseaux où un grand nombre d'œufs peuvent être cachés durant la courte saison de nidification. Nous avons mesuré le contenu énergétique des oeufs de la grande oie des neiges (*Chen caerulescens atlantica* Kennard, 1927) et évalué leur périssabilité lorsque entreposés dans le sol de la toundra durant tout un été. Les œufs ont perdu seulement ~8 % de leur masse sèche durant 60 jours d'entreposage dans le sol. En utilisant des estimations de la digestibilité des nutriments par le renard arctique tirées de la littérature, nous avons évalué que les œufs d'oies frais et entreposés contiennent respectivement 816 et 730 kJ d'énergie métabolisable, une différence de 11 %. À l'aide de données sur le métabolisme du renard arctique, nous avons évalué que 145 oeufs entreposés seraient requis pour soutenir la croissance d'un jeune renard entre l'âge de 1 et 3 mois (l'indépendance alimentaire). De plus, 23 œufs entreposés contiennent autant d'énergie que les réserves de gras moyennes d'un renard durant l'hiver. Finalement, nous avons calculé que 160 à 220 oeufs entreposés seraient nécessaires à la survie d'un renard pendant 6 mois aux températures froides d'hiver en condition de repos. Cette valeur augmente à 480 lorsqu'on considère les coûts de l'activité. À la lumière des taux d'acquisition et d'entreposage d'œufs observés dans plusieurs colonies d'oies, nous concluons que les oeufs entreposés représentent une source d'énergie importante pour un renard en hiver, compte tenu de ses besoins. Le comportement d'entreposage a donc une grande importance pour l'aptitude phénotypique des individus.

[Traduit par la Rédaction]

Introduction

Surviving winter is a great challenge for terrestrial homeotherms living at high latitudes or altitudes because extensive heat loss owing to low temperatures is often associated with food scarcity. In nonmigratory species, such situations have led to evolution of specific morphological, physiological, and behavioural adaptations aimed at storing energy before and saving energy during winter. For instance, arctic terrestrial mammals increase their body insulation in winter,

Received 15 February 2008. Accepted 29 July 2008. Published on the NRC Research Press Web site at cjz.nrc.ca on 3 October 2008.

V. Careau[1,2] and J.-F. Giroux. Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada.
G. Gauthier. Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC G1K 7P4, Canada.
D. Berteaux. Chaire de recherche du Canada en conservation des écosystèmes nordiques et Centre d'études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

[1] Corresponding author (e-mail: vincent.careau@usherbrooke.ca).
[2] Present address: Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada.

doi:10.1139/Z08-102

thereby reducing thermoregulatory costs when exposed to cold ambient temperatures (T_a). Animals can also adapt to periods of food scarcity by storing energy in advance through fat deposition and (or) hoarding behaviour (Scholander 1955; Vander Wall 1990).

The arctic fox (*Vulpes lagopus* (L., 1758), also known as *Alopex lagopus* (L., 1758)) must withstand a very large temperature gradient (up to 90 °C) between T_a and its core body temperature (T_b) during winter, and has thus developed sophisticated adaptations to cope with the severe conditions of the High Arctic environment. Physiological adaptations for energy conservation include a seasonal reduction of basal metabolic rate (BMR), T_b, food intake, and running cost, especially during famine periods (Fuglei 2000). Prestrud (1991) also suggested that fat deposition and food-caching were important physiological and behavioural adaptations of arctic foxes for surviving seasonal shortages of food.

Bird eggs are an important food source for arctic foxes (Chesemore 1968; Stickney 1991; Bantle and Alisauskas 1998; Kapel 1999). More specifically, goose eggs are particularly valuable because they are relatively large, rich in fat, and often occur in dense patches (e.g., colonies). Egg acquisition rate by arctic foxes in goose colonies can reach 2.7–7.3 eggs·h^{-1}, of which 80%–97% are cached for later use (Stickney 1991; Samelius and Alisauskas 2000; Samelius 2006; Careau et al. 2008). Eggshell fragments found in arctic fox scats provide evidence that egg caches supply food during winter (Fay and Stephensen 1989; Prestrud 1992). Many authors suggested that accumulation of cached eggs during summer enhance arctic fox winter survival (Fay and Stephensen 1989; Stickney 1991; Prestrud 1992; Bantle and Alisauskas 1998; Samelius 2000). Recent isotope analysis showed that cached eggs can be recovered and eaten up to 1 year after they were acquired (Samelius et al. 2007). Although perishability is a major factor influencing energy reward associated with long-term hoarding (Vander Wall 1990; Hadj-Chikh et al. 1996; Careau et al. 2007*a*), there is surprisingly no estimate of egg perishability once stored in tundra soil. Low temperatures of storage sites during the arctic summer may slow down decomposition of cached eggs until the soil freezes in fall, after which little or no decomposition presumably occurs.

Herein, we investigate the energetic benefits associated with egg-caching by arctic foxes. In a first step, we estimated the energetic value of goose eggs. We measured fat, protein, and energy contents of goose eggs and estimated experimentally their perishability when stored in tundra soil. In a second step, we used published estimates of arctic fox physiological parameters to calculate the potential contribution of goose eggs to fox reproduction and winter survival. Specifically, we estimated how many goose eggs (*i*) were required to sustain the growth of one pup from the age of 1 to 3 months, after which it becomes nutritionally independent from its parents, (*ii*) are equivalent, in terms of energy content, to the full body fat reserves of a fox in winter, and (*iii*) were required to ensure survival throughout arctic winter. This study is thus about the fitness value of a commonly observed behaviour (food-caching) in a commonly observed arctic predator (the arctic fox).

Materials and methods

We conducted fieldwork on Bylot Island (72°53′N, 79°54′W), Nunavut, Canada, during summers 1989–1990 and 2004. This island is part of Sirmilik National Park and is an important breeding site for greater snow geese (*Chen caerulescens atlantica* Kennard, 1927) (Reed et al. 2002). The core of the colony (highest nest density area) is located in a mosaic of wet polygon fens surrounded by extensive upland habitats (Tremblay et al. 1997). An automated weather station located in the same type of habitat ~30 km from the main goose colony recorded mean hourly T_a with a shielded temperature probe at 2 m above ground from 1995 to 2002. Ground temperature (T_g) was also recorded at a depth of 10 cm below ground surface. Mean, minimum, and maximum daily temperatures were calculated.

Egg collection

Egg collection is strictly limited in Canadian national parks and this imposed strong constraints on our study design. In particular, we were required to keep sample sizes and replicates to a minimum and make full use of existing data. Measurements taken on fresh, cached, and stored eggs (see definitions below) thus differed. Choinière and Gauthier (1995) collected goose eggs at the beginning of incubation (7–18 June 1989: $n = 31$; 9–17 June 1990: $n = 27$) and measured their nutrient content to analyse goose parental investment. We now use their data in a new context. Because these eggs were heated in water at 85 °C for 90 min immediately after collection and kept frozen until analysis, we considered them “fresh” eggs.

On 18 June 2004, at the onset of the incubation period, we collected 20 goose eggs and buried them randomly throughout the study area in upland (mesic) and polygon fen (humid) habitats. We simulated the caching behaviour of fox by placing eggs in excavated holes and covering them with 2–3 cm of mosses and vegetation. Soil temperature has been monitored on Bylot Island since 1993. The warmest monthly mean occurs in July and is 2.8 °C at a depth of 10 cm (Gagnon et al. 2004). Eggs were recovered on 17 August (after 60 days of storage), kept in a cooler, and sent to the laboratory where they were frozen on 23 August. Sample size was reduced from 20 to 16 because of accidental losses. Hereafter, we refer to the 20 eggs cached on 18 June as “cached” eggs and to the 16 eggs recovered on 17 August as “stored” eggs.

Egg content analysis

All eggs were weighed upon collection in the nest (wet mass). Using a relationship between egg density (g·cm^{-3}) and incubation stage (Choinière and Gauthier 1995), we calculated that fresh and cached eggs had been incubated for a mean (SD) of 3 ± 3 and 1 ± 1 days, respectively. In the laboratory, fresh and stored eggs were thawed at 5 °C and shells (with membranes) were discarded and not considered in egg composition, as they contain no energy. Behavioural observations confirmed that foxes never consumed the entire egg shells, although they might ingest some small fragments (V. Careau, personal observation). All eggs were freeze-dried in the laboratory to measure dry mass. We determined the fat content of fresh eggs from a homogenate of the yolk using a Rafatec apparatus (Randall 1974) with petroleum ether as the solvent. Fat content of stored eggs was determined using the same apparatus and solvent, but from a homogenate of whole egg rather than from a homogenate of the yolk. The use of different protocols owing to the requirement of using existing data should not bias the results because the entire fat content of eggs is found in the yolk (Rohwer 1986). We measured ash content of stored eggs by incinerating a subsample in a muffle furnace at 550 °C for 6 h and weighing the ash residue (for additional details on the method see Gauthier et al. 1992). The protein mass was then determined by subtracting fat and ash masses from the whole egg dry mass. Because Choinière and Gauthier (1995) did not measure the ash content of fresh eggs, we subtracted the mean ash mass determined in stored eggs from the total fat-free dry mass of individual fresh eggs. We assumed that ash content did not change over time and was the same in fresh and stored eggs. Although these two assumptions may not be entirely correct, we believe that ignoring completely ash content in both types of eggs would have been a more serious source of bias.

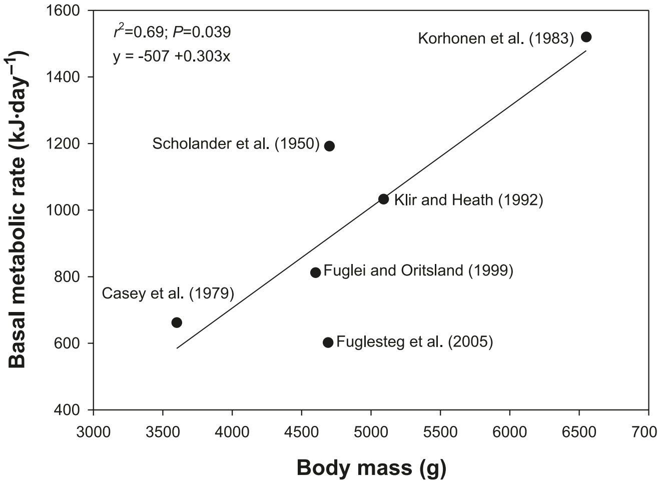
Bioenergetics modeling

We calculated the potential contribution of goose eggs to the energy needs by arctic foxes using published estimates of nutrient digestibility (Ahlstrøm et al. 2003), fat and protein oxidation (Tauson et al. 2002), energy demand during growth (Frafjord 1994), fat deposition (Prestrud and Nilssen 1992; Prestrud and Pond 2003), BMR, and lower critical temperature (T_{lc}) (Scholander et al. 1950; Fuglesteg et al. 2006). In the literature, we found six BMR values for arctic fox (Fig. 1). After accounting for differences in body masses, the estimates provided by Scholander et al. (1950) and Fuglesteg et al. (2006) represent maximal and minimal values, respectively. We used these two estimates (standardized to a mean body mass of 3.5 kg) in our calculations to provide a range of estimates regarding the potential contribution of goose eggs to the winter energy needs of arctic fox. Because fat and protein digestibility of arctic and farm-raised blue foxes (*Vulpes lagopus* (L., 1758), also known as *Alopex lagopus* (L., 1758)) are similar (Ahlstrøm et al. 2003), we used digestibility values reported for blue foxes. In fat- and protein-rich tissues such as goose eggs, fat and protein digestibility are 96% and 88% in blue fox, respectively (Ahlstrøm and Skrede 1995, 1998). We used 39.8 and 18.8 kJ·g^{-1} of metabolizable fat and protein, respectively, as conversion factors to estimate the caloric content of eggs (Enggaard Hansen et al. 1991, cited in Ahlstrøm et al. 2003).

Statistical analyses

We performed ANOVA with Tukey's post hoc procedure to test for differences in dry and wet masses between eggs collected in 1989, 1990, and 2004. Using the relationship between wet and dry masses of fresh eggs, we estimated the dry mass of cached eggs and compared it with the measured dry mass of stored eggs. We attributed the difference to the effect of storage. We compared fat content (% of dry mass) and mass-specific energy content (kJ·g^{-1}) between fresh (pooled 1989–1990) and stored eggs using Welch ANOVA to test the null hypothesis that means were equal while allowing variances to differ as the Brown–Forsythe test indicated unequal variances. We used the JMP version 5.0.1 statistical software (SAS Institute Inc., Cary, North Carolina) and always report values as means ± SD.

Fig. 1. Basal metabolic rate in arctic fox (*Vulpes lagopus*) as a function of body mass and source of data.



Results

Wet and dry masses of eggs

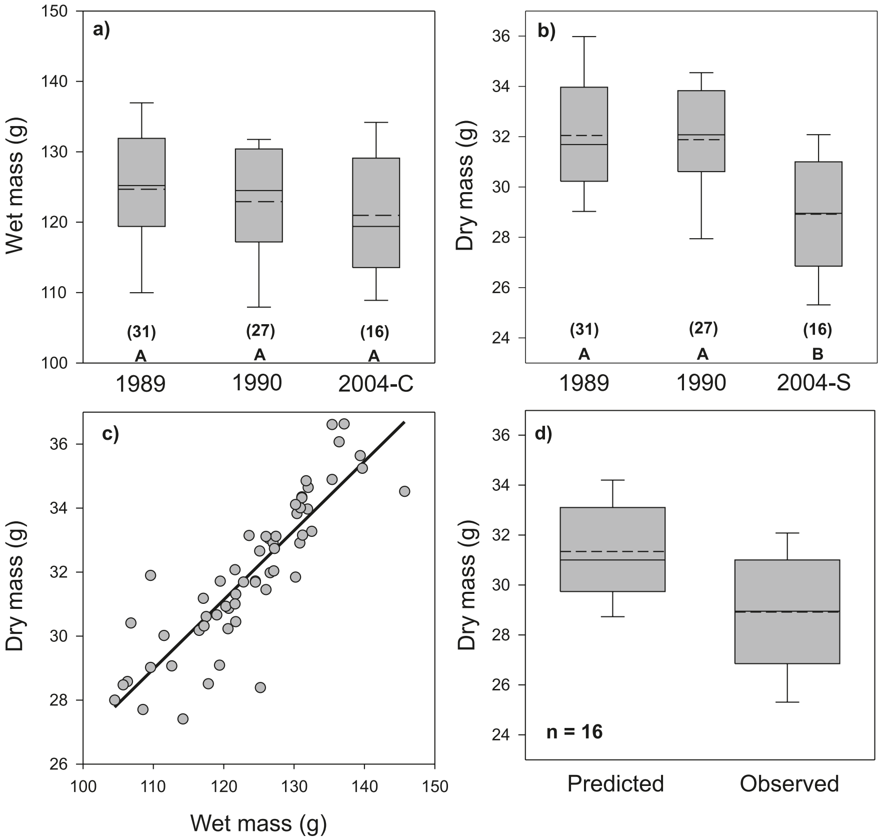
Wet mass of eggs at collection did not differ significantly among years ($F_{[2,71]} = 0.87$, $P = 0.42$; Fig. 2*a*). Dry mass of fresh eggs was not significantly different between 1989 and 1990, but dry mass of stored eggs was significantly lower than that of fresh eggs ($F_{[2,71]} = 10.60$, $P < 0.001$; Fig. 2*b*). Dry mass of fresh eggs can be predicted from their wet mass ($F_{[2,56]} = 169.98$; dry mass = 5.17 + 0.22(wet mass); $r^2 = 0.75$, $P < 0.0001$; Fig. 2*c*). Using this equation, we predicted dry mass of cached eggs (Fig. 2*d*, left bar) and compared it with measured dry mass of stored eggs (Fig. 2*d*, right bar). Dry mass of stored eggs was 8% lower than the predicted dry mass of cached eggs (paired *t* test: $t_{[15]} = 6.43$, $P < 0.001$). We attributed this 8% difference to a loss of dry mass during the 60-day storage period.

Fat, protein, and caloric contents of eggs

Fat proportion (%) was not significantly different between fresh (1989–1990 pooled) and stored (fresh: 44.8% ± 1.9%, $n = 58$; stored: 43.8% ± 3.0%, $n = 16$; Welch ANOVA: $t_{[18,35]} = 1.31$, $P = 0.21$) eggs. Mean ash and protein proportions of stored eggs were 4.8% ± 1.3% and 51.3% ± 3.7%, respectively. Using the mean ash proportion determined in stored eggs, the protein proportion of fresh eggs was thus 50.4% ± 1.9%. These values, combined to the dry masses of fresh (31.97 ± 2.32 g) and stored (28.92 ± 2.38 g) eggs (see Fig. 2*b*), indicate that mean fat and protein contents of fresh eggs were 14.4 ± 1.3 g and 16.1 ± 1.2 g, respectively, while fat and protein contents of stored eggs were 12.7 ± 1.2 and 14.8 ± 1.6 g, respectively.

Mass-specific caloric content (kJ·g^{-1}) was not significantly different between fresh (27.3 ± 0.4 kJ·g^{-1}) and stored (27.1 ± 0.6 kJ·g^{-1}) eggs (Welch ANOVA: $t_{[18,64]} = 1.36$, $P = 0.19$). The total mean caloric content of fresh and stored

Fig. 2. Wet (*a*) and dry (*b*) masses of greater snow goose (*Chen caerulescens atlantica*) eggs collected during early incubation on Bylot Island, Nunavut, Canada, during 1989, 1990, and 2004. Wet mass of all eggs was measured in the field at collection (1989 and 1990) and prior to being cached (2004-C). Dry mass of eggs was measured while they were fresh (boiled eggs, 1989 and 1990) or after they had been stored in the tundra ground for 60 days (2004-S). Means with different letters differ significantly ($P < 0.05$, Tukey's post hoc test) and numbers in parentheses show sample size. Data are presented as box plots with the median (line within the box), mean (broken line), 25th and 75th percentiles (box), and the 10th and 90th percentiles (bars). Using the regression equation between dry and wet masses of fresh eggs (*c*), we predicted initial dry mass of stored eggs from their wet mass when they were cached and compared these with their measured dry mass after a storage period of 60 days (*d*).



eggs were 873 ± 68 kJ (range 730–1016 kJ) and 783 ± 61 kJ (range 686–878 kJ), respectively ($t_{[72]} = 4.81$, $P < 0.001$). Since fat- and mass-specific caloric contents were very similar between fresh and stored eggs, the reduction of 10% in total caloric content of stored eggs corresponded to the reduction in total dry mass during storage.

Bioenergetics modeling

We estimated the mean digestible content of fresh goose eggs at 13.8 g fat (14.4 g × 96%) and 14.2 g protein (16.1 g × 88%). Therefore, the metabolizable energy (ME) of fresh eggs was 816 kJ, i.e., (13.8 g × 39.8 $\mathrm{kJ \cdot g^{-1}}$ fat) + (14.2 g × 18.8 $\mathrm{kJ \cdot g^{-1}}$ protein). Using the same calculations, ME of stored eggs was estimated at 730 kJ (11% lower than fresh eggs). Frafjord (1994) caught four 25-day-olds, wild-born arctic fox pups at their emergence from the den (0.5 kg) and monitored their food intake in outdoor cages. Pups consumed 1112 $\mathrm{kJ \cdot kg^{-1} \cdot day^{-1}}$ and grew 34 $\mathrm{g \cdot day^{-1}}$ until they reached 95 days of age (2.6 kg), that is the age of nutritional independence from their parents (Audet et al. 2002). Thus, 106 107 kJ are required to sustain the energy demand of a growing pup from emergence to independence, which corresponds to 130 fresh eggs or 145 stored eggs.

In arctic foxes, fat is deposited both subcutaneously and viscerally (ranging from 0% to 20% of skinned carcasses) and the mean fat reserve of a 3.5 kg individual during November and December approximates an energy storage of 14 740 kJ (Prestrud and Nilssen 1992). We estimated that this fat reserve was equivalent to only 20–23 fresh or 23–25 stored eggs. This was obtained by using 90%–95% and 60%–70% efficiency for conversion of egg fat and egg protein into deposited fat, respectively (Tauson et al. 2002).

Because no estimate of field metabolic rate (FMR) is currently available for arctic foxes, we used eq. 1 in Nagy et al. (1999) to predict energy requirements of a free-ranging mammal of 3.5 kg. This yielded a FMR of 1 925 $\mathrm{kJ \cdot day^{-1}}$, which represents 350 350 kJ if sustained during 6 months, an amount of energy equivalent to 429 fresh or 480 stored eggs. However, FMRs of free-ranging mammals vary widely among and within species and for arctic foxes, the upper and lower 95% confidence intervals for FMR are 5140 and 721 $\mathrm{kJ \cdot day^{-1}}$, respectively.

Contrary to FMR, several measures of BMR have been taken on arctic foxes of different body size (Fig. 1). To ease comparisons among studies and to provide realistic estimates for wild animals, we standardized BMR values for an average-sized fox of 3.5 kg. The lowest BMR value ever reported in arctic fox is 471 kJ·day^{-1} (corrected to 3.5 kg) associated with a T_{lc} of –7 °C (Fuglesteg et al. 2006). Below –7 °C, metabolic rate (MR) increases following the relationship MR = $-8.76T_{\mathrm{a}} + 408$ until –40 °C. Based on this equation and on the daily mean T_{a} recorded on Bylot Island over 8 years (Fig. 3), a fox in resting conditions would need 143 fresh or 160 stored eggs to meet the expense of thermoregulation from early October to early April (6 months in resting conditions). However, the low BMR and high T_{lc} reported by Fuglesteg et al. (2006) clearly depart from previous measurements in winter acclimatised arctic foxes. For example, Scholander et al. (1950) reported a BMR of 883 kJ·day^{-1} (corrected to 3.5 kg) that was constant from –7 to –40 °C, whereas Fuglei and Oritsland (1999) reported a BMR of 735 kJ·day^{-1} (corrected to 3.5 kg). Using 883 kJ·day^{-1} as the MR level required to maintain T_{b} constant over a temperature range of –7 to –40 °C, 197 fresh eggs or 220 stored eggs would be required to survive 6 months in resting conditions.

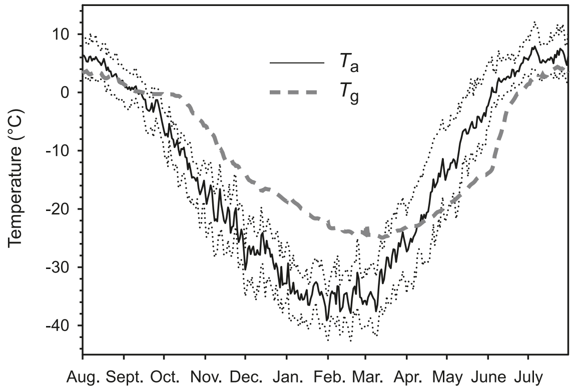
Discussion

Ecological significance of stored eggs

Our experiment suggests that once stored in tundra soil for a whole summer, eggs lose no more than 10% of their dry mass and energy content. This loss may be real and due to for instance bacterial activity, or only apparent due to our constrained experimental design (fresh eggs were boiled, whereas stored eggs were not). A 10% loss of energetic content is thus probably a maximum value for eggs stored in the cold tundra soil during a full summer, and our estimates of the energetic value of stored eggs are likely conservative.

Behavioural observations of foraging arctic foxes have been conducted in many goose colonies. Samelius and Alisauskas (2000) estimated from a mean egg acquisition rate of 4.2–7.3 eggs·h^{-1} that a single fox could acquire up to 900–1500 eggs per summer in a snow goose colony, of which 97% were cached. In a Black brant (*Branta bernicla nigricans* (Lawrence, 1846)) colony at Kokechick Bay, egg acquisition rate by foxes was 3.5 eggs·h^{-1}, of which 80% were cached (Stickney 1991). On Bylot Island, mean egg acquisition rate was 3.8 eggs·h^{-1}, of which 87% were cached (Careau et al. 2008). Using the method of Samelius and Alisauskas (2000) based on 8 h of foraging per day and a nesting season of 27 days, an average-sized fox would cache 605 eggs in Kokechick Bay and 714 eggs on Bylot Island. These estimates along with our bioenergetic calculations indicate that cached eggs can represent an extremely important source of energy relative to the needs of an arctic fox during winter, as 500 eggs correspond to >40 times the full body fat reserves of a fox, or 2–3 times the thermoregulatory costs of a resting fox during the 6 coldest months of the year. Five hundred eggs also correspond roughly to the energetic needs of a free-ranging fox during the 6 coldest months, based on estimates of field metabolic rate derived from Nagy et al. (1999).

Fig. 3. Mean daily ambient (T_{a}) and ground (T_{g}; 10 cm below surface) temperatures recorded on Bylot Island, Nunavut, Canada, averaged over 8 years (1995–2002). Dotted lines indicate the mean of daily minimum and maximum values for T_{a}.



Considering that 145 eggs are theoretically required to feed a single pup throughout its growth to independence and that arctic foxes have the largest litter size in the order Carnivora (up to 16 or 18 pups; Tannerfeldt and Angerbjörn 1998), it is unlikely that they can solely rely on eggs to sustain high reproductive output. However, individuals supplemented with stored eggs during winter and spring may realise higher reproductive output during the next breeding season (Angerbjörn et al. 1991). Long-term hoarding of eggs by arctic foxes seems common, as some eggs stored during summer are recovered in the next spring prior to reproduction (Stickney 1991; Samelius et al. 2007; V. Careau, unpublished data). In this case, stored eggs should have an overall positive effect on reproductive output.

Fat deposition is important for winter survival because body fat increases insulation when chill factor is high and constitutes an onboard fuel reserve when searching for other food sources or waiting for favourable foraging conditions. Prestrud (1991) pointed out that a cache containing 10 little auks (*Alle alle* (L., 1758)) and 4 thick-billed murres (*Uria lomvia* (L., 1758)) represents an energy storage equivalent to the mean fat deposits in a fox. The same amount of energy is contained in ~25 stored eggs of greater snow geese, which a fox can hoard in only a few hours of foraging and caching. Consequently, we agree with Prestrud (1991) that food-caching may have a high survival value for arctic foxes.

Factors limiting the benefit of cached eggs

Arctic foxes forage on goose eggs throughout the nesting season, while digestibility of eggs decreases with time as embryos develop their bones and feathers. One may therefore suggest that foxes need more eggs than we estimated to meet the various demands that we have analyzed. However, acquisition and caching rates of eggs by foxes are much higher during the laying and early-incubation periods than during the late-incubation and hatching periods (Careau et al. 2008), because nest attentiveness and defence by female greater snow geese increases as incubation progresses. Observations of arctic foxes foraging in another goose colony on Banks Island also indicated that egg acquisition rate decreased, although marginally, throughout incubation

(Samelius and Alisauskas 2000). However, these authors did not include the laying period in their study and we have shown that egg acquisition by foxes was 5 times higher during laying than later in the incubation period (Careau et al. 2008). Arctic foxes are therefore constrained to select the best quality eggs for storage and later use. This strongly reduces the potential biases that embryo development could introduce in our estimations.

One could also argue that many caches may never be recovered because they are forgotten or pilfered. However, behavioural mechanisms such as egg re-caching have evolved to reduce such loss (Careau et al. 2007*a*). This behaviour probably increases memory of cache locations and reduces pilfering (DeGange et al. 1989). Extensive behavioural observations in our study area indicated that cache pilfering by other predators such as common ravens (*Corvus corax* L., 1758) is rare (Careau et al. 2007*b*). Other factors may limit the benefit of cached eggs, such as deep snow cover and thick ice layers that may prohibit access to some stored food. Many analyses of stomach contents and scats, however, indicated that arctic foxes can recover cached food during winter (Frafjord 1993). Observations on red foxes (*Vulpes vulpes* (L., 1758)) (Sklepkovych and Montevecchi 1996) and arctic foxes (Frafjord 1993) clearly indicate that they are able to locate cached food through a deep layer of snow and recover it even when the ground is frozen. On Bylot Island, we found indirect evidence that some stored eggs had been recovered and eaten while frozen in the ground. In such case, the fox uncovered the egg, bit a hole in it, and ate its content while the lower part of the shell remained fastened in the frozen ground.

Conclusions

This paper presents a first quantitative look into egg-caching by arctic foxes from an energetic perspective. Collecting new data in the field and bridging the literature on arctic fox physiology and behaviour enabled us to demonstrate that hoarding can be a very profitable strategy for capitalizing on brief periods of resource pulses such as goose eggs (Careau et al. 2008). Our study is largely perfectible because we faced uncertainties while going through the many steps leading to estimations of the fitness value of egg-caching. For example, no measure of FMR is available for arctic foxes in winter and we had to rely on published regressions between body mass and FMR. Yet arctic foxes are known to reduce their winter energy expenditures by entering into metabolic depression, especially during famine periods when increased heat production is not required for thermoregulation (Fuglei and Oritsland 1999). This shows how the fitness value of an amazing behaviour, consisting in caching hundreds of eggs and eating them several months later in one of the harshest terrestrial environments, still needs work to be fully understood.

Acknowledgements

We thank Ambroise Lycke for field assistance and Gérald Picard for laboratory analyses. We are indebted to the Hunters and Trappers Association of Pond Inlet, Nunavut Territory, for assistance and support. V.C. is grateful to Mountain Equipment Coop for providing material and to Sanimal for a scholarship. Funding and support were provided by Polar Continental Shelf Project, Fonds Québécois de la Recherche sur la Nature et les Technologies, Nunavut Wildlife management Board, Natural Sciences and Engineering Research Council of Canada, Canada Network of Centres of Excellence ArcticNet, and Canada Research Chair Program. We thank K. Mathot for a critical review on an earlier draft of the manuscript and two reviewers for constructive criticism. This is Polar Continental Shelf Project contribution no. 052-08.

References

Ahlstrøm, O., and Skrede, A. 1995. Comparative nutrient digestibility in blue foxes (*Alopex lagopus*) and mink (*Mustela vison*) fed diets with diverging fat/carbohydrate ratios. Acta Agric. Scand. A, **45**: 74–80.

Ahlstrøm, O., and Skrede, A. 1998. Comparative nutrient digestibility in dogs, blue foxes, mink, and rats. J. Nutr. **128**: 2676S–2677S. PMID:9868238.

Ahlstrøm, O., Fuglei, E., and Mydland, L.T. 2003. Comparative nutrient digestibility of arctic foxes (*Alopex lagopus*) on Svalbard and farm-raised blue foxes (*Alopex lagopus*). Comp. Biochem. Physiol. A, **134**: 63–68. doi:10.1016/S1095-6433(02)00184-8.

Angerbjörn, A., Arvidson, B., Norén, E., and Strömgren, L. 1991. The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment. J. Anim. Ecol. **60**: 705–714. doi:10.2307/5307.

Audet, A.M., Robbins, B.C., and Larivière, S. 2002. *Alopex lagopus*. Mamm. Species, **713**: 1–10. doi:10.1644/1545-1410(2002)713<0001:AL>2.0.CO;2.

Bantle, J.L., and Alisauskas, R.T. 1998. Spatial and temporal patterns in arctic fox diets at a large goose colony. Arctic, **51**: 231–236.

Careau, V., Giroux, J.F., and Berteaux, D. 2007*a*. Cache and carry: hoarding behaviour of arctic fox. Behav. Ecol. Sociobiol. **62**: 87–96. doi:10.1007/s00265-007-0441-z.

Careau, V., Lecomte, N., Giroux, J.F., and Berteaux, D. 2007*b*. Common ravens raid arctic fox food caches. J. Ethol. **25**: 79–82. doi:10.1007/s10164-006-0193-7.

Careau, V., Lecomte, N., Bêty, J., Giroux, J.F., Gauthier, G., and Berteaux, D. 2008. Hoarding of pulsed resources: temporal variations in egg-caching by arctic foxes. Ecoscience, **15**: 268–276. doi:10.2980/15-2-3097.

Casey, T.M., Whiters, P.C., and Casey, K.K. 1979. Metabolic and respiratory response of arctic mammals to ambient temperature during the summer. Comp. Biochem. Physiol. A, **64**: 331–341. doi:10.1016/0300-9629(79)90452-3.

Chesemore, D.L. 1968. Notes on the food habits of Arctic foxes in northern Alaska. Can. J. Zool. **46**: 1127–1130. doi:10.1139/z68-161.

Choinière, L., and Gauthier, G. 1995. Energetics of reproduction in female and male greater snow geese. Oecologia (Berl.), **103**: 379–389. doi:10.1007/BF00328628.

DeGange, A.R., Fitzpatrick, J.W., Layne, J.N., and Woolfenden, G.E. 1989. Acorn harvesting by florida scrub jays. Ecology, **70**: 348–356. doi:10.2307/1937539.

Enggaard Hansen, N., Finne, L., Skrede, A., and Tauson, A.H. 1991. Energiforsyning hos mink ogræv. Rep. No. 63, Nordic Agricultural Scientists, Copenhagen, Denmark.

Fay, F.H., and Stephensen, R.O. 1989. Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. Can. J. Zool. **67**: 1986–1994. doi:10.1139/z89-283.

Frafjord, K. 1993. Food habits of arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. Arctic, **46**: 49–54.

Frafjord, K. 1994. Growth rates and energy demands in captive juvenile arctic foxes *Alopex Lagopus* in Svalbard. Polar Biol. **14**: 355–358. doi:10.1007/BF00238452.

Fuglei, E. 2000. Physiological adaptations of the arctic fox to high Arctic conditions. Ph.D. thesis, Departement of Biology, University of Oslo, Oslo, Norway.

Fuglei, E., and Oritsland, N.A. 1999. Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (*Alopex lagopus*) at Svalbard. J. Comp. Physiol. B, **169**: 361–369. PMID:10549138.

Fuglesteg, B.N., Haga, O.E., Folkow, L.P., Fuglei, E., and Blix, A.S. 2006. Seasonal variations in basal metabolic rate, lower critical temperature and responses to temporary starvation in the arctic fox (*Alopex lagopus*) from Svalbard. Polar Biol. **29**: 308–319. doi:10.1007/s00300-005-0054-9.

Gagnon, C., Cadieux, M.C., Gauthier, G., Lévesque, E., Reed, A., and Berteaux, D. 2004. Analyses and reporting on 15 years of biological monitoring data from Bylot Island, Sirmilik National Park of Canada. Sci. Rep., Centre d'études nordiques, Université Laval, Québec.

Gauthier, G., Giroux, J.F., and Bédard, J. 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Can. J. Zool. **70**: 2077–2087. doi:10.1139/z92-280.

Hadj-Chikh, L.Z., Steele, M.A., and Smallwood, P.D. 1996. Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. Anim. Behav. **52**: 941–948. doi:10.1006/anbe.1996.0242.

Kapel, C.M.O. 1999. Diet of arctic foxes (*Alopex lagopus*) in Greenland. Arctic, **52**: 289–293.

Klir, J.J., and Heath, J.E. 1992. Metabolic rate and evaporative water loss at different ambient temperatures in two species of fox: the red fox (*Vulpes vulpes*) and the arctic fox (*Alopex lagopus*). Comp. Biochem. Physiol. A, **101**: 705–707. doi:10.1016/0300-9629(92)90347-S.

Korhonen, H., Harri, M., and Asikainen, J. 1983. Thermoregulation of polecat and racoon-dog: a comparative study with stoat, mink and blue foxes. Comp. Biochem. Physiol. A, **74**: 225–230. doi:10.1016/0300-9629(83)90592-3. PMID:6131765.

Nagy, K.A., Girard, I.A., and Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annu. Rev. Nutr. **19**: 247–277. doi:10.1146/annurev.nutr.19.1.247. PMID:10448524.

Prestrud, P. 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. Arctic, **44**: 132–138.

Prestrud, P. 1992. Food habits and observations of the hunting behaviour of Aactic foxes, *Alopex lagopus*, in Svalbard. Can. Field-Nat. **106**: 225–236.

Prestrud, P., and Nilssen, K. 1992. Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. J. Wildl. Manage. **56**: 221–223. doi:10.2307/3808816.

Prestrud, P., and Pond, C.M. 2003. Fat indices of arctic foxes *Alopex lagopus* in Svalbard. Wildl. Biol. **9**: 193–197.

Randall, E.L. 1974. Improved method for fat and oil analysis by a new process of extraction. J. Assoc. Anal. Chem. **57**: 1165–1168.

Reed, A., Hughes, R.J., and Boyd, H. 2002. Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983–1998. Wildfowl, **53**: 53–65.

Rohwer, F.C. 1986. Composition of blue-winged teal eggs in relation to egg size, clutch size, and the timing of laying. Condor, **88**: 513–519. doi:10.2307/1368280.

Samelius, G. 2000. Arctic fox predation on lesser snow geese and their eggs. M.Sc. thesis, University of Saskatchewan, Saskatoon.

Samelius, G. 2006. Foraging behaviours and population dynamics of arctic foxes. Ph.D. thesis, University of Saskatchewan, Saskatoon.

Samelius, G., and Alisauskas, R.T. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. Arctic, **53**: 279–288.

Samelius, G., Alisauskas, R.T., Hobson, K.A., and Larivière, S. 2007. Prolonging the arctic pulse: long-term exploitation of cached eggs by arctic foxes when lemmings are scarce. J. Anim. Ecol. **76**: 873–880. doi:10.1111/j.1365-2656.2007.01278.x. PMID:17714265.

Scholander, P.F. 1955. Evolution of climatic adaptation in homeotherms. Evolution, **9**: 15–26. doi:10.2307/2405354.

Scholander, P.F., Hock, R., Walters, V., and Irving, L. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. **99**: 259–271. doi:10.2307/1538742. PMID:14791423.

Sklepkovych, B.O., and Montevecchi, W.A. 1996. Food availability and food hoarding behaviour by red and arctic foxes. Arctic, **49**: 228–234.

Stickney, A. 1991. Seasonal pattern of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Can. J. Zool. **69**: 2853–2859. doi:10.1139/z91-402.

Tannerfeldt, M., and Angerbjörn, A. 1998. Fluctuating resources and the evolution of litter size in the arctic fox. Oikos, **83**: 545–559. doi:10.2307/3546681.

Tauson, A.H., Chwalibog, A., and Ahlstrøm, O. 2002. Substrate oxidation in male blue foxes (*Alopex lagopus*) during feeding, fasting and realimentation. J. Nutr. **132**: 1793S–1795S. PMID:12042531.

Tremblay, J.P., Gauthier, G., Lepage, D., and Desrochers, A. 1997. Factors affecting nesting success in greater snow geese — effects of habitat and association with snowy owls. Wilson Bull. **109**: 449–461.

Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.