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Hoarding of pulsed resources: Temporal variations in egg-caching by arctic fox[1]

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Abstract: Resource pulses are common in various ecosystems and often have large impacts on ecosystem functioning. Many animals hoard food during resource pulses, yet how this behaviour affects pulse diffusion through trophic levels is poorly known because of a lack of individual-based studies. Our objective was to examine how the hoarding behaviour of arctic foxes (*Alopex lagopus*) preying on a seasonal pulsed resource (goose eggs) was affected by annual and seasonal changes in resource availability. We monitored foraging behaviour of foxes in a greater snow goose (*Chen caerulescens atlanticus*) colony during 8 nesting seasons that covered 2 lemming cycles. The number of goose eggs taken and cached per hour by foxes declined 6-fold from laying to hatching, while the proportion of eggs cached remained constant. In contrast, the proportion of eggs cached by foxes fluctuated in response to the annual lemming cycle independently of the seasonal pulse of goose eggs. Foxes cached the majority of eggs taken (> 90%) when lemming abundance was high or moderate but only 40% during the low phase of the cycle. This likely occurred because foxes consumed a greater proportion of goose eggs to fulfill their energy requirement at low lemming abundance. Our study clearly illustrates a behavioural mechanism that extends the energetic benefits of a resource pulse. The hoarding behaviour of the main predator enhances the allochthonous nutrients input brought by migrating birds from the south into the arctic terrestrial ecosystem. This could increase average predator density and promote indirect interactions among prey.

Keywords: arctic goose colony, food storing, lemming cycle, predator response.

Résumé : Les ressources possédant des pics d'abondance ont un impact important sur le fonctionnement des écosystèmes. Plusieurs animaux mettent de la nourriture en réserve durant un pic d'abondance de nourriture, mais la façon dont ce comportement influence la diffusion du pic d'abondance entre les niveaux trophiques est peu connue – principalement à cause d'un manque d'études au niveau individuel. Notre objectif était d'examiner comment le comportement de mise en réserve du renard arctique (*Alopex lagopus*) était influencé par les variations annuelles et saisonnières de la disponibilité en nourriture. Nous avons observé le comportement des renards s'approvisionnant grâce à une abondance saisonnière d'œufs dans une colonie de grandes oies des neiges (*Chen caerulescens atlanticus*) durant 8 saisons de nidification et couvrant sur 2 cycles complets de lemmings. Le nombre d'œufs acquis et cachés par les renards diminuait de la période de ponte jusqu'à l'éclosion alors que la proportion d'œufs cachés demeurait constante. À l'inverse, la proportion d'œufs cachés variait en fonction du cycle de lemmings, et ce, malgré une augmentation du taux d'acquisition d'œufs d'oies. Les renards ont caché la majorité (> 90 %) des œufs acquis durant les années de haute à moyenne abondance de lemmings. Cette proportion a diminué jusqu'à 40 % durant les années de faible abondance, probablement parce que les renards ont dû consommer une plus grande proportion d'œufs d'oies pour combler leurs besoins énergétiques durant ces années. Cette étude révèle un mécanisme comportemental important qui prolonge les bénéfices énergétiques d'un pic d'abondance. Le comportement de mise en réserve des prédateurs augmente l'intrant allochtone amené du sud par les oiseaux migrateurs dans le système arctique, ce qui en retour pourrait faire augmenter la densité moyenne de prédateurs et favoriser des interactions indirectes entre les proies.

Mots-clés : Arctique, colonie d'oies des neiges, mise en réserve de nourriture.

Nomenclature: Anonymous, 2007.

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Introduction

Resource availability changes over time in all natural systems and has major impacts on ecosystem functioning. Resource pulses are ephemeral events of resource superabundance that occur in a wide range of ecosystems, such as mast fruiting by trees, hurricane-mediated green falls, insect outbreaks, and storm-induced transport of marine resources to terrestrial systems (Ostfeld & Keesing, 2000). Although some general patterns of community response to diverse resource pulses have been described (Paetzold, Bernet & Tockner, 2006; Yang, 2006), little is known on the behavioural adaptations of consumers with regard to management of the energy provided by resource pulses. As a result, the effects of pulsed resources on ecosystems remain unclear, and studies focusing on mechanisms involved at the individual level are needed (Schoener, 1986). While some consumers can anticipate the occurrence of resource pulses (Boutin *et al.,* 2006), they cannot control their timing or intensity. Consumers may, however, use behavioural strategies to maximize the exploitation of resource pulses when they occur, such as tracking pulses over time (Wilmers *et al.,* 2003) or caching large amounts of resources. In that way, hoarding behaviour can be an effective strategy for capitalizing on brief periods of resource abundance (Humphries *et al.,* 2002). Indeed, many birds and mammals are known to hoard large quantities of seeds during mast events, which have consequences on trophic dynamics (*i.e.,* seed germination; Vander Wall, 1990; Schmidt & Ostfeld, 2003). Yet, temporal variation in hoarding of pulsed resources and its potential impact on food webs remain poorly explored in most ecosystems.

Arctic tundra is often characterized by resource pulses that have significant impacts on the functioning of this ecosystem (Ims & Fuglei, 2005). Lemming populations usually exhibit strong fluctuations with a periodicity of 3–5 y (Gilg, Hanski & Sittler, 2003), which affect life history traits of their main terrestrial predator, the arctic fox (*Alopex lagopus*; Tannerfeldt & Angerbjörn, 1996). For example, during peak lemming years (pulse), arctic foxes have high pregnancy rates and large litter sizes, resulting in a numerical response with a 1-y time lag (Angerbjörn, Tannerfeldt & Erlinge, 1999). Conversely, reproductive output of foxes is considerably reduced during low lemming years (inter-pulse period, Gauthier *et al.,* 2004). Arctic foxes can rely opportunistically on seasonal pulsed resources such as seal and reindeer (*Rangifer tarandus*) carcasses as well as eggs of ground- and cliff-nesting birds (Bantle & Alisauskas, 1998; Roth, 2002; Eide *et al.,* 2005).

Several goose species breed in the tundra during the short Arctic summer. Their high nesting synchrony and colonial habit provide arctic foxes with a clumped, superabundant, and predictable pulsed resource (Figure 1). The abundance of this allochthonous resource increases rapidly and reaches its maximum during laying, decreases gradually throughout incubation because of egg predation, and then ends abruptly during the synchronous hatch. Because arctic foxes forage primarily on lemmings when abundant (main prey) and switch to goose eggs (alternative prey) when lemmings are scarce, annual nest predation rate can vary from 20–80% (Bêty *et al.,* 2001; 2002). Foxes living near goose colonies hoard as much as > 80% of eggs they take (Stickney, 1991; Samelius & Alisauskas 2000; Careau,

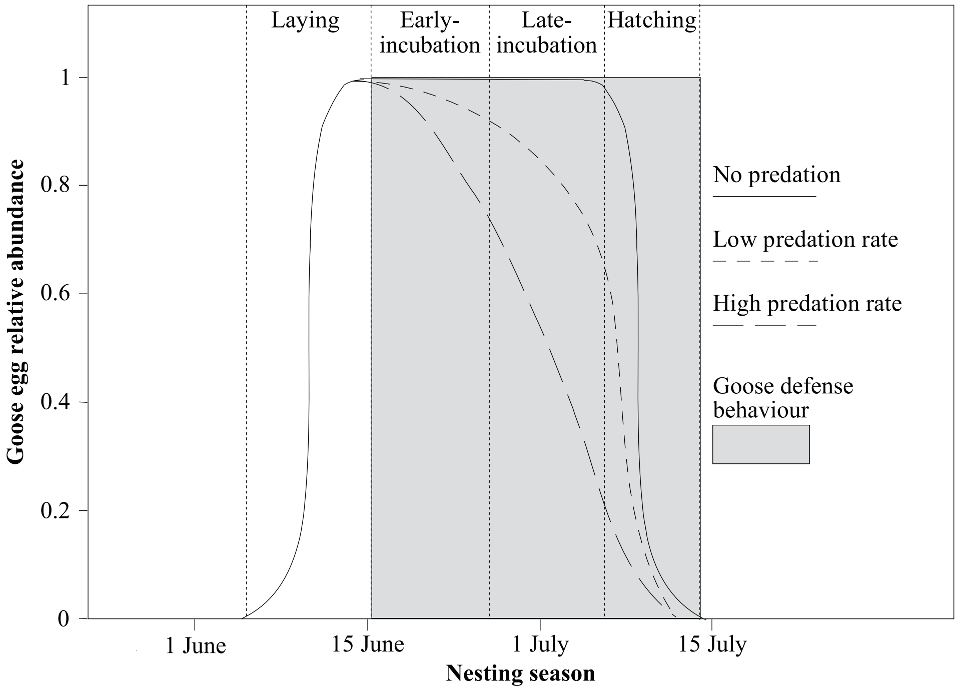

FIGURE 1. Relative abundance and timing of the seasonal pulse of greater snow goose eggs on Bylot Island, Nunavut. The nesting season was divided into 4 periods for the analyses (laying, early incubation, late incubation, and hatching). Nest abandonment is generally rare in greater snow geese (Bêty *et al.,* 2001). Predation by arctic fox is the main cause of decrease in egg abundance during incubation and can vary from ~20% predation rate (low predation years) to 80% (high predation years; Bêty *et al.,* 2002). The shaded portion of the graph represents the period during which geese attend their nest most of the time (~95%, for incubation) and defend their eggs against predators (Choinière & Gauthier, 1995).

Giroux & Berteaux, 2008). Arctic fox may hoard eggs in 2 steps (cache and recache) to increase their acquisition rate and reduce pilferage (Careau, Giroux & Berteaux, 2008). Temporal changes in caching and recaching intensity have been poorly documented in canids and most other carnivores (Vander Wall, 1990). Caching of prey and recovery may occur at any time of the year and seems to be related to food availability and the nutritional status of the predator (Macdonald, 1976; Sklepkovych & Montevecchi, 1996; Samelius *et al.,* 2007). Better knowledge about how temporal fluctuations in food abundance influence caching, recovery, and recaching behaviours should improve our understanding of the mechanisms underlying hoarding of resource pulses.

The objective of our study was to examine how the hoarding behaviour of a carnivore (arctic fox) preying on a seasonally abundant pulsed resource (goose eggs) was affected by temporal changes in resource availability (cyclic lemming populations and egg abundance). We monitored lemming abundance, goose nesting phenology and egg abundance, the rate at which foxes acquired and cached goose eggs, and the fate of depredated eggs (eaten, cached, or recached) over 2 complete lemming cycles of 4 y each. We examined whether caching rate (number of cached items per h), recovery rate (number of recovered caches per h), and caching proportion (% of items cached *versus* consumed) were related to the availability of goose eggs or to variation in lemming abundance. Seasonally, egg abundance and availability reach their maxima during the laying period, when geese spend most of their time feeding away from their nests (Gauthier & Tardif, 1991). Therefore, we expected that foxes cache eggs at a higher rate during this period. As lemmings become scarce from year to year, arctic foxes should consume a greater proportion of goose eggs (the alternative prey) to fulfill their immediate energy requirement. We predicted that they would cache a lower proportion of eggs during low phases of the lemming cycle than during lemming peaks.

Methods

STUDY AREA

The study was conducted on Bylot Island, Nunavut, Canada (72° 53' N, 79° 54' W), during 8 summers from 1996 to 1999 and 2002 to 2005. Bylot Island is part of the Sirmilik National Park of Canada and is the most important breeding site for the greater snow goose (*Chen caerulescens atlanticus*) population, with over 20 000 nesting pairs (Gauthier *et al.,* 2004). We conducted fieldwork in the highest nest density area of the colony, located in a mosaic of wet polygon fens and dry upland surrounded by extensive upland habitats (see Tremblay *et al.,* 1997 for a detailed description).

ANNUAL VARIATION IN LEMMING ABUNDANCE

Brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings coexist on the study area (Gauthier *et al.,* 2004). Starting in 1994, we monitored abundance of these 2 species in late July using snap-trap censuses at a site located 30 km away from our observation site. In 1993, lemming abundance was estimated from lemming nests (see Bêty *et al.,* 2001 for details). Trapping was done in 2 plots (wet polygon fens and mesic upland). In each plot, 50 Museum special traps baited with peanut butter and rolled oat were set every 10 m on 2 parallel transect lines (100 m apart) following the protocol of Shank (1993). Traps were set within 1–2 m of each station, near a lemming burrow when possible, and were checked daily for 10 d. One trapping day was added when the number of misfired traps was greater than 25. Each year, the total number of trap nights was thus around 1000. Years were further classified according to number of years after the occurrence of a lemming peak (time lag since lemming peak).

SEASONAL VARIATION IN GOOSE EGG ABUNDANCE

We searched portions of the colony for goose nests during egg-laying and incubation each year (see Bêty *et al.,* 2001). For nests found during incubation, laying date (day of the first laid egg) was determined by estimating incubation stage or by backdating from hatching date (Lepage, Gauthier & Menu, 2000). Nest initiation usually occurs in June and is highly synchronized: about 70% and 90% of nests are initiated within 4 and 8 d, respectively (Gauthier & Tardif, 1991; Lepage, Gauthier & Menu, 2000). Nest attentiveness by female geese increases as egg-laying progresses (Poussart, Larochelle & Gauthier, 2000). Incubation lasts ~23 d, and hatching occurs in early July. Arctic fox is the main predator of goose eggs and can account for up to 90% of eggs depredated (Bêty *et al.,* 2001). As geese can defend their nest, fox attacks are rarely successful when females are on their nest (< 10% success rate), but success rate can reach > 90% when parents are away from their nest (> 10 m; Bêty *et al.,* 2002). Because egg abundance (number of eggs in the colony) and accessibility (degree of nest attendance and defence) change during the goose nesting season, we divided it into 4 periods: laying, early-incubation, late-incubation, and hatching (Figure 1). Laying and hatching periods span from –5 to +5 d from the respective median dates. Early-incubation period ranged from day 6 to 15 after the median laying date, whereas late-incubation ranged from –11 to –6 d from hatching date. Finally, annual goose nest density (nest density hereafter) has been estimated since 1996 by searching nests in the same sample area (9.6 ha) located in the observation area and in the centre of the colony. This area is known to be representative of the whole colony, including where arctic fox behaviour was sampled (Bêty *et al.,* 2001).

BEHAVIOURAL OBSERVATIONS

Behavioural observations took place from 23 June to 8 July during the laying, incubation, and hatching periods of geese in all years but 2004 and 2005, when observations began 8 June and stopped 14 July to sample the laying and hatching periods more intensively. Each year, observations were conducted by 2 observers and averaged 145 ± 34 $h \cdot y^{-1}$ (mean ± SE) (Table I). Three of us (J. Bêty, N. Lecomte, and V. Careau) collected 73% of the data, while the rest was done by 3 other observers who were trained by one of us at the beginning of each season. During the first lemming cycle (1996–1999), 24 observation periods of 4 h were conducted systematically in rotation throughout the 24-h daylight cycle. During the second lemming cycle (2002–2005), 61% of the observation effort was spent between 2000 and 0400 to maximize the likelihood of

TABLE I. Stage of the lemming cycle, nesting parameters of greater snow geese, and details on the behavioural observations of foraging foxes on Bylot Island, Nunavut, 1996–2005.

Year	Number of years after lemming peak	Goose nests·ha^{-1}	Number of nests monitored	Median laying date	Median hatching date	Periods of observation	Observation effort (h)
1996	0	1.3	367	14-June	11-July	22 June – 6 July	96
1997	1	3.3	326	10-June	7-July	23 June – 6 July	96
1998	2	4.5	349	7-June	4-July	23 June – 1 July	96
1999	3	1.4	185	17-June	12-July	24 June – 8 July	96
2002	2	7.4	470	16-June	11-July	23 June – 10 July	111
2003	3	11	585	9-June	6-July	13 June – 2 July	92
2004	0	0.8	676	11-June	7-July	15 June – 12 July	198
2005	1	3.8	346	12-June	8-July	8 June – 14 July	363

observing foxes. Although fox activity is usually higher at night (V. Careau and J. Bêty, unpubl. data), there was no difference in egg acquisition rate ($F_{1, 95} = 1.45$, $P = 0.23$) and caching rate ($F_{1, 95} = 0.46$, $P = 0.50$) between this period and the rest of the day. Although sampling method slightly changed over time, we believe it has limited impact on the results because (1) a few experienced observers collected most of the observations; (2) behaviour of actively foraging foxes, in terms of rates of egg acquisition and caching, did not change from day to night; and (3) each lemming cycle and nesting season were sampled in a constant way throughout its entire duration.

We observed foxes foraging in the goose colony using a 20–60x spotting scope from 1 blind in 1996–1999, 2 blinds in 2002–2004, and 3 blinds in 2005. From a blind, an observer could accurately monitor foraging behaviour over ~2 km^2 of the colony. Observation limits were set by visibility and topography. We did not conduct behavioural observations under fog or rain conditions because poor visibility reduced our probability of detecting foxes. When 2 foxes were observable, the closest one was sampled except when it was not foraging actively (*e.g.,* when grooming or engaged in intra-specific agonistic interactions). We monitored focal foxes as long as they were foraging actively within the observation limits. Overall, we had visual contact with foraging foxes during a total of 58 h out of 1148 h spent in observation blinds. From 1999 to 2002, foxes were identified on a daily basis by the distinctive patterns of their fur (shedding from winter to summer pelage). Multiple sightings of an individual during an observation period were pooled and treated as a single foraging period (the sample unit). During 2004–2005, identification was facilitated by ear tags fitted to some foxes during a concurrent study. Although none of the marked fox observed in 2004 was sampled in 2005, we cannot exclude this possibility for other years. We marked 41 adult foxes from 2003 to 2006, of which 9 were recaptured (or observed) from 2004 to 2007 (D. Berteaux, unpubl. data). We believe that this relatively low recapture/re-observation rate (22%) is representative of the resighting probability of a given unmarked fox during 2 consecutive years.

Each time a fox acquired a goose egg, we noted the source from which it was taken (nest or cache) and subsequent fate (eaten or cached). The source and fate of an egg were considered unknown when a fox appeared or disappeared with an egg in its mouth. Eggs were considered recovered from a cache when a fox dug up an egg from the ground (Vander Wall, 1990). All these different behaviours were clearly distinguishable as long as the fox was foraging within observation limits. Because we focused on actively foraging and caching foxes, we restricted our analyses to successful foraging periods, which included either acquisition and/or recovery of at least 1 egg.

STATISTICAL ANALYSES

To give an overall estimate of egg acquisition, recovery, and caching rates, we used the slope of the relation (forced through the origin) between number of eggs acquired from nest, recovered from caches, and cached relative to the observation length, respectively (*sensu* Samelius & Alisauskas, 2000). We performed GLM analysis using Poisson distribution (ideal for count data where variances increase with the mean) to test the effects of nesting period, time lag since lemming peak, and nesting density on the number of eggs acquired, recovered, and cached. Observation length was included as a covariate in all models. The correlation between acquisition, recovery, and caching rates—expressed as number of eggs acquired, recovered, and cached divided by observation length—was determined using Spearman correlations (r_s; count data were not distributed normally; Shapiro–Wilk test: $W < 0.90$, $P < 0.001$). Because we were unable to identify foxes from one year to the next, we could not calculate the true (*i.e.,* inter-individual) variances of our measures of foraging behaviour. To avoid potential pseudoreplication, we restricted the number of available degrees of freedom to 25 for each model. This represents the most conservative number of different individuals that we sampled throughout the 8 y of the study, as we monitored 4 to 8 individuals each year, with a potential resighting probability of 22% (see above).

We examined how seasonal and annual variation in food abundance influenced the fate of eggs (whether they were cached or eaten) using logistic regression. In this analysis, the fate of multiple eggs acquired by an individual during a foraging period is a repeated measure. We thus used the generalized estimating equation (GEE) with the logit link function implemented in SAS (procedure GENMOD using the statement REPEATED; SAS Institute Inc. 2005) to model caching behaviour. The GEE method estimates the within-cluster similarity of residuals and uses this estimated correlation to re-estimate the regression parameters and to calculate standard errors (Hanley *et al.,* 2003). We modeled the working correlation matrix with an exchangeable correlation structure (one correlation coefficient for all individuals and repeated measures; Horton & Lipsitz, 1999). The GEE method thus considers each foraging period as independent. We used a type 3 GEE analysis to test for significance of a variable in the model with other variables already included (nesting period and density, time lag after peak lemming year, and egg source). Further correlation in our data exists because some eggs were acquired from the same nest. To overcome the potential problem of a spatial correlation structure, we weighted each egg according to the nest that it came from. For example, if a fox acquired 4 eggs from a given nest, a weight of 0.25 was conferred to each of these eggs. Unbalanced sampling design precluded the inclusion of second-order interaction terms in the ANOVA and the GEE models. All probabilities are 2-tailed, significance level was set at $\alpha = 0.05$, and means are reported with ± SE.

Results

Pulse occurence: Lemming and goose egg abundance

The snap-trap census indicated lemming peaks in 1993, 1996, 2000, and 2004 (Figure 2). Nesting of nomadic predators, such as snowy owls (*Bubo scandiacus*), was confirmed during these 4 y only (Gauthier *et al.,* 2004; G. Gauthier, unpubl. data), providing evidence that our lemming sampling design was sufficient to detect peak lemming years (Wiklund, Kjellen & Isakson, 1998). Our study thus encompassed 2 complete lemming cycles of 4 y. Median dates of goose laying and hatching ranged from 7 to 17 June and 4 to 12 July, respectively. The difference between these two events was relatively constant among years (range 25–27 d; Table I). This means that the duration of the pulse in goose egg abundance was similar among years, although its timing differed annually (Figure 1). Estimated nest density in the observation area varied 14-fold among years (0.8 to 11 nests·ha^{-1}; Table I).

Egg acquisition rate

Foxes obtained 228 eggs from 209 nests and 69 eggs from as many caches during 141 successful foraging periods (*i.e.,* ≥ 1 egg acquired or recovered). Overall, the mean egg acquisition rate from goose nests was 3.5 ± 0.3 eggs·h^{-1}. Acquisition rates differed among nesting periods and phases of the lemming cycle (Table II). Egg acquisition rate declined 7-fold from laying to hatching (Figure 3a). Acquisition rate increased 3.6-fold from the lemming peak years (time lag year 0) to the end of the lemming cycle (Figure 3a). Nest density had no effect on acquisition rate (Table II).

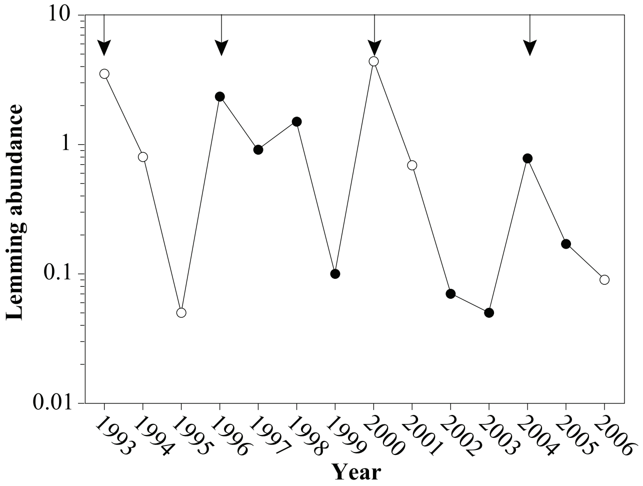

Figure 2. Index of lemming abundance (pooled number of *Lemmus sibiricus* and *Dicrostonyx groenlandicus* caught per 100 trap-nights) recorded on Bylot Island, Nunavut. Arrows indicate peak lemming years and closed circles indicate years with observations of arctic fox behaviour. The value 0.05 was added for years of zero lemming abundance, representing half the smallest index value that could be recorded by our sampling method.

Egg recovery rate

Over the 8 y of the study, egg recovery rate from caches averaged 1.0 ± 0.1 eggs·h^{-1} and varied among nesting seasons and phases of the lemming cycle (Table II). Egg recovery rate was not related to nest density but increased 4-fold from mid- to late incubation (Table II). We did not observe any fox recovering a cached egg during the low phase of the lemming cycle, yielding a recovery rate of 0 for these years (Figure 3b). Acquisition and recovery rates were negatively correlated ($r_s = -0.70$, $P < 0.001$, $n = 141$).

Egg caching rate

The mean caching rate was 3.7 ± 0.3 eggs·h^{-1}. Caching rate was positively correlated with acquisition rate ($r_s = 0.49$, $P < 0.001$, $n = 141$) but negatively correlated with recovery rate ($r_s = -0.20$, $P = 0.016$, $n = 141$). Caching rates varied both seasonally and annually (Table II). On a seasonal basis, caching rates followed the same trend as acquisition rates, declining 6-fold from laying to hatching periods (Figure 3c). On an annual basis, however, caching rate dropped from 4.5 ± 0.5 to 2.4 ± 0.5 eggs·h^{-1} during the first to the third year after a lemming peak, although acquisition rate showed the opposite trend (Figures 3a and 3c).

Table II. GLM analyses testing the effects of the time lag since lemming peak, nesting period, nest density, and observation length on number of (a) eggs acquired from nest, (b) eggs recovered from caches, and (c) eggs cached by arctic fox on Bylot Island, Nunavut, 1996–2005. Statistically significant variables are in bold (see text and Figure 3 for details). Number of degrees of freedom available for each model was 25, since this is the most conservative number of different foxes that we sampled during our study (see Methods).

	df	Sum of squares	Mean squares	*F* value	*P*
a) Acquisition rate					
Time lag since lemming peak	3	49.1	16.4	5.3	0.01
Nesting period	3	130.6	43.5	14.0	0.001
Nest density	1	2.3	2.3	0.7	0.4
Observation length	1	139.7	139.7	44.8	< 0.001
Residuals	16	411.6	3.1		
b) Recovery rate					
Time lag since lemming peak	3	15.9	5.3	11.8	< 0.001
Nesting period	3	5.6	1.9	4.2	0.02
Nest density	1	0.07	0.07	0.2	0.7
Observation length	1	0.8	0.8	1.7	0.21
Residuals	16	58.9	0.5		
c) Caching rate					
Time lag since lemming peak	3	120.1	40.0	12.6	< 0.001
Nesting period	3	104.6	34.9	11.0	< 0.001
Nest density	1	0.3	0.3	0.1	0.76
Observation length	1	136.0	136.0	42.9	< 0.001
Residuals	16	418.4	3.2		

This was explained by a much lower caching proportion during these years (see below).

EGG CACHING PROPORTION

There were no annual or seasonal differences in the proportion of eggs with unknown fate ($n = 20$) when accounting for the source (*i.e.,* nest or cache; $\chi^2 < 6.02$, $df = 3$, $P > 0.05$). We thus discarded eggs with unknown fate to calculate the proportion of eggs cached during 135 foraging periods and found no seasonal ($\chi^2 = 3.26$, $df = 3$, $P = 0.33$) or nest density effects ($\chi^2 = 0.04$, $df = 1$, $P = 0.84$). Overall, foxes cached 87% of the eggs acquired from nests ($n = 219$) and recached 64% of the eggs recovered from caches ($n = 58$; source effect: $\chi^2 = 14.2$, $df = 1$, $P < 0.001$; Figure 4). Time lag after peak lemming year affected egg caching proportion ($\chi^2 = 14.2$, $df = 3$, $P < 0.01$). Foxes cached a lower proportion of eggs during the third year after lemming peak than during any other years (Figure 4; $\chi^2 \geq 20.2$, $df = 1$, $P < 0.001$ for all comparisons between time lag 3 *versus* time lag 0, 1, and 2). Foxes ate a higher proportion of acquired eggs in the low phase of the lemming population cycle. Re-caching proportion was not affected by time lag after lemming peak (time lag 0, 1, and 2 only, as no observations were made with a time lag 3; $n = 58$, $\chi^2 = 1.71$, $df = 2$, $P = 0.43$).

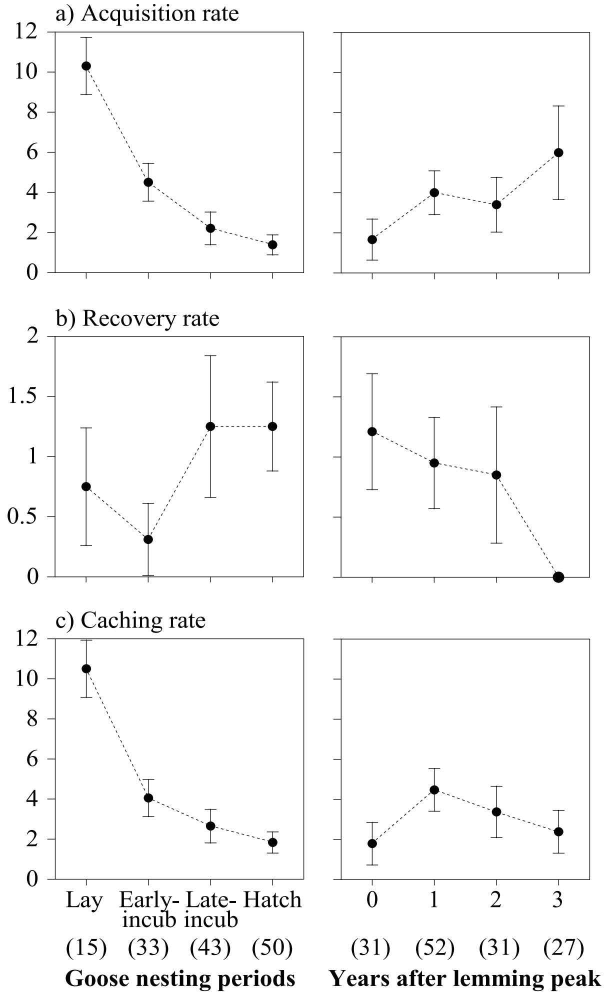

FIGURE 3. Seasonal and annual variations in a) acquisition rate (eggs from nests), b) recovery rate (eggs from caches), and c) caching rate of arctic fox on Bylot Island, Nunavut, 1996–1999 and 2002–2005. Rates were determined using the slope of the regression between number of eggs acquired, recovered, and cached relative to the observation length and are presented with their 95% confidence interval. Numbers in parentheses represent sample size (number of foraging periods). Only successful foraging periods are considered (with the acquisition or recovery of at least 1 egg).

Discussion

The natural experimental setting of the Bylot Island terrestrial ecosystem allowed us to show how foraging and caching behaviour of an arctic carnivore varied with seasonal and annual fluctuations in resource abundance. Arctic foxes cached similar proportions of eggs throughout the nesting season, yet the rate at which they cached eggs decreased from laying to hatching as a consequence of decreasing acquisition rate. Arctic foxes cached a much lower proportion of eggs when lemmings were scarce (*i.e.,* third year after the peak) despite a high acquisition rate. This means that the proportion of alternative prey that is cached is related to the abundance of the primary prey. Such temporal variations in the management of a seasonal resource pulse are part of a behavioural mechanism that optimizes the use of the pulse by delaying its consumption through hoarding.

Although caching proportion is lower during low lemming years, it is likely that arctic foxes hoard similar amounts of eggs each year. Indeed, predation rate on goose eggs increases as lemming become scarce (Bêty *et al.,* 2002), leading to an increase in egg acquisition rate (Figure 3a). In low lemming years, consumption of cached eggs may also be higher during fall and spring (Samelius *et al.,* 2007). By combining our results with those of predator activity budget and density, we could better quantify the energy transfer from resource pulses to consumers and its diffusion through trophic levels in the arctic tundra. Use of the stable isotope technique could also help in quantifying the proportion of cached eggs that are recovered and con-

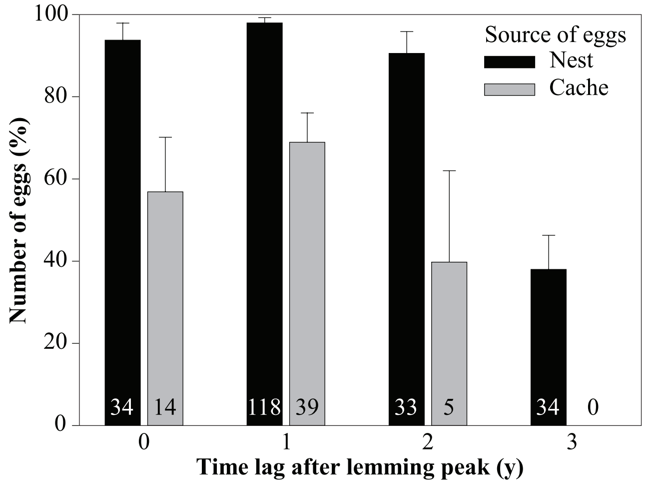

FIGURE 4. Annual variation in the percentage (+SE) of goose eggs cached by arctic foxes according to the source of eggs (nest or cache) and the time lag after the lemming peak on Bylot Island, Nunavut, 1996–1999 and 2002–2005. Sample size is shown within bars.

sumed by arctic foxes throughout the year (Giroux, 2007; Samelius *et al.,* 2007).

ACQUISITION RATE OF A SEASONAL RESOURCE PULSE

Active nest defence by snow geese is the primary factor limiting foraging success of arctic foxes (Samelius & Alisauskas, 2001; Bêty *et al.*, 2002), and this likely explains most of the seasonal pattern in egg acquisition rate. During laying, geese spent most of their time feeding away from their nests (Gauthier & Tardif, 1991). Egg acquisition by foxes should then be limited mostly by travelling time between undefended nests and time spent hoarding. When incubation begins, nest defence by geese lowers the predator acquisition rate (Samelius & Alisauskas, 2001). Foraging theory also predicts a reduction in acquisition rate throughout the nesting season because predation increases the ratio of inactive *versus* active nests (Schmidt, 1999). Therefore, missed opportunities and travelling time between active nests should increase as the nesting season progresses towards hatch.

Acquisition rate should increase with nest density, as travelling time decreases from nest to nest (Schmidt, 1999). Surprisingly, when considering successful foraging periods only (*i.e.,* ≥ 1 egg acquired or recovered), nest density had no effect on acquisition rate despite its large annual variation. Two hypotheses can be put forward to explain this result. First, because geese nest in complex habitats (*e.g.,* polygon fens) that prevent terrestrial predators from travelling directly between nests, nest density may not reflect the actual distance that foxes must travel between nests (Tremblay *et al.,* 1997; Lecomte *et al.,* 2008). Therefore, travelling time and predation success may be more influenced by habitat characteristics than nest density. This habitat effect, coupled with nest defence by geese, may explain why the range of nest density observed during our study did not influence acquisition rate. Second, considered in light of a typical prey-dependent functional response, all observations made during this study may have occurred to the right of the inflection point, along the asymptotic portion of the functional response curve where predator functional response is saturated. Further studies are needed to determine if time spent searching for nests by foxes does vary as a function of goose nest densities.

MANAGEMENT OF THE PULSE

The seasonal abundance and accessibility of goose eggs decrease as the nesting season progresses, while the abundance of cached eggs increases because foxes cache a substantial proportion of eggs acquired both from nests and caches. As observed in other goose colonies (Stickney, 1991; Samelius & Alisauskas, 2000), arctic foxes tend to increase their recovery rate of cached eggs late in the nesting season. This may be a response to declining egg availability in nests and/or a result of an increasing number of cached eggs. Searching for cached eggs represents an important part of the fox time budget towards the end of the nesting season (V. Careau, pers. observ.), and the rate at which they recover eggs may be correlated with the number of cached eggs. Cache recovery rate was null in years when the proportion of eggs cached was the lowest. This suggests that cache recovery rate depends on a combination of prey availability and cache abundance. Recovery rate of cached food by hoarders may also depend on the abundance of their competitors, but our inability to discern between cache recovery and raiding impedes us from drawing conclusions on this effect (Vander Wall, 1990; Samelius & Alisauskas, 2000).

The negative association between egg acquisition and recovery rates could have several causes that are not mutually exclusive. First, arctic foxes could rely more on cached eggs when their acquisition rate is low, as do red foxes (*Vulpes vulpes*) and seed-caching rodents (Reichman & Fay, 1983; Henry, 1986). This is supported by the larger proportion of recovered eggs that were eaten by arctic foxes compared to those obtained in nests. Second, the time spent by foxes eating or recaching recovered eggs may reduce the time they could spend acquiring additional eggs from nests. The relatively high proportion of recovered eggs that were recached (64%) implies that this activity is important and could possibly limit the time available to acquire new eggs (Careau, Giroux & Berteaux, 2008). Third, what we interpreted as recaching could instead be cache pilfering, a common phenomenon in solitary, long-term hoarding animals (Vander Wall & Jenkins, 2003). Because foxes cache eggs in the goose colony, where several home ranges overlap (Anthony, 1997; Eide, Jepsen & Prestrud, 2004), there are many eggs cached by different foxes in the same area. The recaching of recovered or pilfered eggs may become a more advantageous strategy as the nesting season progresses because the abundance of cached eggs increases while the abundance of eggs in nests decreases. This could result in more time spent by foxes searching for cached eggs and moving eggs from existing caches at the expense of egg acquisition in goose nests.

ANNUAL VARIATION IN RESOURCE AVAILABILITY

Bêty *et al.* (2002) showed that foraging decisions by arctic foxes in the Bylot Island goose colony were influenced by the lemming cycle. Lemmings are profitable prey for arctic fox because they maximize the trade-off between energy reward and foraging costs such as injury risk, travel cost, and handling time (Stein, 1977; Careau, Giroux & Berteaux, 2008). In contrast, snow geese defend their nests, which increases injury risk and handling time for foxes preying upon eggs (Bêty *et al.,* 2002; Samelius & Alisauskas, 2006). Lemming abundance influences the fitness reward of goose eggs, and this is reflected in foraging decisions as foxes switch from lemmings to goose eggs in years with low lemming abundance (Bêty *et al.,* 2002). In our study, we found that lemming abundance also influences hoarding decisions by arctic foxes. Arctic foxes feed primarily on lemmings when abundant, but they still acquire goose eggs and cache a high proportion of them for later use. As the preferred prey become scarce, foxes consume a greater proportion of the alternative prey to fulfill their daily energy requirement. Hence, optimal foraging theory (Pyke, Pulliam & Charnov, 1977) could explain why eggs were cached in a lower proportion in the third year after the lemming peak. The abundance of a primary prey determines the proportion of an alternative prey that is consumed immediately rather than stored for later use. Our study reveals a behavioural mechanism of resource management that might extend the effects of resource pulses in arctic systems.

Our results contrast with other behavioural studies conducted on arctic fox foraging in goose colonies (Kokechick Bay: Stickney, 1991; Banks Island: Samelius & Alisauskas, 2000; Karrak Lake: Samelius, 2006). These studies failed to detect annual variations in egg-caching proportion, possibly because they did not encompass a complete lemming cycle or because alternative prey species were relatively scarce compared to eggs. Indeed, lemmings may have been less abundant in these colonies, as suggested by lower lemming trapping indices during peak years (Karrak Lake: 1.7 captures per 100 trap-nights [Samelius *et al.,* 2007]; Bylot Island: ~ 3.2 captures per 100 trap-nights, this study). Goose eggs may thus be the primary prey item on which arctic foxes forage in these other bird colonies, independent of lemming abundance (*i.e.,* no prey-switching mechanism as described above). Nest density was also considerably higher at Banks Island and Karrak Lake (22–34 nests·ha^{-1}) than at Bylot Island. Finally, brant goose (*Branta bernicla*) eggs at Kokechick Bay may be easier to obtain than those of snow geese due to their smaller body size. Therefore, the relatively low availability of goose eggs and the high abundance of lemmings at Bylot Island may have enhanced the effects of lemming abundance fluctuations on egg-caching by arctic foxes compared to other sites. This suggests that generalizations across study systems may not always be acceptable, even when they only differ slightly.

IMPLICATIONS FOR ARCTIC ECOSYSTEMS

Because it is often faster to cache food than to consume it (see Careau, Giroux & Berteaux, 2008), food-storing consumers have the capacity to acquire energy rapidly from pulsed resources. During mast years for instance, eastern chipmunks (*Tamias striatus*) can hoard a winter's worth of energy requirement in a single day (Humphries *et al.,* 2002). Similarly, foxes can accumulate significant energy reserves during a goose nesting season (~30 d). Indeed, the relatively high acquisition rate by actively foraging foxes (10.3 eggs·h^{-1}) during the laying period and the large amount of energy contained in a goose egg (mean of 900 ± 9 kJ·egg^{-1}, Choinière & Gauthier, 1995) make hoarding behaviour highly profitable. The amount of energy required to survive 30 d (~15 640 kJ; Prestrud, 1991) could be stored by an arctic fox in less than 2 h of active foraging and caching during the laying period. The use of a cached food reserve during periods of food scarcity (winter and spring) likely enhances arctic fox survival and the number of pups born in the following year (Angerbjörn *et al.,* 1991). Hoarding behaviour may thus increase the reproductive numerical response of arctic fox to the seasonal pulse of goose eggs.

Like many other arctic breeding goose species, the greater snow goose population has increased 14-fold in the last 40 y, in part due to the food subsidy obtained while feeding in southern agricultural lands during winter and spring (Gauthier, Giroux & Reed, 2005). For relatively unproductive Arctic terrestrial ecosystems, breeding geese represent a significant allochthonous energy input. Indeed, the effect of the pulse diffusion through trophic levels can be detected up to 10 km from the nesting goose colony (Giroux, 2007). By storing large numbers of eggs, arctic foxes lengthen both their access to eggs and that of other predators such as common ravens (*Corvus corax*) that raid food caches made by foxes (Careau *et al.*, 2007). Hence, hoarding behaviour by arctic fox could enhance the diffusion of this allochthonous resource pulse in arctic ecosystems (Gauthier *et al.,* 2004). By increasing the average predator density, the presence of a large goose colony can have long-term indirect effects on other prey species like lemmings and ground nesting birds through apparent competition (Bêty *et al.,* 2002).

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Literature cited

Angerbjörn, A., M. Tannerfeldt & S. Erlinge, 1999. Predator–prey relationships: Arctic foxes and lemmings. Journal of Animal Ecology, 68: 34–49.

Angerbjörn, A., B. Arvidson, E. Norén & L. Strömgren, 1991. The effect of winter food on reproduction in the Arctic fox, *Alopex lagopus*: A field experiment. Journal of Animal Ecology, 60: 705–714.

Anonymous, 2007. Integrated Taxonomic Information System. [Online] URL: http://www.itis.gov/ (accessed 4 April 2007).

Anthony, R. M., 1997. Home ranges and movements of Arctic fox (*Alopex lagopus*) in western Alaska. Arctic, 50: 147–157.

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

Bêty, J., G. Gauthier, J.-F. Giroux & E. Korpimäki, 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos, 93: 388–400.

Bêty, J., G. Gauthier, E. Korpimäki & J.-F. Giroux, 2002. Shared predators and indirect trophic interactions: Lemming cycles and arctic-nesting geese. Journal of Animal Ecology, 71: 88–98.

Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi & A. A. Dhondt, 2006. Anticipatory reproduction and population growth in seed predators. Science, 314: 1928–1930.

Careau, V., J. F. Giroux & D. Berteaux, 2008. Cache and carry: hoarding behaviour of Arctic fox. Behavioral Ecology and Sociobiology, 62: 87–96.

Careau, V., N. Lecomte, J. F. Giroux & D. Berteaux, 2007. Common ravens raid Arctic fox food caches. Journal of Ethology, 25: 79–82.

Choinière, L. & G. Gauthier, 1995. Energetics of reproduction in female and male greater snow geese. Oecologia, 103: 379–389.

Eide, N. E., J. U. Jepsen & P. Prestrud, 2004. Spatial organization of reproductive Arctic foxes *Alopex lagopus*: Response to changes in spatial and temporal availability of prey. Journal of Animal Ecology, 73: 1056–1068.

Eide, N. E., P. M. Eid, P. Prestrud & J. E. Swenson, 2005. Dietary responses of Arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. Wildlife Biology, 11: 109–121.

Gauthier, G., J. F. Giroux & A. Reed, 2005. Interactions between land use, habitat use and population increase in greater snow geese: What are the consequences for natural wetlands? Global Change Biology, 11: 856–868.

Gauthier, G. & J. Tardif, 1991. Female feeding and male vigilance during nesting in greater snow geese. Condor, 93: 701–707.

Gauthier, G., J. Bêty, J. F. Giroux & L. Rochefort, 2004. Trophic interactions in a High Arctic snow goose colony. Integrative and Comparative Biology, 44: 119–129.

Gilg, O., I. Hanski & B. Sittler, 2003. Cyclic dynamics in a simple vertebrate predator–prey community. Science, 302: 866–868.

Giroux, M.-A., 2007. Effets des ressources allochtones sur une population de renards arctiques à l'île Bylot, Nunavut, Canada. Mémoire de maîtrise, Université du Québec à Rimouski, Rimouski, Québec.

Hanley, J. A., A. Negassa, M. D. D. Edwardes & J. E. Forrester, 2003. Statistical analysis of correlated data using generalized estimating equations: An orientation. American Journal of Epidemiology, 157: 364–375.

Henry, J. D., 1986. Red Fox: The Catlike Canine. Smithsonian Institution Press, Washington, DC.

Horton, N. J. & S. R. Lipsitz, 1999. Review of software to fit generalized estimating equation regression models. American Statistician, 53: 160–169.

Humphries, M. M., D. W. Thomas, C. L. Hall, J. R. Speakman & D. L. Kramer, 2002. The energetics of autumn mast hoarding in eastern chipmunks. Oecologia, 133: 30–37.

Ims, R. A. & E. Fuglei, 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. BioScience, 55: 311–322.

Lecomte, N., V. Careau, G. Gauthier & J.-F. Giroux, 2008. Predator behaviour and predation risk in the heterogeneous Arctic environment. Journal of Animal Ecology, 77: 439–447.

Lepage, D., G. Gauthier & S. Menu, 2000. Reproductive consequences of egg-laying decisions in snow geese. Journal of Animal Ecology, 69: 414–427.

Macdonald, D. W., 1976. Food caching by red foxes and some other carnivores. Zeitschrift für Tierpsychologie, 42: 170–185.

Ostfeld, R. S. & F. Keesing, 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution, 16: 232–237.

Paetzold, A., J. F. Bernet & K. Tockner, 2006. Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. Freswater Biology, 51: 1103–1115.

Poussart, C., J. Larochelle & G. Gauthier, 2000. The thermal regime of eggs during laying and incubation in greater snow geese. Condor, 102: 292–300.

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

Pyke, G., H. R. Pulliam & E. L. Charnov, 1977. Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology, 52: 137–154.

Reichman, O. J. & F. H. Fay, 1983. Comparison of the diets of a caching and a noncaching rodent. American Naturalist, 122: 576–581.

Roth, J. D., 2002. Temporal variability in Arctic fox diet as reflected in stable-carbon isotopes: The importance of sea ice. Oecologia, 133: 70–77.

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

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

Samelius, G. & R. T. Alisauskas, 2001 Deterring arctic fox predation: The role of parental nest attendance by lesser snow geese. Canadian Journal of Zoology, 79: 861–866.

Samelius, G. & R. Alisauskas, 2006. Sex-biased costs in nest defence behaviours by lesser snow geese (*Chen caerulescens*): Consequences of parental roles? Behavioral Ecology and Sociobiology, 59: 805–810.

Samelius, G., R. T. Alisauskas, K. A. Hobson & S. Larivière, 2007. Prolonging the arctic pulse: Long-term exploitation of cached eggs by Arctic foxes when lemmings are scarce. Journal of Animal Ecology, 76: 873–880.

Schmidt, K. A., 1999. Foraging theory as a conceptual framework for studying nest predation. Oikos, 85: 151–160.

Schmidt, K. A. & R. S. Ostfeld, 2003. Songbird populations in fluctuating environments: Predator responses to pulsed resources. Ecology, 84: 406–415.

Schoener, T. W., 1986. Mechanistic approaches to community ecology: A new reductionism? American Zoologist, 26: 81–106.

Shank, C. C., 1993. The Northwest Territories Small Mammal Survey: 1990–1992. Manuscript Report 72, Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories.

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

Stein, R. A., 1977. Selective predation, optimal foraging, and the predator–prey interaction between fish and crayfish. Ecology, 58: 1237–1253.

Stickney, A., 1991. Seasonal pattern of prey availability and the foraging behavior of Arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Canadian Journal of Zoology, 69: 2853–2859.

Tannerfeldt, M. & A. Angerbjörn, 1996. Life history strategies in a fluctuating environment: Establishment and reproductive success in the Arctic fox. Ecography, 19: 209–220.

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

Vander Wall, S. B. 1990. Food Hoarding in Animals. University of Chicago Press, Chicago, Illinois.

Vander Wall, S. B. & S. H. Jenkins, 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology, 14: 656–667.

Wiklund, C. G., N. Kjellen & E. Isakson, 1998. Mechanisms determining the spatial distribution of microtine predators on the arctic tundra. Journal of Animal Ecology, 67: 91–98.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith & W. M. Getz, 2003. Resource dispersion and consumer dominance: Scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters, 6: 996–1003.

Yang, L. H., 2006. Interactions between a detrital resource pulse and a detritivore community. Oecologia, 147: 522–532.