Foraging Patterns of Arctic Foxes at a Large Arctic Goose Colony

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ABSTRACT. Arctic foxes (*Alopex lagopus*) are the main predators of many arctic-nesting birds, and such predation can have a large impact on the nesting performance of geese in some years and in some parts of the Arctic. We examined foraging patterns of arctic foxes at a large lesser snow goose (*Chen caerulescens caerulescens*) colony on Banks Island, Canada, from 1996 to 1998 and were especially interested in the proportion of food that was cached for later use and the impact that fox predation had on goose productivity. Arctic foxes took mostly eggs when foraging among geese, and most of these eggs (97%) were cached for later use. Adult geese and lemmings were taken in low numbers, and most of these foods (83% of geese and 75% of lemmings) were eaten immediately. In years with high fox abundance, the foxes spent considerable effort moving eggs from old caches. This behaviour may have resulted from high rates of cache pilfering, or foxes may have been moving caches to deter cache pilfering. The impact of fox predation was low in all years, and foxes took only about 4–8% of all eggs available at the colony during incubation each year. However, caching and use of cached eggs may influence the survival of arctic foxes by forming significant parts of their winter diet or by supplementing the diets of growing young: during nesting each year, foxes took on average 900–1570 eggs per fox.

Key words: arctic fox, *Alopex lagopus*, Banks Island, food caching, foraging behaviours, lesser snow goose, *Chen caerulescens caerulescens*

RÉSUMÉ. Le renard arctique (*Alopex lagopus*) constitue le prédateur principal de nombreux oiseaux nicheurs de l'Arctique, et cette prédation peut avoir des conséquences majeures sur le succès de la couvaison des oies durant certaines années et dans certaines parties de l'Arctique. Notre étude, réalisée de 1996 à 1998, sur les schémas de recherche de nourriture du renard arctique dans une vaste colonie de petites oies des neiges (*Chen caerulescens caerulescens*) située dans l'île Banks, au Canada, portait surtout sur la proportion de nourriture qui était dissimulée dans des caches pour consommation ultérieure ainsi que sur l'impact qu'avait la prédation du renard sur la productivité de l'oie. Le renard arctique prélevait surtout des œufs quand il cherchait de la nourriture parmi les oies, et la plupart des œufs (97 p. cent) étaient dissimulés pour consommation ultérieure. Les oies adultes et les lemmings étaient prélevés en faible quantité, et la plupart de ces aliments (83 p. cent des oies et 75 p. cent des lemmings) étaient consommés dans l'immédiat. Durant les années d'abondance du renard, les renards faisaient des efforts considérables pour déplacer les œufs d'anciennes caches. Ce comportement peut avoir été dû à un taux élevé de vols de caches, ou bien les renards peuvent avoir déplacé leurs caches pour en décourager le vol. L'impact de la prédation du renard était faible durant toutes les années, et les renards ne prenaient annuellement qu'environ 4 à 8 p. cent de tous les œufs disponibles à la colonie durant l'incubation. La dissimulation dans des caches et l'utilisation des œufs qui y sont conservés pourraient avoir une influence sur la survie du renard arctique, car les caches représentent une partie importante du régime hivernal du renard ou complètent le régime des petits en croissance: durant la nidification annuelle, les renards prélevaient une moyenne de 900 à 1570 œufs par individu.

Mots clés: renard arctique, *Alopex lagopus*, île Banks, dissimulation de nourriture, comportements de recherche de nourriture, petite oie des neiges, *Chen caerulescens caerulescens*

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INTRODUCTION

Arctic foxes are opportunistic predators and scavengers that rely heavily on lemmings and voles throughout most of their range (Chesemore, 1968; Macpherson, 1969; Fay and Stephenson, 1989). However, other foods, such as birds, eggs, carrion from sea mammals, and marine invertebrates can be important in years and areas of low lemming abundance (Chesemore, 1968; Fay and Stephenson, 1989; Prestrud, 1992; Hersteinsson and Macdonald, 1996;

Bantle and Alisauskas, 1998). In fact, Prestrud (1992) suggested that the ability to learn new hunting skills and exploit local variation in foods is a crucial factor for the survival of arctic foxes.

Arctic foxes commonly cache foods for later use when prey is abundant (Fay and Stephenson, 1989; Stickney, 1991; Sklepkovych and Montevecchi, 1996). Cached foods can form considerable portions of arctic fox diets during periods of food shortage (Fay and Stephenson, 1989; Prestrud, 1992; Stickney, 1991; Bantle and Alisauskas,

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1998) or may supplement the diets of growing young (Vander Wall, 1990). Caching and use of cached foods may be especially frequent for arctic foxes living at large bird colonies, where food is often superabundant during the birds' breeding season (Fay and Stephenson, 1989; Stickney, 1991; Bantle and Alisauskas, 1998). However, little is known about caching behaviours and the extent of food caching in arctic foxes or other carnivores (Vander Wall, 1990).

Geese can suffer high rates of nest loss to predation by arctic foxes in some years and in some parts of the Arctic (MacInnes and Misra, 1972; Raveling, 1989; Stickney, 1991; Syroechkovskiy et al., 1991; Sedinger et al., 1993). This is especially true in years when lemming numbers are low and foxes may switch from lemmings to bird prey (Summers, 1986; Summers and Underhill, 1987; Summers et al., 1998). However, other factors, such as nest density, colony size, and ability to defend against arctic foxes, can also influence the impact of arctic fox predation (Bousfield and Syroechkovskiy, 1985; Raveling, 1989; Stickney, 1991; Syroechkovskiy et al., 1991; Bantle 1998). Most studies have examined fox predation indirectly (but see Stickney, 1991; Syroechkovskiy et al., 1991; Bantle, 1998), and little attention has been devoted to the foraging behaviours of arctic foxes.

The objective of this study was to examine foraging patterns of arctic foxes in a large arctic goose colony. Specifically, we examined (1) which foods foxes took when in the colony; (2) the extent to which foods were cached, as opposed to consumed; and (3) the foraging efficiency of arctic foxes and how predation by foxes may affect the productivity of lesser snow geese.

METHODS

Study Area

This study was performed at Egg River on Banks Island (72°25′N, 124°32′W), Canada, during the summers of 1996 to 1998 (Fig. 1). Egg River is the largest lesser snow goose (hereafter, 'snow goose') colony in Canada's western Arctic: it contained about 186 000–439 000 nesting geese from 1996 to 1998 (Samelius and Alisauskas, 1998; Kerbes et al., 1999). The number of geese that nested there each year varied with spring arrival and was higher in 1996 and 1998, when snowmelt was earlier, than in 1997 (Samelius and Alisauskas, 1998). Geese nested in the large valleys of the Egg and Big Rivers, with average nesting densities of 26–34 nests per ha in 1996 to 1998 (Samelius and Alisauskas, unpubl. data). About 5000–30 000 geese died from avian cholera in each year, and the mortality appeared to be higher in 1997, the year of late snowmelt (Samelius and Alisauskas, 1998; Samuel et al., 1999).

In addition to snow geese, other nesting birds included brant geese (*Branta bernicla*), king eiders (*Somateria spectabilis*), sandhill cranes (*Grus canadensis*), glaucous gulls (*Larus hyperboreus*), long-tailed jaegers (*Stercorarius longicaudus*), and lapland longspurs (*Calcarius lapponicus*). Terrestrial mammals common in the colony were arctic foxes, collared lemmings (*Dicrostonyx torquatus*), and muskoxen (*Ovibos moschatus*). Lemming abundance at Egg River varied among years, with peak lemming numbers in 1996 and low numbers in 1997 and 1998 (Samelius and Alisauskas, 1998). Reproductive effort of arctic foxes varied among years and appeared to follow lemming abundance (Samelius and Alisauskas, unpubl. data). The number of fox dens within 1.5 km of the colony that had young was 18 of 20 dens in 1996, 10 of 19 dens in 1997, and 16 of 24 dens in 1998. Dens within 1.5 km of the colony were considered to be associated with the colony because foxes carrying eggs were frequently seen 1.5 km outside the colony.

Observations of Foraging Patterns of Foxes

Foraging behaviours of arctic foxes were monitored throughout the incubation period of geese (i.e., from peak onset of incubation to peak hatch). Periods of observation were 6–29 June in 1996, 11 June–3 July in 1997, and 1–23 June in 1998. Observations were made opportunistically and were performed between 20:00 and 8:00, the period that corresponds to peak fox activity (Eberhardt et al., 1982; Garrott et al., 1984; Anthony, 1997; Bantle, 1998). However, length and timing of observations varied with weather conditions (heavy fog and occasional snow prevented observations) and other research activities. Four observers were involved in the study in 1996 and three observers in 1997 and 1998. To improve consistency among observers, researchers made the first observations each year as a group.

We observed foraging behaviours of arctic foxes by using spotting scopes (15–45×) from hills and ridges inside or near the colony following Altman (1974). Once a fox was located, we monitored it for as long as it was inside the colony, until it was lost behind an obstacle, or until the distance was too great for accurate observations. For each observation, we monitored (1) time of foraging bouts or partial bouts, (2) food objects taken by foxes, and (3) fate of food objects (see below). We excluded time periods and food objects taken when foxes were out of sight or had temporarily left the colony. Similarly, we excluded time periods when foxes were lying down or performing maintenance behaviours such as grooming or resting (26, 39, and 28 minutes from 4, 2, and 2 observations in each year, respectively). Multiple observations of an individual fox during the same night were treated as one observation. Foxes were identified by the patterns of their pelts, which were changing from winter to summer pelage.

Food objects taken by foxes were categorized as eggs, geese, lemmings, or unknown objects. Eggs taken by foxes included nest contents, eggs lying outside of goose nests (hereafter called dump-eggs), and eggs from caches (i.e., buried eggs). Nest contents were almost exclusively eggs
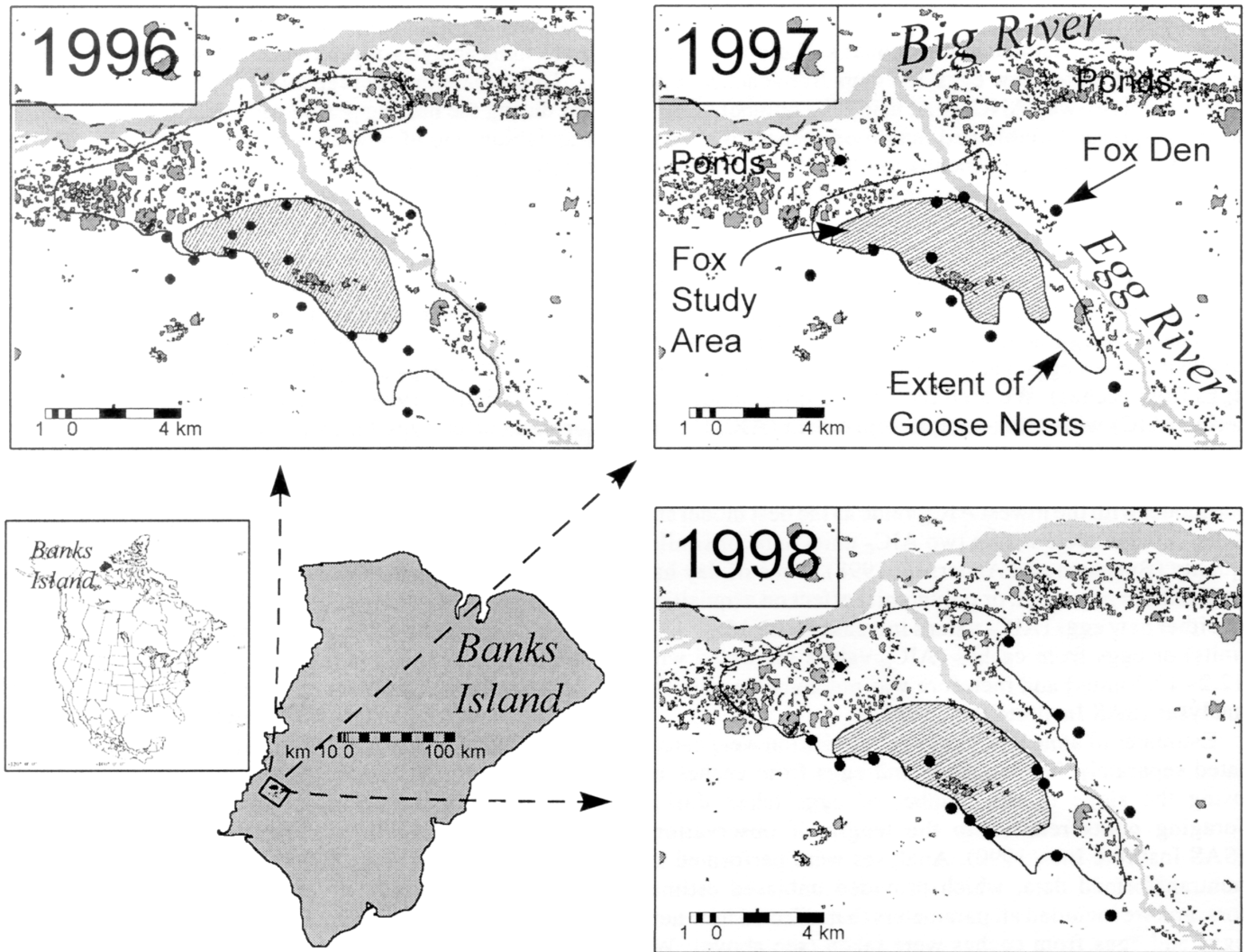
FIG. 1. Extent of Egg River snow goose colony on Banks Island, Canada, in 1996–98 (map modified from Samelius and Alisauskas, 1998). The area covered by goose nests is outlined in black and the study area is indicated by grey stippling. Black circles indicate fox dens with young found within 1.5 km of the colony.

except for a few newly hatched goslings in late incubation of each year (nest contents are called 'eggs' hereafter). Foxes often took eggs from old caches, and we considered an egg to be from a cache if it was dug up from the ground and then moved (Vander Wall, 1990). Eggs taken by foxes were separated into two groups: new eggs (eggs from nest bowls, dump-eggs, or eggs from unknown sources) or eggs from caches. Eggs from unknown sources (12 in 1996, 78 in 1997, and 26 in 1998) were included as new eggs because these eggs were almost exclusively single eggs from unattended nests or dump-eggs. One observer did not monitor eggs taken from caches in 1996. Eggs taken from nest bowls were categorized as being from attended nests (one or both parent geese present at the nest) or unattended nests (no geese near the nest). Females were always incubating when present at nests, and we never observed a single goose standing beside an unattended nest. Adult geese taken by foxes were classed as scavenged or killed.

We defined food objects as (1) eaten, if foxes consumed part or all of the object; (2) cached, if foxes buried part or all of the object; (3) lost, if foxes dropped the object without recovering it during the same observation; and (4) unknown, if foxes were carrying the object as they left the colony or disappeared from view. Fate of eggs was monitored by two observers in 1996, one in 1997, and three in 1998. We excluded eggs taken during two observation bouts in 1997 and one observation bout in 1998 because of observer error.

Interactions among Foxes

Foxes occasionally encountered other foxes while in the colony. We categorized these interactions as (1) aggressive, if a fox chased or bit another fox, or (2) non-aggressive, if two foxes observed or approached each other without any apparent aggression. Multiple encounters between the same foxes during an observation were considered as one encounter.

Statistical Analysis

We examined annual and seasonal variation in rate of egg acquisition for new eggs and eggs from caches separately by multi-way ANCOVA, using the number of eggs as the response variable and length of observation (minutes), year, and stage of incubation (0–23 days) as independent variables (SAS Institute Inc., 1990). Data showed heterogeneity of variance for length of observation, so data were rank-transformed following Conover and Iman (1981). We used the observation bout as the sampling unit and included all main effects and two-way interactions in the model of egg acquisition (n = 248 observations for analysis on new eggs and 227 observations for analysis on eggs from caches). We used the Akaike Information Criterion (AIC) with small-sample adjustment (AIC_C) to select the model that best explained variation in egg acquisition (Burnham and Anderson, 1998). We selected the model with the lowest AIC_C value as the best model and considered models within two AIC_C units to be of similar quality (Burnham and Anderson, 1998). Time of day had no linear, exponential, or polynomial effect on acquisition of either new eggs (AIC_C values increased with 15.8–17.8 units) or eggs from caches (AIC_C values increased with 12.2–13.3 units) and therefore was not considered in the analyses (SAS Institute Inc., 1990).

Estimates of annual rates of egg acquisition were calculated separately for new eggs and eggs from caches by using the slope of the number of eggs taken during foraging bouts relative to the length of observations (SAS Institute Inc., 1990). Analyses were performed on nontransformed data, which provided unbiased estimators, and we included all parameters that affected how new eggs and eggs from caches were taken (see above). We regressed data through the origin when estimating egg acquisition rates that were affected only by length of observation (SAS Institute Inc., 1990).

Annual variation in acquisition of foods other than eggs was examined separately for each prey using a chi-square test; we arranged data by number of prey taken and length of observation each year (n = 26 geese and 10 lemmings; SAS Institute Inc., 1990). Lemming data had too many cells with expected frequencies less than 5, so we used the Fisher exact test (SAS Institute Inc., 1990). Similarly, annual variation in encounter rates among foxes was examined by a chi-square test, for which we arranged data by number of encounters and length of observation each year (n = 38 interactions, SAS Institute Inc., 1990).

We examined whether fate of foods varied among years and relative to food type in two steps, using Fisher exact tests, for which data were arranged by (1) fate and year for each food type separately and (2) fate and food type for each year separately (SAS Institute Inc., 1990). Analyses were performed on food objects with known fate (n = 341 new eggs, 163 eggs from caches, 22 geese, and 4 lemmings). Food objects with unknown fate or fate that fitted into more than one category were not included in the analyses. Fate of food objects did not differ among years for any food type, so we pooled data from all years before performing analysis on differences in fate among food types.

To estimate the average number of new eggs taken per fox during the nesting period each year, we multiplied the acquisition rate of new eggs by daily foraging effort and length of the nesting period. We assumed that foxes spent 8 hours foraging per day (Eberhardt et al., 1982; Anthony, 1997; Bantle, 1998) during 4 days of egg-laying and 23 days of incubation (Bousfield and Syroechkovskiy, 1985; Cooke et al., 1995). This estimate does not include eggs taken from abandoned nests after geese had departed the colony; nor does it account for nest predation often being higher during egg-laying than during incubation (Bantle, 1998; Samelius, 1999). To calculate the range of estimates for number of eggs taken per fox, we multiplied confidence intervals for rate of egg acquisition by daily foraging effort and length of the nesting period.

We evaluated the impact of fox predation on the nesting performance of geese at Egg River by estimating the proportion of eggs taken by foxes during incubation each year (egg-laying was not included in this estimate, as data on goose productivity were not available for this period). The number of eggs available at Egg River was calculated using data from Samelius and Alisauskas (1998), and the number of eggs taken from nest bowls was estimated using both (1) the number of foxes known to breed within 1.5 km of the colony and (2) the number of foxes seen in the study area, scaled for the whole colony (i.e., assuming an even distribution of foxes throughout the colony). In addition to the proportion of eggs taken from nest bowls, we also calculated a conservative estimate of fox predation that included only eggs taken from nests attended by birds. This was done because an unknown portion of eggs was taken from unattended nests where geese had already failed (through death or abandonment), and where removal of eggs had no effect on productivity.

RESULTS

From 1996 to 1998, we observed 2020, 2332, and 2429 minutes of fox and goose interactions distributed on 75, 89, and 84 foraging bouts, respectively. Length of observations ranged from 3 to 137 minutes in 1996, 2 to 79 minutes in 1997, and 2 to 104 minutes in 1998. The minimum number of foxes seen in the study area was 13 in 1996, 21 in 1997, and 18 in 1998. However, some foxes were observed more frequently than others.

Food Acquisition

Eggs were by far the most common food object taken by arctic foxes while in the colony: foxes took 681 new eggs and 338 eggs from caches in all years combined, compared to 24 geese, 10 lemmings, and 18 unknown food objects taken (Table 1). Foxes took new eggs at similar rates each

TABLE 1. Number of food objects taken by arctic foxes while foraging at Egg River colony in 1996 to 1998. Eggs from caches were the only food object taken differently among years.[1] Total observation hours are included to show sampling effort each year.

Year	Eggs		Other foods		Unknown foods	Total observation (hrs)
	New	Caches	Geese	Lemming		
1996	206	24	6	1	2	34
1997	288	205	8	5	5	39
1998	187	109	10	4	11	40
Total	681	338	24	10	18	113

[1] Variation in acquisition of food objects among years was examined by ANCOVA (on number of eggs taken relative to length of observations) for eggs and by chi-square (on number of objects taken relative to sampling effort) for other foods.

year and at a rate that decreased marginally throughout incubation, as shown by the best model including length of observation and stage of incubation ($AIC_C = 895.4$, Table 2). The effect of incubation was weak, however, and explained only 2.4% of the variation after accounting for length of observation. Alternative models showed similar results: two of three models within two AIC_C units of the best model included weak negative effects of incubation ($r^2 < 0.030$ after accounting for length of observation, Table 2). On average, each fox took 7.0 new eggs per hour in 1996 (95% C.I. = 5.8–8.1), 7.3 in 1997 (95% C.I. = 5.8–8.7), and 4.2 in 1998 (95% C.I. = 3.2–5.1).

Most of the new eggs taken by arctic foxes were removed from nest bowls (94% in 1996, 66% in 1997, and 83% in 1998) and only a few eggs were dump-eggs (<1%, 7%, and 3% in each year, respectively) or from unknown sources (6%, 27%, and 14% in each year, respectively). Dump-eggs were taken especially frequently in 1997, a late snowmelt year, when many geese laid their eggs outside of nests while waiting for the snow to melt (Samelius and Alisauskas, unpubl. data). About half of the eggs taken from nest bowls were removed from nests unattended by geese (65%, 55%, and 44% in each year, respectively). The remaining eggs were taken from geese that the foxes forced away from nests before removing eggs.

Foxes took eggs from caches more frequently in 1997 and 1998 than in 1996 as the best model included length of observation and an interaction between length of observation and year ($AIC_C = 766.0$, Table 3). Acquisition of eggs from caches increased marginally throughout incubation as illustrated by all alternative models within 2 AIC_C units of the best model including weak positive effects of incubation ($r^2 < 0.043$ after accounting for length of observation, Table 3). On average, the number of eggs per hour that each fox took from caches was 1.0 in 1996 (95% C.I. = 0.7–1.4); 6.7 in 1997 (95% C.I. = 5.3–8.1); and 3.0 in 1998 (95% C.I. = 2.5–3.6).

Foxes frequently attacked geese, but had considerable difficulty catching them. Consequently, foxes killed only four geese, whereas they scavenged 20 dead geese. Overall, geese were taken equally in all years ($\chi^2_{(2)} = 0.397$, $p = 0.820$, Table 1). Three of the geese killed were nesting females, and the fourth was an unpaired bird of unknown sex that was not associated with a nest. Of the three females killed, one was paired and two were unpaired. When feeding on geese, either freshly killed or scavenged, foxes generally consumed only parts of the goose, feeding mostly from the breast. Although foxes managed to kill only four geese, they occasionally caught and held geese for up to 5 seconds before the geese escaped. During one of those attacks, a fox broke a wing of an unpaired female, then took her eggs and left the injured female alone. In most attacks on geese, however, either the fox or the goose retreated without physical contact (Samelius and Alisauskas, unpubl. data).

Foxes took lemmings with equal frequency in all years (Fisher exact test $p = 0.415$, Table 1). In addition to their successful lemming catches, foxes occasionally made what appeared to be unsuccessful attempts to catch lemmings. During one of these attempts, a lemming was captured temporarily before escaping from the fox.

Fate of Foods

Fate of food objects differed according to food types (Fisher Exact test on food object with known fate, $p < 0.001$); new eggs and eggs from caches were mostly cached, whereas geese and lemmings were mostly eaten (Table 4). A large proportion of lemming catches (60%) had an unknown fate, since the foxes disappeared from

TABLE 2. Values of the Akaike Information Criterion adjusted for small sample size (AIC_C) for the five models that best explained variation in the arctic foxes' acquisition of new eggs at Egg River in 1996–98. Also included are the number of model parameters (K) and the difference between each model and the best model (Δ_i). Effects of continuous model variables are indicated in parentheses.

Model	K	AIC_C	Δ_i
length of observation (+), stage of incubation (-)	4	895.4	0
length of observation (+), length of observation*stage of incubation (+)	4	895.8	0.5
length of observation (+)	3	896.0	0.6
length of observation (+), year*stage of incubation	5	896.8	1.5
length of observation (+), stage of incubation (-), length of observation*stage of incubation (+)	5	897.4	2.1
Full model (length of observation, stage of incubation, year, and all two-way interactions)	13	911.2	15.9

TABLE 3. Values of the Akaike Information Criterion adjusted for small sample size (AIC$_C$) for the five models that best explained variation in arctic foxes' acquisition of eggs from caches at Egg River in 1996–98. Also included are the number of model parameters (K) and the difference between each model and the best model (Δ_i). Effects of continuous model variables are indicated in parentheses.

Model	K	AIC$_C$	Δ_i
length of observation (+), length of observation*year	5	766.0	0
length of observation (+), length of observation*year, year*stage of incubation	8	766.1	0.1
length of observation (+), length of observation*year, length of observation*stage of incubation (+)	6	766.6	0.6
length of observation (+), length of observation*year, stage of incubation (+)	6	767.0	1.1
length of observation (+), length of observation*year, length of observation*stage of incubation (+), year*stage of incubation	9	768.1	2.2
Full model (length of observation, stage of incubation, year, and all two-way interactions)	13	777.0	11.0

view carrying the food. However, only 12% of new eggs, 15% of eggs from caches, and 4% of geese had an unknown fate. The fate of one goose was mixed: part was eaten, part was cached, and the rest was lost when another fox chased the feeding fox. Eggs were the only other food lost: two foxes each lost an egg when chased by another fox, and two foxes each lost an egg when mobbed by ganders.

Food objects were generally cached within 50–200 m from where they were taken, and foxes invested about five minutes in the process. However, the distance that food objects were moved before caching varied from less than 5 m to over 1 km, and foxes occasionally invested more than 15 minutes in caching of foods. Foxes generally appeared undecided about where to cache food objects and often started to dig at several locations before caching foods. Foxes had considerable difficulty moving goose carcasses and dropped them frequently, either to rest or because they were mobbed by ganders. On two separate occasions, we observed a fox feeding on a goose carcass only after dropping it several times when attacked by ganders.

All food objects seen to be cached were cached individually, but foxes also cached foods at den sites and at sites that appeared to be temporary dens (i.e., small dens without the grass or other vegetation that characterizes older dens, see Chesemore, 1969; Garrott et al., 1983). The largest food cache was a temporary den with four entrances: it had 71 goose eggs and a goose neck placed on the ground and more than 20 eggs in each entrance (each entrance >1 m deep). The den, found in 1997, showed no signs of previous occupancy (see above), but we observed young there the following year.

Interactions among Foxes

More encounters between foxes occurred in 1997 and 1998 than in 1996 ($\chi^2_{(2)}$ = 5.835, p = 0.054). We observed four interactions between foxes in 1996, 16 in 1997, and 18 in 1998. Eight interactions in 1997 and ten in 1998 appeared aggressive: in 17 cases, one fox pursued another fox at high speed for distances of 200 m to more than 1 km, and in one case a fox bit another fox. The remaining interactions appeared nonaggressive: the foxes either observed each other from ca 30 m apart (n = 3), approached to within 10 m (n = 7), briefly sniffed or rolled around with

TABLE 4. Known fate of foods taken by foxes at Egg River (all years pooled). The number of food objects in each category is given in parentheses. Fourteen new eggs and 16 eggs from caches were excluded from analyses because of observer error.

| Fate | Eggs | | Other foods | |
	New	From Caches	Geese	Lemmings
Cached	97%(330)	93%(151)	13% (3)	25% (1)
Eaten	2% (7)	7% (12)	83% (19)	75% (3)
Lost	1% (4)	0% (0)	0% (0)	0% (0)
Mixed	0% (0)	0% (0)	4% (1)	0% (0)
Sample size	341	163	23	4

each other (n = 5), left the area together (n = 2), or took eggs from geese while another fox was interacting with the birds (n = 3).

Impact of Fox Predation on Productivity of Geese

While geese were nesting, each fox took on average about 1500 new eggs (range = 1260–1750) in 1996, 1570 (range = 1250–1880) in 1997, and 900 (range = 690–1100) in 1998. The proportion of total available eggs taken by foxes during incubation each year ranged from 2.5 to 5.7% for the breeding population of foxes, and from 4.2 to 8.2% for the fox population scaled from number of foxes seen in the study area (Table 5). The proportion of total available eggs taken by foxes by forcing geese away from their nests ranged from 1.6 to 2.2% for the breeding population of foxes, and from 2.7 to 3.6% for the fox population scaled from number of foxes seen in the study area (Table 5).

DISCUSSION

Food Acquisition

Arctic foxes took mostly eggs when in the colony, whereas few geese and lemmings were taken. This foraging pattern was similar to those of arctic foxes at other waterfowl nesting areas (e.g., Stickney, 1991; Syroechkovskiy et al., 1991) and appeared to reflect availability of food and ease of acquisition. Eggs are easy for foxes to

TABLE 5. Proportion of snow goose eggs present at Egg River taken by foxes during incubation at Egg River in 1996–98. The proportion of eggs that foxes took by forcing birds off their nests is given in parentheses. Nesting failure of geese is included for comparison of fox predation to overall nesting failure (Samelius and Alisauskas, 1998).

Year	Proportion of eggs taken by foxes		Nesting failure of geese
	Breeding foxes[1]	Total population[1]	
1996	5.7% (2.1%)	7.3% (2.7%)	5.9%
1997	5.0% (2.2%)	8.2% (3.6%)	35.3%
1998	2.5% (1.6%)	4.2% (2.7%)	11.7%

[1] Impact of fox predation was calculated using two measures of the fox population: (1) the number of foxes known to breed within 1.5 km of the goose colony, and (2) the number of foxes seen in the study area, scaled for the whole goose colony.

handle and keep well when cached (Stickney, 1991; Bantle and Alisauskas, 1998), which may result in short and successful searches where foods are efficiently cached for later use (Stickney, 1991). Foxes may also have avoided geese and goose carcasses because they are difficult to carry. Additionally, foxes were continuously mobbed by geese when in the colony (Samelius, 1999); they may have avoided killing geese because the risk of injury was too great, or because of negative experiences from previous interactions (Lima and Dill, 1990).

The foraging efficiency of arctic foxes was similar in all three years, despite variation in lemming abundance and reproductive effort. Similar results have been reported for arctic foxes at other waterfowl nesting areas (e.g., Stickney, 1991; Bantle, 1998), and these results support Stickney's (1991) hypothesis that eggs may be the main food of arctic foxes in waterfowl nesting areas where nest densities are high and eggs are relatively easy to obtain. Nest densities at these locations may often be considerably higher than lemming densities, even in years when lemming numbers are high—especially at large goose colonies, where intense grazing by geese has deteriorated the lemming habitat (Bantle, 1998; Samelius and Alisauskas, 1998). Switching from lemmings to bird prey in years with low lemming abundance may, thus, be limited to areas where lemming densities are generally considerably higher than nest densities (e.g., nesting areas of wading birds or sparse waterfowl nesting areas) and does not appear to occur at large goose colonies or waterfowl areas (see Summers, 1986; Summers and Underhill, 1987; Summers et al., 1998). Variation in impact of fox predation at large goose colonies and waterfowl areas may instead reflect the number of foxes frequenting the area rather than variation in foraging efficiency of individual foxes (see MacInnes and Misra, 1972).

Arctic foxes took and cached new eggs at similar rates each year, despite variation in breeding effort and additional costs of raising young. This pattern of prey acquisition was similar to that of arctic foxes at other waterfowl nesting areas (e.g., Stickney, 1991; Bantle, 1998), and it

accords with observations that carnivores may cache foods independently of current energetic demands, acquiring and caching as much food as possible when food is abundant (Smith and Reichman, 1984; Vander Wall, 1990). This behaviour may be especially adaptive in environments where food abundance varies greatly and cached foods keep well (Smith and Reichman, 1984; Vander Wall, 1990). The amount of food that foxes acquire may be limited instead by the foraging capacity of the foxes, or by their need to perform other (e.g., territorial) behaviours (Kamil and Sargent, 1981; Stephens and Krebs, 1986).

Foraging efficiency of arctic foxes at Egg River was higher than that recorded for arctic foxes at other waterfowl areas during incubation. Foxes at Egg River took 4.2–7.3 eggs/hour, whereas foxes at Kokechik Bay in Alaska took 3.5 eggs/hour (Stickney, 1991) and foxes at Karrak Lake in the central Canadian Arctic took 2.7 eggs/hour (Bantle, 1998). Greater variation among, rather than within, geographic regions further suggests that foraging efficiency of arctic foxes may be limited by foraging capacity and not by current energetic demands. Nest densities were substantially lower at Kokechik Bay than at Egg River, and prey acquisition of foxes at Kokechik Bay may thus have been limited by travelling time (Stickney, 1991). However, this was not the case at Karrak Lake, where nest densities were higher than at Egg River; instead, more frequent mobbing by geese may have limited prey acquisition by foxes at Karrak Lake (Bousfield and Syroechkovskiy, 1985; Bantle, 1998).

We found that arctic foxes located and moved considerably more eggs from caches in 1997 and 1998 than they did in 1996. These two years were characterized by high fox densities and reduced breeding effort by foxes (Samelius and Alisauskas, unpubl. data), both of which suggest a large overlap in home range among foxes (Syroechkovskiy et al., 1991; Bantle, 1998). This overlap was further reflected by higher encounter rates and more aggressive interactions among foxes in 1997 and 1998. Higher rates of cache recovery in these two years may have resulted from increased cache pilfering, or foxes may have moved caches to deter cache pilfering (Vander Wall, 1990). Moving and pilfering of caches reduced the time that foxes could spend obtaining new eggs and may appear to be nonadaptive, unless moving the eggs decreased the chances of cache pilfering, or unless eggs from caches were stolen faster than new eggs could be obtained (Andersson and Krebs, 1978; Smith and Reichman, 1984; Vander Wall, 1990). In such cases, movement and pilfering of caches could be advantageous in years of high fox abundance, even though foxes invest considerable time in the process (Andersson and Krebs, 1978; Smith and Reichman, 1984; Vander Wall, 1990). Annual variation in cache recovery may alternatively have reflected differences in cache abundance. This appeared unlikely, however, as foxes took and cached eggs at similar rates in each year, suggesting that abundance of caches was comparable among years.

Arctic foxes rarely killed or injured geese, and most interactions between foxes and adult geese resulted in no injury to foxes or birds. Of the geese that were killed or injured, however, four out of five were incubating females (the fifth bird was of unknown sex), suggesting that female geese may have been exposed to greater risk of injury or death than males. Male geese may have escaped foxes better than female geese because guarding males could retreat more easily than incubating females; or male geese may have been in better condition, since the females invest more energy during nesting (Ankney, 1977; Ankney and MacInnes, 1978). Thus, different roles during nesting (rather than more risk-taking behaviour by females) may have exposed females to greater risk of injury than males (Montgomerie and Weatherhead, 1988).

Fate of Food Objects

Most eggs, but only a few geese and lemmings, taken by arctic foxes were cached for later use; this contrast may have reflected the perishability of different foods (Reichman, 1988; Hadj-Chikh et al., 1996). Eggs may keep better than geese and lemmings because the protective shell reduces decomposition (Stickney, 1991; Bantle and Alisauskas, 1998). We found that most eggs the foxes consumed were cracked (eggs dropped by foxes or dump-eggs cracked by freezing) or old (eggs from caches), which supports the suggestion that perishability was a determinant of immediate food consumption. Additionally, foxes had considerable difficulty moving goose carcasses and occasionally fed on geese after first having tried to move them. So handling time and ease of moving foods may also have influenced whether they were cached or eaten immediately. Nutritional variation among foods may also have played a role (Vander Wall, 1990; Bantle and Alisauskas, 1998).

The foxes' apparent indecisiveness about where to cache food objects may mean that they associate successful cache recovery with certain cache locations (Brodin and Kunz, 1997) or that foxes were reluctant to cache eggs because of high densities of conspecifics (Lathi and Rytkönen, 1996). The latter appeared unlikely, however, as foxes seemed wary in all years, despite variation in fox abundance and encounter rates.

Impact of Fox Predation on Productivity of Geese

The impact of fox predation was low in all years, and foxes took only about 4–8% of all eggs available at Egg River during incubation each year. This predation rate was low compared to that reported from Wrangel Island, Russia, where foxes destroyed almost all snow goose nests in some years (Bousfield and Syroechkovskiy, 1985; Syroechkovskiy and Krechmar, 1981 in Syroechkovskiy et al., 1991). Such extreme predation pressure was unusual, however, and occurred only in years with low

numbers (<15 000) of nesting geese (Bousfield and Syroechkovskiy, 1985). Arctic fox predation at large goose colonies, such as Egg River, may be low because foxes are swamped by large numbers of geese (Wittenberger and Hunt, 1985; Raveling, 1989). Further, predation pressure by arctic foxes may also vary among species in relation to the ability of geese to defend themselves (Stickney, 1991; Syroechkovskiy et al., 1991; Bantle, 1998). Thus, the impact of fox predation at Egg River may have been relatively low because the colony was so large and snow geese defend themselves effectively against the foxes.

Fox predation could account for most nesting failure of geese in 1996, but fox predation was relatively low compared to nesting failure in 1997 and 1998. This suggests that factors other than fox predation had greater influence on nesting performance of geese in years when spring arrived late. Late springs have had a strong effect on nesting performance of snow geese at other colonies (Davies and Cooke, 1983; Bousfield and Syroechkovskiy, 1985) and apparently at Egg River as well (Samelius and Alisauskas, 1998; Samelius, 1999). That fox predation was low compared to nesting failure in 1997 and 1998 further suggests that there was a large number of eggs left at the colony after goose dispersal, upon which foxes and avian predators could scavenge. So arctic foxes may have taken a large number of eggs after goose dispersal, in addition to those taken during nesting. This could explain why arctic foxes at a large goose colony in the central Canadian Arctic had not increased their home range one month after goose departure (Bantle, 1998). However, the absence of an increase in home range may also have reflected the use of caches, or movement of foods from caches to den sites. Moving caches to den sites may increase accessibility and use during winter or serve to supplement the diets of growing young (Fay and Stephenson, 1989; Vander Wall, 1990; Sklepkovych and Montevecchi, 1996). Anthony (1997) noted that near a large brant goose colony, where Stickney (1991) had found that egg caching was common, arctic foxes generally stayed within their summer home range in winter.

Implications of Food Caching for Fox Survival

The average 900–1570 eggs per fox taken and cached during nesting each year may have a significant effect on fox survival by forming a crucial part of the winter diet (Fay and Stephenson, 1989; Stickney, 1991; Prestrud, 1992; Bantle and Alisauskas, 1998) or by supplementing the diets of growing young (Vander Wall, 1990). Some den sites at Banks Island were open during winter (J. Lucas Jr., Sachs Harbour, pers. comm. 1998), suggesting that foxes may have used cached foods during this period. However, foxes were also seen on the ice of the Beaufort Sea (J. Lucas Jr., Sachs Harbour, pers. comm. 1998) and the extent of fox reliance on cached foods was unknown. Caching and use of cached foods may be adaptive

compared to dispersing to search for other food, as this practice allows foxes to stay in a familiar area with a predictable food supply (Fay and Stephenson, 1989; Vander Wall, 1990). Further, caching of foods appears to be especially frequent at large bird colonies, where temporarily abundant concentrations of prey may allow foxes to cache enough food to avoid shortages during the winter (Fay and Stephenson, 1989; Stickney, 1991; Bantle and Alisauskas, 1998).

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