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ORIGINAL PAPER

Cache and carry: hoarding behavior of arctic fox

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Abstract Food-hoarding animals are expected to preferentially cache items with lower perishability and/or higher consumption time. We observed arctic foxes (*Alopex lagopus*) foraging in a greater snow goose (*Anser caerulescens atlanticus*) colony where the main prey of foxes consisted of goose eggs, goslings, and lemmings (*Lemmus* and *Dicrostonyx* spp.). We recorded the number of prey consumed and cached and the time that foxes invested in these activities. Foxes took more time to consume a goose egg than a lemming or gosling but cached a greater proportion of eggs than the other prey type. This may be caused by the eggshell, which presumably decreases the perishability and/or pilfering risk of cached eggs, but also increases egg consumption time. Arctic foxes usually recached goose eggs but rarely recached goslings or lemmings. We tested whether the rapid-sequestering hypothesis could explain this recaching behavior. According to this hypothesis, arctic foxes may adopt a two-stage strategy allowing both to maximize egg acquisition rate in an undefended nest and subsequently secure eggs in potentially safer sites. Foxes spent more time carrying an egg and traveled greater distances when establishing a secondary than a primary cache. To gain further information on the location and subsequent fate of cached eggs, we used dummy eggs containing radio transmitters. Lifespan of primary caches increased with distance from the goose nest. Secondary caches were generally located farther from the nest and had a longer lifespan than primary caches. Behavioral observations and the radio-tagged egg technique both gave results supporting the rapid-sequestering hypothesis.

Keywords Caching decisions · Handling-time hypothesis · Optimal foraging · Rapid-sequestering hypothesis · Short-term cache

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Introduction

Food hoarding is common in a wide variety of animals (arthropods, birds, and mammals) that rely on prey whose abundance fluctuates greatly (Smith and Reichman 1984; Vander Wall 1990). Whereas hoarders can use their food reserves to survive periods of food scarcity, nonhoarders are forced to migrate, enter torpor, or suffer loss in body mass. When hoarding, animals can exert a certain control on their food supply. Food hoarding can also allow animals to optimize foraging and feeding, thereby potentially increasing their competitive ability when foraging on patches of ephemeral food (Vander Wall 1990).

The value of a food item for hoarding animals has two components: its current value if consumed immediately and its potential value if stored and consumed later (Kotler et al. 1999). Both current and future values influence the decision of what to eat or cache (caching decision). These values are largely determined by the food item characteristics, such as its perishability and the time needed for its consumption (Vander Wall 1990). Food perishability has been implicated as a primary determinant of caching decisions in many food-hoarding rodents (Smallwood and Peters 1986; Reichman 1988; Post and Reichman 1991; Gendron and Reichman 1995; Smallwood et al. 2001). Because perishability decreases the future value of stored items, animals should avoid caching perishable food. For short-term hoarding animals constrained by time when foraging and caching, the time required to eat an item can override the effects of perishability. This is referred to the consumption time hypothesis, also known as the handling time hypothesis (Jacobs 1992). For instance, captive grey squirrels (*Sciurus carolinensis*) cached items with the higher consumption time to maximize both foraging and caching efficiency (Jacobs 1992). The perishability and consumption time hypotheses are not mutually exclusive (Hadj-Chikh et al. 1996).

When food-hoarding animals recover a cached item, they do not always consume it immediately but can transfer it to another cache (Clarke and Kramer 1994; Jenkins et al. 1995; Vander Wall 1990, 1995; Vander Wall and Joyner 1998). Although recaching behavior is well documented, its adaptive significance is still poorly understood. The rapid-sequestering hypothesis predicts that animals feeding on a temporarily abundant food resource will first cache food near the source to maximize harvest rate by reducing travel costs (Jenkins and Peters 1992). However, if other foragers visit the food source, primary caches may be susceptible to pilfering as they are relatively concentrated around the food source. In this context, transferring a food item to a more distant and potentially more secure site may reduce pilferage (Vander Wall and Jenkins 2003).

Hoarding behavior is common in arctic fox (*Alopex lagopus*) (Frafjord 1993; Sklepkovych and Montevecchi 1996). This small carnivore consumes a variety of foods such as lemmings, reindeer, and seal carcasses as well as eggs and juveniles of many bird species (Elmhagen et al. 2000; Roth 2003; Eide et al. 2005). Recaching of eggs is especially prominent in goose colonies (Stickney 1991; Samelius and Alisauskas 2000). Food resources fluctuate greatly in the Arctic, making food-hoarding a potentially highly advantageous strategy, especially because low temperatures of permafrost extend the conservation of energy-rich but ephemeral food resources (Smith and Reichman 1984). Hoarding behavior by arctic fox is known to change according to seasonal and annual variations in pulsed resources; during years of very low lemming abundance, the proportion of eggs being cached decreases as a result of more eggs being eaten to fulfill daily energy requirements (Careau 2006).

Few detailed studies have been conducted on caching behavior of free-ranging carnivores despite the substantial scientific attention that this behavior has attracted. This is explained by the extreme difficulty and the vast effort required for observing predatory behavior of carnivores (Vander Wall 1990). Under the continuous sunlight of the Arctic summer, we conducted behavioral observations on free-ranging arctic foxes in an open tundra habitat where they forage on prey with different characteristics: goose eggs, goslings, and lemmings. Given that eggs possess physical and chemical mechanisms that protect them against microbial invasion (Board and Fuller 1974), they should be less perishable than lemmings and goslings. However, the eggshell, which is not consumed, could increase consumption time relative to small vertebrates. If it takes longer to eat an egg than a lemming or gosling, both the perishability and consumption time hypotheses predict that arctic fox will cache goose eggs in higher proportion than goslings and lemmings.

We examined some predictions of the rapid-sequestering hypothesis using artificial eggs tagged with radio transmitters that we tracked as they were transferred from artificial nests to primary and subsequent caches. Arctic fox should spend more time and travel longer distances when performing a secondary than a primary cache. Secondary caches should therefore be located further away from the origin (nest) than the primary caches. If secondary caches are located in safer places, their lifespan (the time elapsed between cache creation and recovery) should be longer than primary caches. We also expected that lifespan of primary caches would increase with distance from the nest.

Materials and methods

Study site

We investigated fox hoarding behavior during the summers of 2004 and 2005 on Bylot Island, (72°53′N, 79°54′W), Nunavut, Canada in a breeding colony of greater snow geese (*Anser caerulescens atlanticus*). Nest density was 0.8 and 3.8 nests/ha in 2004 and 2005, respectively. Density of other ground-nesting species was low relative to that of geese. Geese began laying in early June and hatching occurred one month later in early July. Although most geese leave the nesting area after hatching, some stayed in the area for brood rearing. The brown lemming (*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx groenlandicus*) coexist on Bylot Island (Gauthier et al. 2004). Lemming abundance was high (peak lemming year) in 2004 and moderate (declining phase) in 2005 (snap-trap census, Gauthier G., personal communication).

Behavioral observations

Each year, we observed foraging behavior of arctic foxes from June 8 to July 14. We standardized data collection among observers (three each year for a total of four) at the beginning of each field season. Although we observed foxes during both day and night, we spent more time (60%) observing from 20:00–04:00, when foxes are more active (Anthony 1997). We observed foraging foxes using a 20–60× spotting scope from two blinds in 2004 and three in 2005, and we covered approximately 2 km^2 from each blind. We identified individual foxes based on their distinctive fur patterns due to variation in timing of spring molt or from ear tags fitted to some individuals during a concurrent study. When two foxes were present in the observation area, we sampled the closest one unless it was not actively foraging. An observation session was considered as the total time spent on a given day waiting for and observing foxes. Multiple focal observations of an individual during an observation session were pooled and considered as a single observation period.

Using a digital voice recorder, we noted the time that foxes spent consuming, carrying, and caching food items. *Carrying* time was defined as the period between the moment the item was acquired and its consumption or caching. When a fox carrying a prey started digging the ground, this behavior was recorded as *caching* and ended when the fox stopped packing the soil over the item with its snout and left the cache site. *Consumption* time was recorded when the fox began chewing or licking the prey. All these activities include short periods during which the fox stopped to scan its surroundings. We excluded periods when foxes were resting (lying down) or performing maintenance behaviors such as grooming. Hoarding behavior is highly stereotyped in canids (Phillips et al. 1991), so carrying and caching activities were clearly distinguishable and the sum of these two activities was considered the *hoarding* time.

We noted the type of food items (goose egg, lemming, gosling) acquired, the source of these items (*new* or *cache*), and their fate (eaten, cached, unknown). Eggs acquired in goose nests and live captures of lemmings and goslings were considered to be a *new* source. We considered a lemming to be live captured when a fox caught it after a pounce or a sprint or after vigorous digging. Foxes captured live goslings by attacking goose families or by finding goslings left behind in abandoned nests. Items were considered to be acquired from a cache if the fox gently dug the ground before retrieving the food (Vander Wall 1990). We estimated by eye the relative distance (<100 or >100 m) over which the fox carried a food item before caching it. We noted the location of the cache site so that we could detect whether foxes recovered caches that had been previously made during the same observation period (short-term caches).

In June and July, we visited all fox dens surrounding the goose colony to check for signs of reproduction (fresh scats, tracks, prey remains, or recent digging). Dens with signs of activity were revisited to determine the presence of pups and to identify adults. When a breeding fox carrying a prey left the observation area in the direction of its den, we assumed that the food was taken to the den. If the fox left the area in another direction or if it was not associated to a den, the fate of the food item was recorded as unknown.

Radio-tagged eggs

We used dummy eggs containing radio transmitters (hereafter called radio-tagged eggs; Advanced Telemetry Systems, Model# A2670) that we could substitute for real eggs. Each radio-tagged egg had a plastic shell and included a transmitter with an internal antenna and a minimum battery lifespan of 130 days. The width, length, and weight of the radio-tagged eggs averaged (±SE) 56.8±0.2 mm, 80.9±0.3 mm, and 118±1 g (n=30), respectively, which is within the range of fresh greater snow goose eggs (width 48–58 mm; length 73–89 mm; weight 88–138 g; n=50).

We created artificial nests in the high-density goose nesting area by restoring previous year nests with goose down collected during the preceding summer. In each artificial nest, we included a natural egg collected from a nearby goose nest and a radio-tagged egg. We did not put radio-tagged eggs into real goose nests because nest defense behavior could have prevented foxes from acquiring them. To reduce odor contamination, we stored radio-tagged eggs in goose down for at least 1 day before use and manipulated them with rubber gloves.

We visited each artificial nest daily until it was preyed upon. From the observation blinds, we watched the first 24-h exposure of a sample of artificial nests to determine how arctic foxes reacted to dummy eggs. We tracked radio-tagged eggs by telemetry immediately after we detected a predator visit to a nest. We used nest remains to identify predators (birds or arctic fox). Nests depredated by foxes were characterized by a small hole in the goose down covering eggs, the absence of eggshell around the nest, and sometimes fresh fox faeces in the nest. In contrast, scattered goose down and, generally, broken eggs or eggshells were found around nests depredated by avian predators (sensu Bêty et al. 2002). Usually, when the predator was a fox, both eggs disappeared and the radio-tagged egg was cached.

On the ground, radio-tagged eggs were detected up to 200–600 m depending on topography and egg position. Supplemental tracking was conducted from a helicopter when signals were lost. All the cached radio-tagged eggs were visited every second day during the goose nesting season in June and July and at 5-day intervals from 1 to 18 August. The time elapsed between the creation of a cache and its recovery by the same or a different fox was referred to as the cache lifespan. We used the midpoint date between two successive checks as the time of occurrence of an event such as a cache creation or recovery. We marked caches using a 0.5-cm diameter and 15-cm high-flagged stick located 10 m away from the cache and another unflagged similar stick located midway between the cache and the flagged stick. This marking was designed to reduce the chance that common ravens (*Corvus corax*) or other foxes would cue on marks to locate and raid caches. We performed subsequent surveys of the cached radio-tagged eggs by checking the signal from >10 m.

Statistical analysis

There were two different correlation structures in our behavioral observation data: one due to repeated sampling of individual foxes throughout the season and another due to the fact that a single fox usually acquired multiple prey within a single observation period. We used mixed-effect models that included observation period nested in fox identity as a random effect, thereby taking into account both correlation structures of the data (among and within observation periods). This allowed us to avoid potential biases generated by pseudoreplication, while using all information provided by each individual fox preying upon multiple prey (Machlis et al. 1985; Pinheiro and Bates 2000). Because annual variation in resource availability occurred, we also included year as a random factor in all models. We used PROC GLIMMIX and PROC MIXED for logistic responses and continuous responses, respectively (SAS Institute 2003). We restricted degrees of freedom to $n-1$, where n is the number of individual involved in the test. We rank transformed the data when log-transformation did not approximate a normal distribution (Conover and Iman 1981). We used mixed models to test the following predictions: (1) foxes cached a higher proportion of goose eggs compared to the proportion of lemmings or goslings, (2) consumption time and hoarding time were different among prey, (3) foxes were more likely to transport eggs over 100 m when recaching than when caching, and (4) *carrying* and *caching* times were longer when recaching than caching.

We could not use mixed-effects models on data collected with radio-tagged eggs because we did not know the identity of foxes that cached and recached them. When the radio-tagged egg of a primary cache was recached in a secondary cache, we used a paired *t* test on rank-transformed data to test the predictions that (1) distances between secondary and primary caches was greater than distances between the primary cache and the nest and (2) secondary caches were located further away from the artificial nest than primary caches. We analyzed the lifespan of radio-tagged egg caches using survival time analysis (Nur et al. 2004) implemented in JMP 5.0.1 statistical package (SAS Institute, Cary, NC), with an exponential distribution and likelihood ratio tests. Survival time analysis has the advantage of allowing the use of right-censored data, which are events that have not been observed because the study ended before it could have happened. In our case, this was useful as we had to leave the field on 18 August, whereas some radio-tagged eggs were still cached (exact time of recovery unknown but greater than we could measure). Caches that "survived" past the experiment were right censored (type I censoring), which avoided underestimating the lifespan of caches. The model considered that the lifespan of right-censored caches was greater than—rather than equal to—what we measured (see Tableman and Kim 2004 for a thorough discussion on data censoring). We ran a parametric regression model to test the prediction that the lifespan of a primary cache increased the distance from the nest. We ran another model including distance from the nest and date at which the cache was found as covariates to test the prediction that secondary caches had a longer lifespan than the primary ones. We used time quantile estimates to model survival functions and calculate the time span necessary for half of the caches in a group to be recovered (i.e., half life). In our case, "survivorship" was the probability that a cache had not been recovered after a given number of days since its creation. Means are reported ±SE, tests were two-tailed, and significance level was set at $\alpha=0.05$.

Results

In 2004 and 2005, we respectively sampled the behavior of six and eight individual arctic foxes during 1,454 and 2,227 min on 39 and 59 observation periods that lasted from 3 to 134 min (38±28, median=31 min). None of the four marked foxes observed in 2004 was seen in 2005. In 2004, we sampled four foxes whose reproduction was confirmed at two dens, respectively located at 1,380 and 550 m from the limits of the observation area. In 2005, only one fox included in our observations was associated to a breeding den that was located 600 m from the observation area.

Source and fate of food items

Foxes acquired predominantly lemmings in 2004 and goose eggs in 2005 (Table 1). Goslings were preyed upon at about the same rate in both years. Foxes were observed carrying up to five lemmings or three goslings simultaneously, but never more than a single goose egg at a time. They were more likely to cache goose eggs than lemmings ($F_{1,13}$=58.9, $p<0.001$) or goslings ($F_{1,13}$=24.5, $p<0.001$; Fig. 1). We detected no difference in caching frequencies between goslings and lemmings ($F_{1,13}$=0.1, p=0.7).

The source of items (whether they were newly acquired or recovered from a cache) significantly affected their fate. Overall, foxes were more likely to eat eggs acquired from caches than those from nests ($F_{1,13}$=17.94, $p<0.01$). The proportion of lemmings and goslings carried by foxes outside the observation area (fate = unknown or den) was higher when these items were acquired from caches than when they were first captured (lemmings and goslings pooled: $F_{1,13}$=16.49, $p<0.01$; Fig. 1). It is unlikely that this effect was created by the position of the observer because (1) these live prey were readily dispersed throughout the observation area and (2) foxes did not seem to cache them in a particular direction relative to the observer's position.

Consumption and hoarding times of food items

Consumption time was significantly longer for goose eggs than for lemmings ($F_{1,11}$=73.3, $p<0.001$) or goslings ($F_{1,10}$=39.7, $p<0.001$; Fig. 2). Consumption time was slightly longer for goslings than lemmings ($F_{1,12}$=6.9, p=0.02; Fig. 2). Hoarding time was longer for goose eggs than for lemmings ($F_{1,12}$=24.8, $p<0.001$) or goslings ($F_{1,12}$=6.3, p=0.03), but was similar between lemmings and goslings ($F_{1,10}$=0.15, p=0.71; Fig. 2). Consumption time was significantly longer than hoarding time for goose eggs ($F_{1,12}$=11.9, $p<0.01$) but not for lemmings ($F_{1,11}$=1.7, p=0.23) or goslings ($F_{1,7}$=0.83, p=0.40; Fig. 2).

Short-term caches

None of the 148 eggs cached by foxes was recovered within a continuous observation period, whereas this occurred for 35 and 44% of cached lemmings (n=34) and goslings (n=9), respectively. The 16 cases of short-term caching were performed by six individuals, including five individuals whose reproduction was confirmed in one of the three dens surrounding the observation area. Foxes that were reproducing were more likely to perform short-term caching than those whose reproduction was not confirmed (χ^2=7.02; df=1, n=14, $p<0.01$). The time between creation and recovery of these short-term caches averaged 18±4 min (range 6–42). During this time, foxes acquired a mean of 1.4±0.2 (range 0–3) additional food items (live-captured lemmings or goslings). When foxes recovered short-term caches, they always went out of sight while carrying the food (towards the den in 12 cases; fate unknown in four cases).

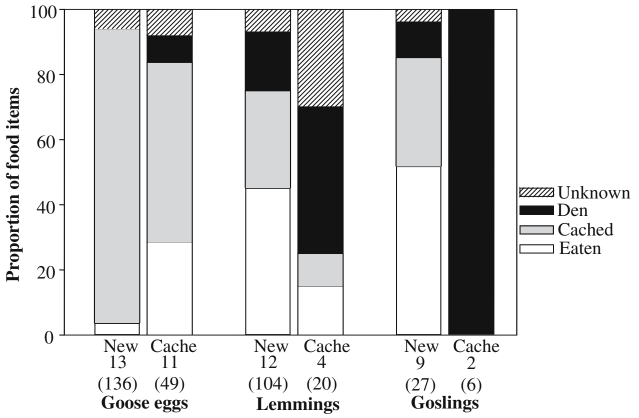

Fig. 1 Fate of goose eggs, lemmings, and gosling acquired by arctic foxes according to the source, Bylot Island, Nunavut 2004–2005. Source is considered to be "new" when a fox took an egg in a nest or live captured a lemming or a gosling. We considered that food items were brought to the den when foxes left the observation area in the direction of their den. Otherwise, the fate was unknown. Numbers below categories refer to the numbers of individual foxes and numbers in parentheses refers to number of food items

Recaching behavior

Foxes recached 55% of eggs they recovered from caches (n=49; Fig. 1). They were more likely to move eggs more than 100 m away when recaching than when caching (73% vs 10%; $F_{1,11}$=23.9, $p<0.001$). Foxes spent significantly less time hoarding eggs obtained from nests than from

Table 1 Number of food items taken by arctic foxes while foraging in a greater snow goose colony, Bylot Island, Nunavut 2004–2005

Item	Goose egg		Lemming		Gosling		Observation effort (h)
Source	Nest	Cache	Live captured	Cache	Live captured	Cache	
2004	18	18 (0)	81	20 (12)	10	5 (3)	198
2005	118	31 (0)	23	0 (0)	17	1 (1)	363
Total	136	49 (0)	104	20 (12)	27	6 (4)	561

The source of the different items is also shown. Numbers in parentheses represent recovered prey that were cached during the same observation period (short-term caches).

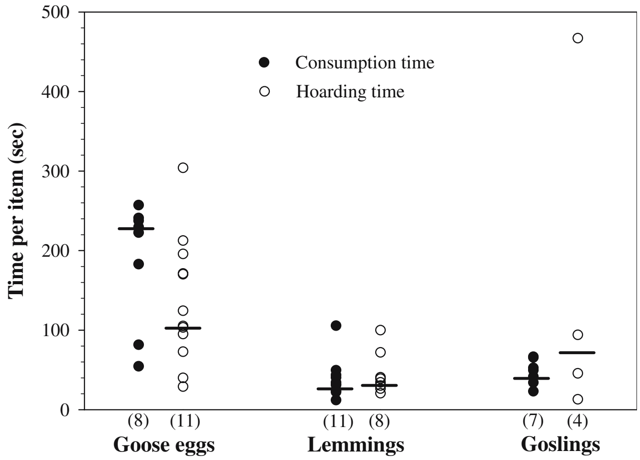

Fig. 2 Time spent by arctic foxes consuming and hoarding goose eggs, lemmings, and goslings, Bylot Island, Nunavut 2004–2005. Hoarding time includes carrying and caching times. Each dot represents an individual (pooled mean), and the line shows the median. Numbers in parentheses show total number of individuals for each category

caches, and this difference was due to a longer carrying phase when recaching (carrying phase: $F_{1,11}=44.2$, $p<0.001$; caching phase: $F_{1,11}=1.8$, $p=0.20$; Fig. 3).

Radio-tagged eggs

We created 71 dummy nests and watched the first 24-h exposure for 29 of these. We observed five individual foxes acquiring seven radio-tagged eggs in seven dummy nests. They spent similar amounts of time hoarding radio-tagged eggs and real eggs (carrying phase: $F_{1,4}=3.6$, $p=0.13$; caching phase: $F_{1,4}=t=0.03$, $p=0.90$). We found 20 additional primary caches for a total of 27 cached radio-tagged eggs. Primary caches were located at a median distance of 82 m from the original artificial nests (range 5–985 m, $n=27$). The lifespan of a primary cache increased with the distance from the artificial nest (survival time analysis; $\chi^2=5.46$; $df=1$; $p=0.02$; ten caches right censored). Time quantile estimates indicated that half life of primary caches located at 50 m from their nests was threefold lower than primary caches located at 500 m (Fig. 4).

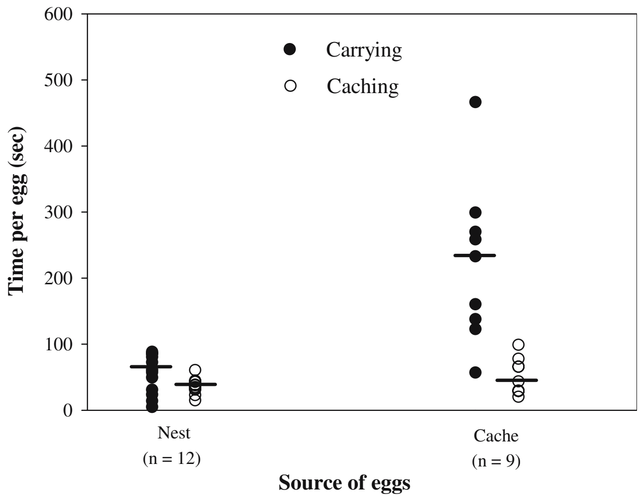

Fig. 3 Time spent by arctic foxes carrying and caching goose eggs acquired from nests (primary caches) and caches (recaching), Bylot Island, Nunavut 2004–2005. Data are presented as in Fig. 2

Foxes moved 11 radio-tagged eggs to secondary caches (Fig. 5). Generally, radio-tagged eggs were moved away from primary caches over a median distance of 256 m (range 36–1040 m), which is significantly greater than the distance between the primary cache and the artificial nest (paired t test; $t=2.67$; $df=10$; $p<0.05$). Only one secondary cache was moved toward the source nest, whereas all others were moved further away (median distance from artificial nest=358 m; paired t test; $t=3.58$; $df=10$; $p<0.01$). Secondary caches had a longer lifespan than primary caches (survival time analysis; $\chi^2=7.02$; $df=1$; $p<0.01$; six secondary caches right censored). Half life of primary and secondary caches was 9.2 and 38.5 days, respectively. Because our study ended before the recovery of some cached radio-tagged eggs, our estimates represent the lower limit of cache lifespan.

Tertiary and quaternary caches were few (5 and 1, respectively); they were moved away from their original caches over a median distance of 94 m (range 22–230 m). Foxes continued to move radio-tagged eggs away from the artificial nests when performing tertiary and quaternary caches (median distance from nest=534 m; range 121–979 m).

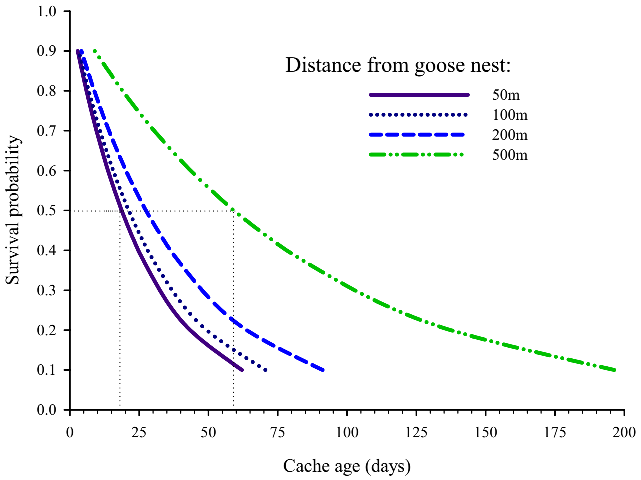

Fig. 4 Survival probability of primary caches (radio-tagged eggs cached by arctic fox on Bylot Island, Nunavut 2004–2005) according to distance from the source (artificial goose nest). Curves were modeled with $\alpha=0.05$ using time quantile estimates for primary caches created at different distances from the nest (50, 100, 200, and 500 m) at the end of June

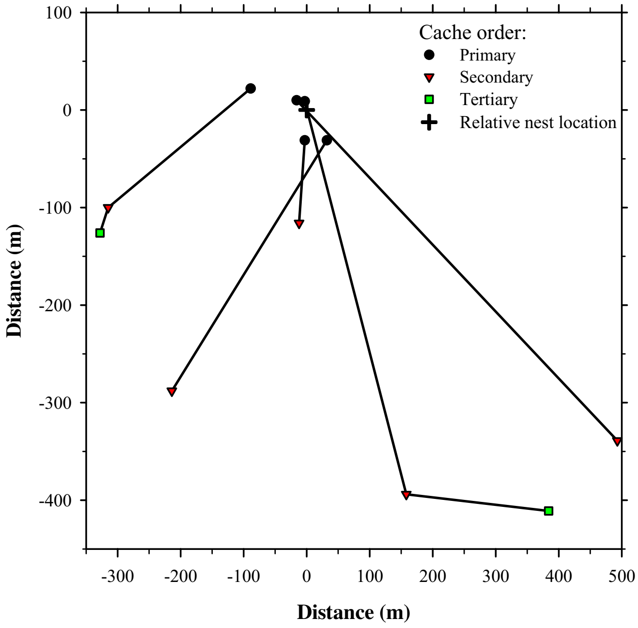

Fig. 5 Representative examples of arctic foxes caching radio-tagged eggs (*n*=5) in a greater snow goose colony, Bylot Island, Nunavut 2004 and 2005. Although foxes acquired radio-tagged eggs from artificial nests located throughout the colony, all nests are placed at the center of the graph shown by the crosshair to facilitate illustration. Lines link radio-tagged eggs from primary to secondary and tertiary caches

Discussion

Fate of food items according to their characteristics

Arctic foxes allocated more time and traveled longer distances per item when hoarding goose eggs than when hoarding lemmings or goslings. They also cached a greater proportion of eggs than of the other two food types. Assuming that eggs, because they possess antimicrobial agents (Board and Fuller 1974), are less likely to spoil than lemmings and goslings, our results support the perishability hypothesis. The perishability of eggs is definitely low, as they loose only ~8–9% of their dry mass over 60 summer days of storage in the partially frozen permafrost of the tundra (*n*=16, unpublished data). As we did not evaluate perishability of stored lemmings or goslings, we lack evidence for the basic assumption of differential shelf life between prey items. Alternatively, the shell of an egg could diminish the odor emitted by the stored item, which would decrease its detection probability by pilferers cueing on odor (as foxes do, Macdonald 1976). Hence, differences in pilfering risk could also explain why goose eggs were cached in higher proportion than lemmings and goslings.

Consumption time was longer for goose eggs than for lemmings or goslings, possibly because of the time required to crack the eggshell without losing its semiliquid contents. Given that arctic foxes may be foraging under time constraints during the short goose nesting season and that they cached goose eggs in less time than what is required to consume them, the consumption time hypothesis may also explain why arctic fox cache a greater proportion of eggs (Jacobs 1992). Although our data cannot determine the relative effects of perishability, pilfering risk, and consumption time on caching decisions of arctic foxes, these hypotheses may be acting simultaneously and result in a greater proportion of eggs being cached compared to other prey.

Similarly, James and Verbeek (1984) found that clams were the most frequently hoarded item by northwestern crows (*Corvus caurinus*). Clams have a shell that protects the edible portion against dehydration and arthropod invasion, thus decreasing perishability. Moreover, clams must be dropped from the air by crows to be opened, which results in a long consumption time (James and Verbeek 1983; Richardson and Verbeek 1986). Hard covering, such as eggshells, seed pericarp, and mollusc shells, which influence both present and future values of food items, is thus an important attribute determining caching decisions in food-hoarding animals (Vander Wall 1990).

Short-term caches

On several occasions, arctic foxes recovered lemmings and goslings that had been captured and cached during the same observation period and left the observation area while carrying multiple prey. Most individuals involved in short-term caching were associated with a breeding den where juveniles had to be fed. Arctic foxes behaved similarly when foraging on the ledge of a steep seabird-nesting cliff in Svalbard (Prestrud 1992). When they are rearing juveniles, arctic foxes can be considered as central place foragers because they must bring back food to the den (central point) to provision their cubs (Tannerfeldt and Angerbjorn 1998). If we assume that a fox increases its fitness by maximizing the delivery rate of energy to its den, it should be advantageous to return to the den with multiple prey. Because holding one or more prey in the mouth is likely to adversely affect a fox ability to capture additional prey (Orians and Pearson 1979), a short-term caching strategy is likely favored to increase capture rate and provisioning. Foxes were never observed caching eggs on such a short-term basis, probably because they can carry only one egg at a time.

The short hoarding time of lemmings and goslings (~60 sec) reported in this study suggests that the time costs associated with finding a short-term cache location is relatively low. Short-term caching may minimize the risk of losing food to scroungers when attacking other prey, but does not eliminate this risk completely because pilfering of short-term caches by avian predators such as common ravens and glaucus gulls (*Larus hyperboreus*) has been reported (Prestrud 1992; Careau et al. 2007).

Recaching behavior

Behavioral observations and telemetry gave consistent results that fit the rapid-sequestering hypothesis. We observed that arctic foxes invested more time carrying goose eggs and transported them over longer distances when recaching them than when caching them for the first time. Tracking radio-tagged eggs showed that arctic foxes traveled longer distances when performing a secondary than a primary cache and that the secondary cache had a longer lifespan than the primary ones. The rapid sequestering hypothesis is likely favored because of the short accessibility of goose eggs during the breeding season. Geese are present at their nest for ~94% of the time during incubation, they usually feed and drink relatively close to their nest (<20 m) while remaining vigilant to predators, and they can effectively deter arctic foxes from their nests (Reed et al. 1995; Bêty et al. 2002). After having discovered an undefended nest containing multiple eggs, an arctic fox can rapidly deplete it by caching eggs nearby. Caching may thus allow arctic fox to maximize benefits when a food supply is only available for a limited period of time, as observed by Macdonald (1976) in red fox (*Vulpes vulpes*).

The recaching of rapidly sequestered eggs is probably a strategy of reducing pilfering risk. Primary caches are vulnerable to pilfering because arctic fox home ranges overlap extensively in goose colonies (Anthony 1997; Eide et al. 2004). Hence, foxes may benefit from investing time and effort to recache eggs in potentially safer sites (outside the goose colony and/or closer to their den). Increased cache lifespan with distance from the food source was observed in Japanese squirrels (*Sciurus lis*, Tamura et al. 1999), eastern chipmunks (*Tamias striatus*, Clarke and Kramer 1994) and willow tits (*Parus montanus*, Brodin 1993), presumably because food sources attract other foragers. In our study, the lifespan of caches also increased with distance from the nest. This may be because cache pilfering and/or the benefit of recaching decreases when distance from the food source increases.

The rapid-sequestering hypothesis has been supported by two laboratory experiments on Merriam's kangaroo rats (*Dipodomys merriami*, Jenkins and Peters 1992; Jenkins et al. 1995) but not during a field experiment on eastern chipmunks (Clarke and Kramer 1994). These authors have shown that scatter hoard placement was more related to the pilferage avoidance hypothesis (Macdonald 1976) than to the need for rapidly sequestering food items from an ephemeral food patch. Subordinate chipmunks (juveniles) were more likely to recache their food after a competitor had searched the vicinity of the cache (Clarke and Kramer 1994). In three cases, Careau et al. (2007) observed common ravens in the vicinity of newly made caches that were aggressively defended by foxes until the birds flew away. Contrary to what is predicted by the pilfering-avoidance hypothesis, the foxes always left the area without recaching.

Because the rapid-sequestering hypothesis does not explain the subsequent recaching from secondary to tertiary caches, our results raise other questions about the adaptive significance of recaching in arctic fox. Given the relatively short distances over which radio-tagged eggs were carried from secondary to tertiary caches, recaching could be a mean of monitoring the quality and quantity of the food reserve (see DeGange et al. 1989). However, this cache management hypothesis assumes that the hoarder is retrieving its own food, which may not be always be the case. If a foraging fox encounters a cache that it did not make, it can increase its own knowledge of the stored resource and reduce the knowledge of its competitors by moving the eggs to a new location (Vander Wall 1995). Therefore, what we interpret as recaching could instead becache pilfering (Daly et al. 1992; Vander Wall and Jenkins 2003).

Conclusions

The pattern of caching decisions observed in arctic foxes suggests that they are sensitive to prey characteristics such as perishability, pilfering risk, and consumption time. Although the low temperature of the storage sites (surface of permafrost, ~0°C) suggests that perishability is less likely to influence caching decisions, the fact that arctic fox can store for long time and potentially rely on hoards to survive winter probably makes goose eggs their most preferred prey to cache (Stickney 1991; Samelius and Alisauskas 2000). Alternatively, lemmings and goslings were preferentially eaten on site or brought to the dens, especially by individuals that were attending young. Our findings support argument of Partridge and Green (1985) that there is danger in ignoring age, sex, and reproductive status of observed individuals in foraging studies. Finally, our results on recaching in arctic fox represent the first field study supporting the rapid-sequestering hypothesis. There is clearly a need for more studies on hoarding behavior in nonrodent species to better understand this behavior in mammals.

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