FORAGING BEHAVIOURS AND POPULATION DYNAMICS
OF ARCTIC FOXES

A Thesis Submitted to the College of

Graduate Studies and Research

in Partial Fulfilment of the Requirements

for the Degree of Doctorate of Philosophy

in the Department of Biology,

University of Saskatchewan,

Saskatchewan

By

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2006

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ABSTRACT

Northern environments are often characterised by large seasonal and annual fluctuations in food abundance. In this thesis, I examined how arctic foxes (*Alopex lagopus*) used seasonally superabundant foods (geese and their eggs) and how access to these foods influenced population dynamics of arctic foxes. I addressed this against a backdrop of variation in lemming and vole abundance (small mammals hereafter) – the main foods of arctic foxes throughout most of their range. Field work was done at the large goose colony at Karrak Lake and surrounding areas in the Queen Maud Gulf Bird Sanctuary in Nunavut, Canada, in the spring and summers of 2000 to 2004.

Behavioural observations of individually-marked arctic foxes showed that they took and cached 2,000-3,000 eggs per fox each year and that the rate at which they took eggs was largely unrelated to individual attributes of foxes (e.g. sex, size, and breeding status) and nesting distribution of geese. Further, the rate at which foxes took eggs varied considerably within individuals in that foxes were efficient at taking eggs at times and inefficient at other times. This may have resulted from foxes switching between foraging actively and taking eggs opportunistically while performing other demands such as territorial behaviours.

Comparison of stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of fox tissues and those of their foods showed that the contribution of cached eggs to arctic fox diets was inversely related to collared lemming (*Dicrostonyx torquatus*) abundance. In fact, the contribution of cached eggs to overall fox diets increased from <28% in years when collared lemmings were abundant to 30-74% in years when collared lemmings were scarce. Furthermore, arctic foxes used cached eggs well into the following spring (almost 1 year after eggs were acquired) – a pattern which differs from that of carnivores generally storing foods for only a few days before consumption.

A field-study of experimental caches showed that survival rate of these caches was related to age of cache sites in the first year of the study (e.g. 0.80 and 0.56 per 18-day period for caches from new and 1 month old cache sites, respectively) and departure by geese after hatch in the second year of the study (e.g. 0.98 and 0.74 per 18-day period during and after goose nesting, respectively). Food abundance and deterioration of cache sites (e.g. loss of soil cover and partial exposure of caches) were,

thus, important factors affecting cache loss at Karrak Lake. Further, annual variation in the importance of these factors suggests that strategies to prevent cache loss are not fixed in time but vary with existing conditions. Evolution of caching behaviours by arctic foxes may, thus, have been shaped by multiple selective pressures.

Comparisons of reproductive output and abundance of arctic foxes inside and outside the goose colony at Karrak Lake showed that (*i*) breeding density and fox abundance were 2-3 times higher inside the colony than they were outside the colony and (*ii*) litter size, breeding density, and annual variation in fox abundance followed that of small mammal abundance. Small mammal abundance was, thus, the main governor of population dynamics of arctic foxes whereas geese and their eggs elevated fox abundance and breeding density above that which small mammals could support. These results highlight both the influence of seasonal and annual variation on population dynamics of consumers and the linkage between arctic environments and wintering areas by geese thousands of kilometres to the south.

ACKNOWLEDGEMENTS

DEDICATION

this thesis is dedicated to all the people who helped me in the field

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1. INTRODUCTION

1.1 Foraging Behaviour

1.1.1 Foraging Theory

All animals confront the problem of finding enough food for growth, maintenance, and reproduction while faced with needs to perform other demands and confronted with dangers from other animals (Perry and Pianka 1997). This conflict forms a central aspect in foraging theory and predicts that optimal foraging behaviours result from feeding strategies that maximise lifetime reproductive output (Stephens and Krebs 1986, Perry and Pianka 1997). However, other factors such as anatomical and physiological limitations can also affect foraging behaviours (Stephens and Krebs 1986, Grier and Burk 1992). Foraging behaviours, thus, reflect both intrinsic and extrinsic constraints on what and where to feed (Perry and Pianka 1997).

1.1.2 Prey Selection

Predation is often skewed towards weak and sick prey (Taylor 1984). However, selection of debilitated prey is generally more common among predators that focus on prey that are difficult to capture or that offer great resistance (Temple 1987). Animals in poor condition may also take higher risks than animals in good condition (McNamara and Houston 1987, Sinclair and Arcese 1995). Further, learned behaviours such as negative experiences and familiarity with prey may also influence prey selection (Lima and Dill 1990, Grier and Burk 1992). Prey selection is, thus, generally a complex process affected by several factors.

1.1.3 Food Caching

Caching of foods is common among many birds and mammals and may be an adaptive strategy to avoid food shortage in environments where food abundance fluctuates greatly and where cached foods keep well (Vander Wall 1990). Use of stored foods allows animals to remain in familiar areas without having to put on large amounts of body fat and is an alternative strategy to migration, torpor, hibernation, and fat

storage (Smith and Reichman 1984, Vander Wall 1990). Food hoarding may also be adaptive to supplement diets of growing young or to reduce time spent foraging when other behaviours are more important (Smith and Reichman 1984, Vander Wall 1990). A critical aspect for the evolution of food caching is that caching individuals have a greater chance of recovering caches than do other individuals (Andersson and Krebs 1978). However, the importance of cached foods to overall diets is poorly understood in most animals (Vander Wall 1990).

Animals generally cache foods in either many small caches scattered in space (*scatter-hoarding*) or in a few closely spaced caches with many foods in each cache (*larder-hoarding*, Vander Wall 1990). The strategy of how foods are cached appears to be influenced by the ability to defend caches against competitors; scatter-hoarded foods are typically not defended whereas larder-hoarded foods are more likely to be defended (Smith and Reichman 1984, Vander Wall 1990). Further, scatter-hoarding animals generally rely on secretive behaviours and inconspicuous caches whereas larder-hoarding animals often devote considerable time and energy in defending larders (Vander Wall 1990). For example, animals often delay or avoid caching foods when competitors are nearby (Heinrich and Pepper 1998, Bugnyar and Kotrschal 2002). Other strategies to reduce cache loss includes selection of cache sites, optimal spacing of caches, and storage of more foods than needed (Smith and Reichman 1984, Vander Wall 1990). However, the relative importance of factors affecting cache loss is unknown in most animals (Vander Wall 1990).

1.2 Population Dynamics

1.2.1 Population Dynamics and Demographic Processes

Population dynamics is the study of abundance and distribution of organisms and factors that regulate populations in space and time (Begon et al. 1996, Williams et al. 2002). Fluctuations in population size are caused by changes in birth, death, immigration, and emigration rates (Begon et al. 1996). These vital rates, in turn, vary with biotic factors such as predation and competition and with abiotic factors such as extreme weather conditions (Williams et al. 2002). Further, biotic factors are generally

density-dependent whereas abiotic factors are typically density-independent (Begon et al. 1996). The study of population dynamics is often complex even in relatively simple food webs (see Krebs et al. 1995, Post et al. 2000) and ecological patterns typically vary among ecosystems (Lawton 1999). Yet, understanding how abundance and distribution of animals vary in space and time is fundamental for both theoretical and applied biology (Begon et al. 1996, Thompson et al. 1998). In fact, Begon et al. (1996) argue that identifying and understanding the distribution and abundance of organisms is the main aim of ecology.

1.2.2 Generalist and Specialist Predators

Predators are often categorised as generalist or specialist predators depending on their degree of specialisation on their prey; generalist predators switch among prey opportunistically whereas specialist predators are closely linked to specific prey and rarely switch among prey (Andersson and Erlinge 1977). Generalist predators tend to have a stabilising effect on prey numbers by feeding on the most abundant prey and thereby dampening prey fluctuations (Andersson and Erlinge 1977, Hanski et al. 1991). However, generalist predators can also suppress rare or secondary prey as such predators can be maintained at high levels by their primary prey (Holt 1977). Specialist predators tend to have a destabilising effect on their prey because the delay in the numerical response is often very pronounced among specialist predators (Hanski et al. 1991). Generalist predators can function as specialist predators in patchy environments or in ecosystems with few prey species simply because they encounter only one or a few prey species (O'Donoghue et al. 1997, Warburton et al. 1998).

1.2.3 Population Dynamics and Fluctuating Foods

Large seasonal and annual fluctuations in food abundance are common in northern environments. These fluctuations, in turn, influence both the abundance and distribution of animals that feed on them (Krebs et al. 1995, Krebs et al. 2001). For example, reproductive events such as litter size and pregnancy rates are often closely related to female condition and food abundance (Bronson 1989, Stearns 1992).

Similarly, changes in immigration and emigration rates often reflect changes in food abundance (Begon et al. 1996). However, animals seldom respond instantaneously to changes in food abundance so there is often a delay in the numerical response of most animals (Begon et al. 1996).

I was interested in understanding what role large temporal and spatial fluctuations in prey abundance had on predator populations. As well, I wished to increase the understanding about food storage as an alternative strategy to fat storage, migration, hibernation, and torpor for surviving extreme nutritional constraints. I was interested in a relatively simple food web so that a clear focus could be maintained on the interaction between predator and prey. Reduced species richness in polar regions tend to result in food webs that are simpler than those found in temperate or equatorial ecosystems. As well, arctic terrestrial habitats show large seasonal increases in migratory animals (especially birds) that function as potential superabundant prey for resident predators. Consequently, my choice of model predator and ecosystem, described below, was governed by these considerations.

1.3 Study Animal

1.3.1 Diet and Foraging Behaviours

Arctic foxes (*Alopex lagopus*) are generalist predators and scavengers that rely heavily on small mammals throughout most of their range (Audet et al. 2002). However, other foods such as birds and their eggs can be important in arctic fox diets in some years and parts of the arctic (Hersteinsson and MacDonald 1996, Bantle and Alisauskas 1998). Arctic foxes commonly cache foods when foods are abundant (Stickney 1991, Samelius and Alisauskas 2000). Caching of foods appears to be especially common among arctic foxes at large bird colonies where foxes cache >1,000 eggs each during the nesting season by birds (Stickney 1991, Samelius and Alisauskas 2000). Small mammals often fluctuate dramatically over 3-5 year periods whereas large influxes of birds and their eggs provide arctic foxes with predictable and seasonally superabundant food. Large bird colonies therefore provide ideal settings to study food

caching by arctic foxes and how use of these foods vary in relation to fluctuations in other foods.

1.3.2 Abundance and Demography

Arctic fox numbers often fluctuate considerably among years (Audet et al. 2002). These fluctuations are especially pronounced among arctic foxes that rely heavily on small mammals (Macpherson 1969, Angerbjörn et al. 1995). Fluctuations in arctic fox numbers appear to be closely related to variation in recruitment of young which, in turn, is highly correlated with food abundance (Macpherson 1969, Angerbjörn et al. 1991, Angerbjörn et al. 1995). In fact, arctic foxes have the largest litter size in the order Carnivora and may have up to 18 pups when foods are abundant (Tannerfeldt and Angerbjörn 1998). Mortality factors for arctic foxes include starvation, trapping, diseases, and predation by avian and mammalian predators – although starvation is likely the main cause of death (Audet et al. 2002).

1.4 Thesis Outline and Objectives

The objectives of this thesis were to examine how arctic foxes used seasonally superabundant foods (geese and their eggs) and how use of these foods influenced population dynamics of arctic foxes. I addressed this against a backdrop of annual variation in small mammal abundance. Specifically, I evaluated the role of intrinsic and extrinsic variables on foraging behaviours of individually-marked foxes (Chapter 3), examined when and to what extent arctic foxes used cached eggs by comparing stable isotope ratios (δ^{13}C and δ^{15}N) of fox tissues to that of their foods (Chapter 4), evaluated how nesting distribution by geese and age of cache sites influenced survival rates of experimental food caches (Chapter 5), and compared reproduction and abundance of arctic foxes inside and outside a large goose colony and in relation to annual variation in small mammal abundance (Chapter 6). Field work was conducted at the large goose colony at Karrak Lake and surrounding areas in the Queen Maud Gulf Bird Sanctuary in Nunavut, Canada, in the spring and summers of 2000 to 2004 (although Chapter 3 was conducted in 2001-2003 and Chapter 5 in 2001 and 2003).

2. STUDY AREA

This study was done at Karrak Lake (67°14'N, 100°15'W) and surrounding areas in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada, in May to July, 2000 to 2004 (Figure 2.1). Karrak Lake is the largest goose colony in the sanctuary (Kerbes 1994) and consisted of about 700,000 to 1,000,000 nesting Ross's (*Chen rossi*) and lesser snow geese (*Chen caerulescens*) in 2000 to 2004 (R. Alisauskas, Canadian Wildlife Service, personal communication). Geese arrived at Karrak Lake in late May and departed the colony after hatch in early July. Average nesting density ranged 22-34 nests/ha from 2000 to 2004 (R. Alisauskas, Canadian Wildlife Service, personal communication). Ross's and lesser snow geese nesting at Karrak Lake winter in the southern parts of North America and spend 1-2 months at staging areas in the central parts of the continent in spring and fall (Alisauskas 2002). Karrak Lake and surrounding areas consist of gently rolling tundra that is dominated by rock outcrops, sedge meadows, and marshy areas interrupted by shallow tundra ponds (Ryder 1972). Arctic fox diets at Karrak Lake are dominated by small mammals, geese, and eggs (Bantle and Alisauskas 1998).

In addition to foxes and geese, other animals common in the area included king eiders (*Somateria spectabilis*), longtailed ducks (*Clangula hyemalis*), gulls (*Larus* spp.), parasitic jaegers (*Stercorarius parasiticus*), ptarmigan (*Lagopus* spp.), shore-birds (Charadriiformes), passerine birds (Passeriformes), caribou (*Rangifer tarandus*), collared lemmings (*Dicrostonyx torquatus*), and red-backed voles (*Clethrionomys rutilus*). Wolves (*Canis lupus*), wolverines (*Gulo gulo*), grizzly bears (*Ursus arctos*), muskoxen (*Ovibos moschatus*), arctic hares (*Lepus arcticus*), and brown lemmings (*Lemmus sibiricus*) were rare during this study. Caribou, wolves, and the majority of birds are migratory and present in the area only during spring and summer (although some caribou and wolves remain in the area throughout winter). Small mammal abundance varied considerably among years and was high in 2000, low in 2002 and 2004, and intermediate in 2001 and 2003 (Chapter 6).

Figure 2.1. Karrak Lake is the largest goose colony in Queen Maud Gulf Bird Sanctuary, Nunavut, Canada, and consisted of 700,000 to 1,000,000 nesting Ross's and lesser snow geese in 2000 to 2004.

3. THE ROLE OF INTRINSIC AND EXTRINSIC FACTORS ON FORAGING BEHAVIOURS OF ARCTIC FOXES

Abstract: Foraging behaviours generally reflect numerous internal and external factors on what and where to feed. However, few studies have examined how foraging behaviours are influenced by more than one or a few parameters. In this study, I examined how foraging behaviours of arctic foxes at a large goose colony were influenced by a suite of intrinsic (sex, size, and breeding status) and extrinsic factors (nesting density by geese, proportion of two sympatric goose species, and stage of incubation). Behavioural observations of individually-marked arctic foxes showed that they took and cached 2,000-3,000 eggs per fox each year and that the rate at which they took eggs was largely unrelated to intrinsic and extrinsic factors. In fact, repeated observations showed that the rate at which arctic foxes took eggs varied considerably within individuals in that foxes were efficient at taking eggs at times but inefficient at other times. This may have resulted from foxes switching between foraging actively and taking eggs opportunistically while performing other demands such as territorial behaviours.

3.1 Introduction

The conflict of finding enough food for growth, maintenance, and reproduction while faced with the need to perform other demands such as territorial maintenance, finding mates, and predator avoidance forms a central aspect of foraging theory (Stephens and Krebs 1986, Perry and Pianka 1997). Foraging behaviours by most animals are also influenced by intrinsic and extrinsic factors such as age, sex, breeding status, individual variation, and spatial and temporal variation in foods (Perry and Pianka 1997, Bolnick et al. 2003). Foraging behaviours by most animals are, thus, constrained by intrinsic and extrinsic factors on what and where to feed. However, the relative importance of these constraints is poorly understood in most animals because few studies have examined more than one or a few factors concurrently. This is

especially true for foraging behaviours of predators as they are rarely seen in the wild (but see Gese et. al 1996).

Arctic foxes are generalist predators and scavengers that rely heavily on lemmings and voles (small mammals hereafter) throughout most of their range (Audet et al. 2002). However, other foods such as birds and their eggs can be important in arctic fox diets in some years and parts of the arctic (Hersteinsson and MacDonald 1996, Bantle and Alisauskas 1998). Arctic foxes commonly cache foods when foods are abundant (Audet et al. 2002). Caching of foods appears to be especially common among arctic foxes at large bird colonies where foxes cache >1,000 eggs per fox during the nesting-season by birds (Stickney 1991, Samelius and Alisauskas 2000). Small mammals often fluctuate dramatically over 3-5 year periods whereas bird colonies provide arctic foxes with seasonally superabundant foods. The objective of this study was to examine how intrinsic and extrinsic factors influence foraging behaviours by arctic foxes at a large goose colony. Specifically, I examined how sex of foxes, size of foxes, breeding status of foxes, nesting density by geese, proportion of two sympatric goose species, and stage of incubation influenced food acquisition by arctic foxes.

3.2 Methods

3.2.1 Trapping and marking of foxes

Adult arctic foxes (≥1 year old) were captured and ear-tagged in May and early June each year (see Samelius et al. 2003 for capture procedures). For each fox, the weight, sex, and the size of the right hind-foot was recorded. Breeding status of foxes was determined from repeated visits to den sites (Chapter 6). A subset of foxes were fitted with radio-collars (Telonics MOD-105, weight = 70 g) to help locate foxes for behavioural observations.

3.2.2 Behavioural observations

Foraging behaviours of individually marked foxes was observed with spotting scopes (15-45×) from hills and ridges associated with the colony following Samelius

and Alisauskas (2000). Observations were made during the peak incubation period by geese which was mid June to early July (although nesting chronology varied by about 1 week among years during this study). Observations were made opportunistically between 20:00 and 10:00 which corresponded to peak fox activity (Anthony 1997, Bantle 1998). Twenty-four hour daylight and limited vegetation provided ideal conditions for observing interactions between foxes and geese although heavy rain, snow, fog, and strong winds prevented observations occasionally. There were 3 observers per year in this study so the first observations in each year were made as a group to improve consistency among observers (82% of the observations were made by 2 observers that were involved in all years).

Once a fox was detected, it was observed for 60 minutes or until it went out of view, was too far away for accurate observation, or left the colony. For each observation, (*1*) duration of observation, (*2*) food objects taken by foxes, (*3*) proportion of Ross's versus lesser snow geese along the foraging path of the fox (see below), (*4*) and fate of food objects (see below) were recorded. Time periods and food objects acquired when foxes were temporarily out of sight were excluded. Food objects were categorised as eggs, adult geese (geese hereafter), nest contents from passerine nests (we could not determine how many eggs or nestlings foxes took from these nests), small mammals, and unknown foods. Eggs were separated into *new eggs* (eggs from nest bowls) and *eggs from existing caches* (eggs dug up from the ground). Food objects were defined as (*1*) cached if buried by the fox, (*2*) eaten if consumed by the fox, (*3*) lost if dropped and not recovered by the fox, (*4*) brought to den if carried to a den site by the fox, and (*5*) unknown if carried by the fox when disappearing from view.

The proportion of Ross's and lesser snow geese along foraging paths of foxes (species composition hereafter) was determined at the start of each observation and every 5 minutes thereafter by deciding to what species the closest 3 breeding pairs within about 100 m belonged. Nesting density by geese was determined at sample plots that were distributed systematically throughout the colony in a 1×1 km grid (Alisauskas, unpublished data). Average nesting density of the 3 sample plots closest to the area in which foxes foraged was used as an index of nesting density for each observation. I acknowledge that these large scale estimates of nesting density were not

direct estimates of nesting density along foraging routes by foxes but suggest that they were representative for nesting density in the general area in which foxes foraged.

3.2.3 Statistical analysis

I examined how acquisition of new eggs and eggs from existing caches varied with size of foxes, sex of foxes, breeding status of foxes, nesting density, species composition, and stage of incubation by a multi-way ANCOVA (Proc GLM, SAS Institute Inc., 1990). I performed analyses separately for new eggs and eggs from existing caches. Other foods were taken too infrequently to allow for detailed analyses. Acquisition of eggs varied with length of observation so I used the residual number of eggs taken when controlling for length of observation. I regressed data through the origin (noint option, SAS Institute Inc. 1990) and used year-specific residuals to control for annual variation in the rate at which eggs were acquired. Similarly, I limited analyses on new eggs to observations ≥ 10 minutes ($n = 66$ observations from 16 foxes) and analyses on eggs from existing caches to observations ≥ 20 minutes ($n = 33$ observations from 14 foxes) to ensure that foxes were observed long enough for these behaviours to occur (see Results for rate at which these foods were acquired). Sex and size of foxes were closely correlated ($r^2 = 0.42$) so I used size corrected for sex (i.e. the residual within each sex) in the analyses. I derived 48 *a priori* candidate models for each of these analyses where models ranged from none to all combinations of up to 3 of the independent variables above. I used variation around the grand mean as a null model (i.e. no effect of either of the variables examined). I used Akaike's information criterion ($AIC = n[\ln(SSE/n)] + 2K$, where K = number of model parameters, including the intercept and σ^2) with small-sample adjustment ($AIC_c = AIC + [(2K(K + 1))/(n - K - 1)]$) to select the most parsimonious models that best explained variation in acquisition of new eggs and eggs taken from existing caches (Burnham and Anderson 1998). I selected the model with the lowest AIC_C value as the most parsimonious model and considered models within 2 AIC_C units to be of similar quality (Burnham and Anderson 1998).

I estimated the rate at which foxes took new eggs and eggs from existing caches as the slope between number of eggs acquired and duration of observation. I regressed data through the origin (noint option, SAS Institute Inc. 1990). I estimated the average number of new eggs taken per fox during the nesting period by geese by multiplying the rate at which foxes took new eggs by daily foraging effort and the length of the nesting period. I assumed that foxes spent 8 hours foraging per day during 30 days of nesting following Samelius and Alisauskas (2000). This estimate should be used with caution as the variation in daily foraging effort is poorly understood (but see Bantle 1998 who found that arctic foxes at Karrak Lake showed >60% activity between 16:00-08:00).

I provide mean ± 95% confidence limits unless otherwise stated.

3.3 Results

One thousand six hundred eighty five minutes of foraging behaviours by arctic foxes were observed during which they took 257 new goose eggs, 48 goose eggs from existing caches, 1 goose egg from another fox (an egg that was dropped by a fox as it was chased by the focal fox), 17 small mammals, 3 geese (of which 1 was scavenged and 2 were killed), nest contents from 3 passerine nests, and 13 unknown foods (of which 1 was dug up from the ground). Foxes took 47% of new eggs after pushing geese off nests and the remaining 53% from nests unattended by geese (of which 6% may have been eggs outside of nest bowls). The rate at which foxes took new eggs was similar among years with foxes taking 13 ± 4, 8 ± 2, and 12 ± 4 new eggs per hour in 2001-2003, respectively. This corresponds to an average of 1,900-3,100 new eggs per fox each year. The rate at which foxes recovered eggs from existing caches, in contrast, varied among years with foxes taking 1.2 ± 0.6, 2.4 ± 0.5, and 0.7 ± 0.5 eggs per hour from existing caches in 2001 to 2003, respectively.

Foxes cached 96% of new eggs and 90% of eggs from existing caches for which fate could be determined (i.e. eggs from existing caches were largely recached) whereas they cached only 8% of fleshy foods (i.e. small mammals and geese) for which fate could be determined (Table 3.1). In contrast, 92% of fleshy foods for which fate could

Table 3.1. Fate of foods taken by arctic foxes at Karrak Lake in 2001-2003.

| Fate | Eggs | | Other foods | | |
	new eggs, % $n = 257$	from caches, % $n = 48$	geese, % $n = 3$	small mammals, % $n = 17$	passerine nests, % $n = 3$
cached	87	77	0	6	67
eaten	2	8	0	12	33
brought to den	<1	0	67	41	0
lost	<1	0	0	0	0
unknown[1]	10	15	33	41	0

[1] foods carried by foxes when disappearing from view

be determined were either consumed immediately or brought to den sites for consumption by young whereas only 3% of new eggs and 10% of eggs from existing caches for which fate could be determined were consumed immediately or brought to den sites. Most foods were cached within 100 m from where they were taken and foxes generally spent about 2-5 minutes in the process. However, foxes occasionally moved foods >1 km before caching them and spent >10 minutes in the process. Foxes often appeared undecided of where to cache foods and often started to dig at several locations before caching foods. All foods were cached individually (except for a few foods cached temporarily at den sites).

Model {nesting density} was the only model that described variation in the rate at which foxes took new eggs better than the *null model* of no effect of either of the variables examined (Table 3.2). Foxes took an additional 0.021 ± 0.024 new eggs as nesting density increased with 1 nest/ha. However, the influence of nesting density was very weak and explained only 4% of the overall variation in the rate at which foxes took new eggs ($r^2 = 0.04$). Similarly, repeated observations showed that variation in the rate at which foxes acquired new eggs was similar within ($s^2 = 6.9$) and among foxes ($s^2 = 7.9$). In fact, individual variation explained only 13% of the overall variation in the rate at which foxes acquired new eggs ($r^2 = 0.13$). Variation in the rate at which foxes took new eggs was greater among male foxes than among female foxes although they took similar number of new eggs overall ($s^2 = 11$ and 4.9 for male and female foxes, respectively, Figure 3.1).

Models {stage of incubation}, {stage of incubation + nesting density + species composition}, {stage of incubation + species composition}, {stage of incubation + breeding status of foxes}, and {stage of incubation + nesting density} described variation in the rate at which foxes recovered eggs from existing caches better than other models (Table 3.2). However, models that included nesting density, species composition, and breeding status of foxes did not improve the model fit compared to the model where these parameters were not included. These parameters, thus, had limited, if any, impact on the rate at which foxes took eggs from existing caches. Foxes took an additional 0.060 ± 0.051 eggs from existing caches as the incubation period progressed
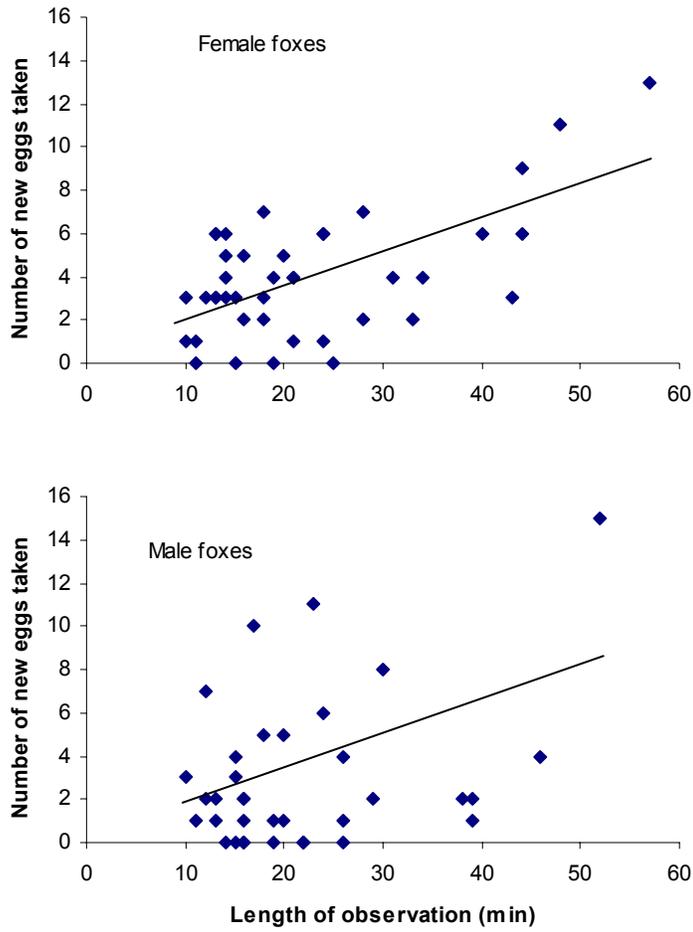
Figure 3.1. Variation in the rate at which arctic foxes took eggs at Karrak Lake in 2001-2003.

Table 3.2. Model selection for the rate at which arctic foxes took new eggs and eggs from existing caches at Karrak Lake in 2001-2003. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), model weights (w_i), and coefficient of determination (r^2). I used variation around the grand mean as the null model. AIC_c values for the best models were 139.85 and -4.79 for models new eggs and eggs from existing caches, respectively.

Model	K	Δ_i	w_i	r^2
new eggs				
nesting density	3	0	0.11	0.04
null model	2	0.79	0.07	na
nesting density + stage of incubation	4	0.99	0.07	0.06
nesting density + sex of foxes	4	1.70	0.05	0.05
stage of incubation	3	1.70	0.05	0.02
nesting density + breeding status of foxes	4	1.72	0.05	0.05
sex of foxes	3	1.92	0.04	0.02
nesting density + species composition	4	2.27	0.04	0.04
eggs from existing caches				
stage of incubation	3	0	0.16	0.15
stage of incubation + nesting density + species composition	5	0.39	0.13	0.27
stage of incubation + species composition	4	1.27	0.08	0.19
stage of incubation + breeding status of foxes	4	1.76	0.07	0.18
stage of incubation + nesting density	4	2.01	0.06	0.17

by 1 day. However, the influence of stage of incubation was weak and explained only 15% of the overall variation in the rate at which foxes took new eggs ($r^2 = 0.15$). Similarly, repeated observations showed that variation in the rate at which foxes took eggs from existing caches was similar within ($s^2 = 0.77$) and among foxes ($s^2 = 0.98$). In fact, individual variation explained only 22% of the overall variation in the rate at which foxes took eggs from existing caches ($r^2 = 0.22$). Variation in the rate at which foxes took eggs from existing caches was similar among male ($s^2 = 0.8$) and female foxes ($s^2 = 1.0$).

A sub-sample of observations from known-aged foxes showed that 1-year old foxes and foxes ≥ 2 years old took new eggs at similar rates (AIC$_C$ value of the model with age included was 0.7 units above the model where age was not included, $r^2 = 0.09$). There were too few observations ≥ 20 minutes to permit analyses on age-specific rates at which foxes took eggs from existing caches.

Foxes interacted with other foxes on 12 occasions. Four of these interactions appeared aggressive (non-breeding males chasing foxes of unknown sex) whereas the remaining 8 interactions appeared non-aggressive (2 interactions between breeding foxes and their mates, 4 interactions between non-breeding foxes of different sex, 1 encounter where a non-breeding female appeared unaffected by a non-breeding fox of unknown sex, and 1 encounter where a non-breeding fox appeared to avoid a non-breeding male).

3.4 Discussion

This study showed that arctic foxes at Karrak Lake took and cached about 2,000-3,000 eggs per fox each year and that the rates at which arctic foxes took eggs were largely unrelated to intrinsic and extrinsic variables such as life history characteristics and nesting distribution by geese. Limited influence of these variables may largely have reflected a superabundance of foods and the ease with which eggs were obtained. For example, arctic foxes took about half of the eggs from unattended nests that offered no resistance to foxes (see Samelius and Alisauskas 2001). Intrinsic and extrinsic variables may instead be more important in affecting foraging behaviours

when preying on foods that are more difficult to capture (Temple 1987). Furthermore, the rate at which foxes took eggs varied considerably within individuals in that foxes were efficient at taking eggs at times but inefficient at other times. This may have resulted from foxes switching between foraging actively and taking eggs opportunistically while performing other demands such as territorial behaviours. In fact, animals seldom focus on foraging to the exclusion of other demands (Perry and Pianka 1997) and I suggest that switching among active and passive foraging is common among opportunistic predators such as the arctic fox. Variation in the rate at which foxes took eggs was especially pronounced among male foxes which may have resulted from male foxes spending more time performing territorial behaviours than female foxes. For example, male foxes often appeared to ignore geese and either spent considerable time sniffing and marking prominent features such as nests and boulders or travelled at a faster pace and in more directed routes than during most observation (although male foxes took eggs occasionally during these observations).

Arctic foxes at Karrak Lake took and cached new eggs at similar rates among years despite annual variation in both small mammal abundance and breeding effort by foxes. This was similar to that by arctic foxes at other large goose colonies and waterfowl nesting areas (e.g. Stickney 1991, Samelius and Alisauskas 2000) and suggests that arctic foxes acquire and cache foods independently of availability of alternative foods and current energetic demands. Arctic foxes may, instead, acquire and cache as much food as possible when foods are available to compensate for unpredictable changes in small mammal abundance. This may be an adaptive strategy in northern environments where cached foods keep well and food abundance fluctuates considerably among years and seasons (Vander Wall 1990). Arctic foxes at Karrak Lake took new eggs 2-4 times as frequently as arctic foxes at other large goose colonies or waterfowl nesting areas (Stickney 1991, Samelius and Alisauskas 2000). Furthermore, variation in the rate at which arctic foxes took new eggs at these locations was more pronounced among than within areas which suggest that foraging efficiency by foxes was driven by local conditions such as nesting density and species composition. For example, nesting densities at Karrak Lake were greater than that at a large waterfowl nesting area in western Alaska (Stickney 1991). Similarly, arctic foxes

at Karrak Lake had access to both Ross's and lesser snow geese whereas arctic foxes at a large goose colony on Banks Island had access only to lesser snow geese (Samelius and Alisauskas 2000).

Arctic foxes acquiring new eggs at similar rates among years at large goose colonies despite annual variation in small mammal abundance (see above) contrasts sharply with that of arctic foxes at small goose colonies switching between small mammals and eggs in accordance to small mammal abundance (Bêty et al. 2002). These differences may largely reflect the relative abundance of small mammals and eggs at these locations. Specifically, high nesting densities and a superabundance of eggs at large colonies may result in eggs being much more abundant than small mammals whereas eggs at small goose colonies may be outnumbered by small mammals in some years. Furthermore, arctic foxes taking eggs at similar rates among years at large goose colonies suggest that the impact of arctic fox predation on nesting performance of geese at large colonies reflect the number of foxes frequenting the colony rather than variation in foraging efficiency of foxes (i.e. reflecting the numerical rather than the functional response of foxes as suggested by Samelius and Alisauskas 2000). Annual variation in the rate at which arctic foxes take eggs at small colonies, in contrast, suggests that the impact of arctic fox predation at small colonies reflect both the numerical and the functional response of foxes (see Bêty et al. 2002). Furthermore, the impact of arctic fox predation on nesting performance of geese generally decreases as colony size and nesting density increase because of predator swamping (Raveling 1989).

Arctic foxes at Karrak Lake took eggs from existing caches more frequently in the summer of 2002 than in the summers of 2001 and 2003. The summer of 2002 was characterised by intermediate fox densities and low small mammal abundance (Chapter 6). This was similar to arctic foxes at a large goose colony on Banks Island, Canada, that recovered cached eggs more frequently in years when arctic foxes were abundant and small mammals were scarce (Samelius and Alisauskas 2000). High rates of cache recovery in years when foxes were abundant and small mammals were scarce may have resulted from increased pilfering or from higher prevalence of rearranging cached eggs to deter pilfering (Vander Wall 1990). For example, animals often rearrange cached foods when competitors are abundant and pilfering rates are high (Hansson 1986,

Preston and Jacobs 2001). However, animals may also rearrange cached foods more frequently in years when alternative foods are scarce and cached foods may become more important than in years when alternative foods are abundant and easy to obtain (see Jokinen and Suhonen 1995). Annual variation in the rate at which arctic foxes recovered cached eggs may, alternatively, have reflected differences in the abundance of cached eggs although this appeared unlikely because foxes cached similar number of eggs among years at both Karrak Lake and Banks Island (see above).

Eggs were almost exclusively cached whereas most fleshy foods were consumed immediately or brought to den sites for consumption by young. This was similar to findings by Samelius and Alisauskas (2000) and may largely have reflected differences in perishability of these foods (Gendron and Reichman 1995, Hadj-Chikh et al. 1996). Specifically, eggs keep >1 year if properly cached because the shell, several protective membranes, and physio-chemical properties of albumen prevent microbial activity (Freeman and Vince 1974, Stickney 1991). Fleshy foods, in contrast, start to decompose in a few days (Samelius, personal observation). The rate at which arctic foxes cached foods may also have reflected nutritional value of foods in that foxes consumed nutritionally more valuable foods and cached less valuable foods (Vander Wall 1995).

4. ARCTIC FOX DIETS REVEALED THROUGH STABLE ISOTOPE ANALYSES: THE IMPORTANCE OF CACHED FOODS

Abstract: Food storage (termed food hoarding or food caching) is common among many animals. However, the extent to which animals use cached foods and how such use may change in response to abundance of alternative foods is unknown for most species. Arctic foxes cache thousands of eggs annually at large goose colonies and I estimated the contribution of cached eggs to spring and fall diets of arctic foxes by comparing stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of fox tissues to those of their foods using a multi-source mixing model (IsoSource). Geese were not present in the study area in spring or fall so egg signatures in fox tissues therefore represented cached eggs. The contribution of cached eggs to arctic fox diets was inversely related to collared lemming abundance; the contribution of cached eggs to overall fox diets increased from <28% in years when collared lemmings were abundant to 30-74% in years when collared lemmings were scarce. Further, arctic foxes used cached eggs well into the following spring (almost 1 year after eggs were acquired) – a pattern which differs from that of carnivores generally storing foods for only a few days before consumption.

4.1 Introduction

Food storage (termed food hoarding or food caching) is common among many birds and mammals and may be adaptive to avoid food shortage in environments where food abundance fluctuates dramatically; use of stored foods allows animals to remain in familiar areas and is an alternative strategy to migration, torpor, hibernation, and fat storage (Smith and Reichman 1984, Vander Wall 1990). Food hoarding may also be adaptive to supplement diets of growing young or to reduce time spent foraging when other behaviours are more important (Smith and Reichman 1984, Vander Wall 1990). However, the extent to which animals use stored foods is unknown for most species (Vander Wall 1990). This is especially true for members of the order Carnivora among which many species cache foods but for which the actual use of these foods is unknown (Vander Wall 1990).

Arctic foxes are generalist predators and scavengers that rely heavily on lemmings and voles (small mammals hereafter) throughout most of their range (Audet et al. 2002). However, other foods such as birds and their eggs can be important in arctic fox diets in some years and regions of the Arctic (Hersteinsson and MacDonald 1996, Bantle and Alisauskas 1998). Additionally, arctic foxes commonly cache foods when they are abundant (Stickney 1991, Samelius and Alisauskas 2000). Caching of foods appears to be especially frequent among arctic foxes at large bird colonies where foxes cache >1,000 eggs per fox each nesting season (Fay and Stephenson 1989, Samelius and Alisauskas 2000). Small mammals often fluctuate dramatically over 3-5 year periods whereas large influxes of migratory birds and their eggs provide arctic foxes with predictable and seasonally superabundant food. Large bird colonies therefore provide ideal settings to study food caching by arctic foxes and how use of these foods vary in relation to fluctuations in other foods.

The objectives of this study were to examine (1) when and to what extent arctic foxes at a large goose colony used cached eggs and (2) how use of cached eggs varied with small mammal abundance. Specifically, I examined arctic fox diets in spring (May) and fall (Sept-Nov) by comparing isotope signatures (δ^{13}C and δ^{15}N) of fox tissues with those of their foods. Geese were not present in the study area in spring or fall so egg signatures therefore represented cached eggs. Stable isotope analyses have been used widely in ecological studies and are based on the fact that stable isotope signatures in animal tissues reflect those of their foods (Hobson 1999, Kelly 2000).

4.2 Methods

4.2.1 Foods Available to Foxes in Spring and Fall

Foods available to arctic foxes in spring and fall included collared lemmings, red-backed voles, arctic hares, caribou, muskoxen, ptarmigan, and cached eggs. Goslings and geese are rarely cached by arctic foxes (Samelius and Alisauskas 2000) and are therefore rarely available to arctic foxes outside of the nesting season by geese. Goslings and geese are also acquired at much lower rates than are eggs (Samelius and Alisauskas 2000) so I did not include goslings and geese in the analyses. Similarly,

arctic hares were rare during this study and are rarely consumed by arctic foxes at Karrak Lake (Bantle and Alisauskas 1998) so I did not include arctic hares in the analyses. Most caribou in the Karrak Lake area are migratory and present only in spring and summer although some caribou remain in the area throughout the year (Gunn et al. 2000). Brown lemmings were not encountered during this study and therefore I did not include them in the analyses.

4.2.2 Collection of Fox Tissues

Blood was collected from the cephalic vein and winter-fur was clipped from the main trunk of the body of adult foxes ($\geq$1 year old) captured in May and early June (see Samelius et al. 2003 for capture procedures). Traps were baited with sardines for 5-10 days prior to capture to improve capture success (see inclusion of sardines in diet analyses below). Foxes were marked with plastic ear-tags which were used to distinguish local foxes from potential immigrants (see below). The metabolic turn-over rate of blood is about 1 month whereas fur is metabolically inactive (Hobson 1999); stable isotope signatures in blood therefore represented spring diets whereas those from winter-fur represented diets from the previous fall when the fur was grown (Roth 2002).

Arctic foxes can make considerable long-distance movements (Audet et al. 2002) although they tend to stay in an area once they have settled (Tannerfeldt and Angerbjörn 1996, Anthony 1997, Landa et al. 1998). Similarly, arctic foxes marked at Karrak Lake appeared to use similar areas throughout the year (Samelius, unpublished data, see Anthony 1997 for similar observation in a waterfowl-nesting area in Alaska). So, to avoid inclusion of foxes that may have immigrated from areas where they may have eaten foods with different isotopic signatures, I included only (*i*) foxes that were ear-tagged in previous years in *analyses of fall diets* and (*ii*) breeding foxes and foxes that were ear-tagged in previous years in *analyses of spring diets* (foxes started to breed 1-2 months prior to capture and therefore must have been resident in the study area for at least that period).

4.2.3 Collection of Prey Tissues

Goose eggs and muscle samples from small mammals, caribou, muskoxen, and ptarmigan were collected opportunistically in spring and summer. I have no muscle samples from fall, but since diets of small mammals, caribou, muskoxen, and ptarmigan are similar in spring and fall (Rodgers and Lewis 1986, Holder and Montgomerie 1993, Gunn and Adamczewski 2003, Miller 2003), I assumed that isotope signatures in muscle of these herbivores were similar within species in spring and fall (see Barnett 1994 and Drucker et al. 2001 for similarity of isotope signatures of caribou muscle in spring and fall and Roth 2002 for similar assumption on small mammals). Fur from 3 ringed seals (*Phoca hispida*) from the Queen Maud Gulf was collected to examine whether foxes used marine foods. Also, 10 sardine samples were prepared to examine whether consumption of sardines during pre-bating of traps (see above) influenced stable isotope signatures of foxes.

4.2.4 Small Mammal Abundance

Small mammal abundance was monitored at 3 permanent trap-lines established in 1994 following Shank (1993). Trap-lines consisted of 25 trap-sites with 1 snap-trap placed within 1 m of each trap-site. One trap-line was monitored during the second half of June and the other two were monitored during the second half of July. Small mammal abundance was monitored for 10 consecutive nights and I used number of captures per 100 trap-nights as an index of small mammal abundance for each year. I subtracted 0.5 trap-nights for each trap that was snapped without capture to correct for variation in sampling effort (Beauvais and Buskirk 1999). Trap-lines included habitats ranging from wet lowland areas to dry upland hills.

4.2.5 Stable Isotope Analyses

I freeze-dried muscle, blood, and egg (homogenised eggs without the shell) samples to remove water and I used a 2:1 chloroform-methanol solution to remove lipids from muscle and egg samples. Similarly, I removed surface oil from fur samples by using this solution. Muscle, blood, and egg samples were powdered with a mortar

whereas fur samples were clipped into fine pieces of fur. Samples of about 1 mg were weighed into tin cups and combusted in an Europa 20:20 continuous flow ratio mass spectrometer (CFIRMS) at the Department of Soil Sciences at University of Saskatchewan. I used 2 laboratory standards (egg albumen and whale baleen) for every 5 tissue samples analysed. Stable isotope ratios were expressed in δ-notation as parts per thousand (‰) deviations from Pee Dee Belemnite ($\delta^{13}C$) and atmospheric air ($\delta^{15}N$) standards according to $\delta X = [(R_{sample}-R_{standard})/R_{standard}] \times 1000$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Laboratory measurement error was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$.

4.2.6 Data Analyses and Comparisons

I used Program IsoSource (Phillips and Gregg 2003) to estimate spring and fall diets of arctic foxes. This program uses mass balance mixing models too provide *ranges* of possible source contributions when the number of sources is to large to permit unique solutions from general mass balance mixing models (Phillips and Gregg 2003). I used source increments of 1% and mass balance tolerance of ±0.1‰. I performed analyses on spring and fall diets separately for each year (*n* = 4-9 foxes per year for analyses on spring diets and 4-7 foxes per year for analyses on fall diets)[1]. Prey items of arctic foxes were isotopically distinct and did not vary among years except for signatures of caribou muscle that differed among years and overlapped with muscle signatures of red-backed voles in 2003 and muskoxen in 2000, 2002, and 2004 (MANOVA, F_{18} = 80.12, *P* < 0.001, Tukey's pair-wise test to identify difference among groups, Figure 4.1, Table 4.1). I suspect that annual variation in isotopic signatures of caribou muscle was related to caribou wintering in different areas (see Gunn et al. 2000 for this herd of caribou wintering in areas >300 km apart) but suggest that caribou signatures were similar among years in fall before caribou moved south. I therefore used year-specific caribou signatures in analyses of spring diets whereas I pooled means of caribou signatures from all years in analyses of fall diets. Further, I pooled means for (i) caribou and red-backed
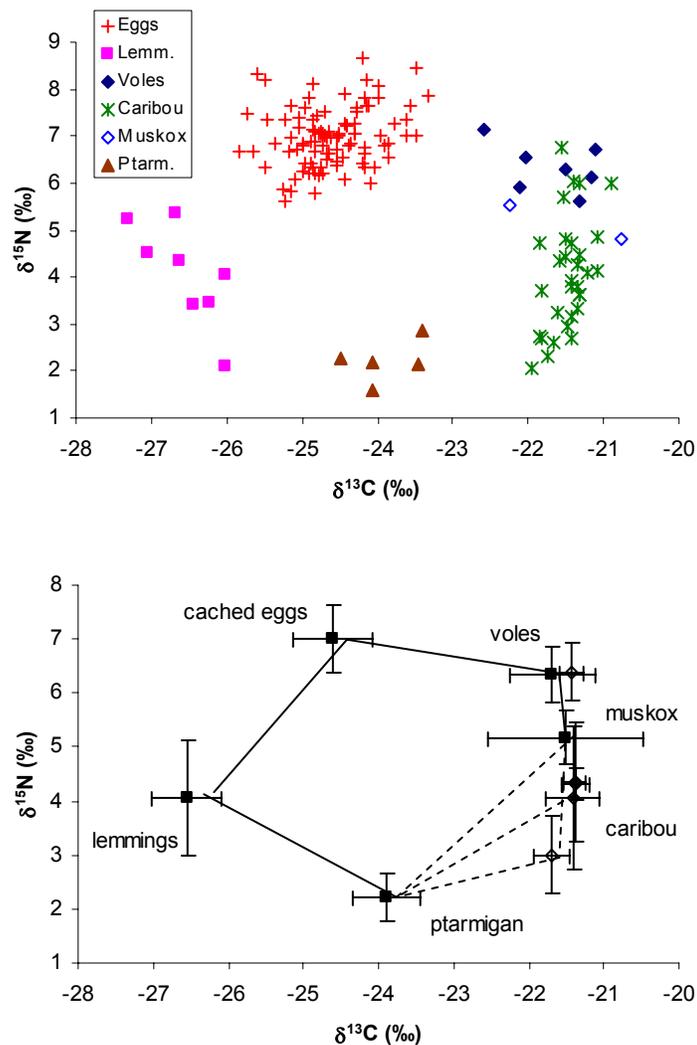
Figure 4.1. Isotopic signatures of food items included in analyses of arctic fox diets at Karrak Lake in 2000 to 2004. Top graph shows distribution of samples and bottom graph shows mean ± 1 SD. Outlined in the lower graph is the source polygon used in analyses of arctic fox diets. I used year-specific signatures of caribou muscle for analyses of spring diets whereas I pooled the means of caribou muscle from all years in analyses of fall diets. The source polygon therefore differed somewhat among years for analyses on spring diets (indicated by dashed lines). Open circles indicate year-specific signatures of caribou muscle.

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[1] sample size was 1 fox for analyses of spring diets in 2000 as there were no previously marked foxes at the onset of this study

Table 4.1. Isotope signatures of foods included in analyses of arctic fox diets at Karrak Lake in 2000 to 2004 (mean ± SD). Also provided in the table are the proportions of C and N of different foods (mean ± SD).

Food	δ^{13}C, ‰	δ^{15}N, ‰	%C	%N	Sample size
goose eggs	-24.6 ± 0.5	7.0 ± 0.6	47 ± 2	13 ± 1	97
collared lemming muscle	-26.6 ± 0.5	4.3 ± 0.8	47 ± 3	14 ± 1	8
red-backed vole muscle	-21.7 ± 0.6	6.3 ± 0.5	48 ± 2	14 ± 1	7
caribou muscle 2000 [a,b]	-21.4 ± 0.2	4.3 ± 0.3	49 ± 2	15 ± 1	6
caribou muscle 2001 [a]	-21.7 ± 0.2	3.0 ± 0.7	47 ± 2	14 ± 1	7
caribou muscle 2002 [a,b]	-21.4 ± 0.1	4.4 ± 1.1	50 ± 1	15 ± 1	9
caribou muscle 2003 [a,b]	-21.4 ± 0.2	6.4 ± 0.5	49 ± 1	15 ± 1	2
caribou muscle 2004 [a,b]	-21.4 ± 0.4	4.1 ± 1.3	48 ± 1	14 ± 1	5
muskox muscle	-21.5 ± 1.0	5.2 ± 0.5	48 ± 3	16 ± 0.3	2
ptarmigan muscle	-23.9 ± 0.5	2.2 ± 0.5	48 ± 1	14 ± 1	5

[a] I used year specific signatures of caribou muscle in analyses of spring diets whereas I pooled means of caribou muscle from all years in analyses of fall diets

[b] caribou signatures overlapped with red-backed vole signatures in 2003 and with muskox signatures in 2000, 2002, and 2004 – I therefore pooled means for these tissues in analyses of spring diets in those years

voles in analyses of spring diets in 2003 and (*ii*) caribou and muskoxen in analyses of spring diets in 2000, 2002, and 2004. I did not include seals or sardines in final analyses because their contributions to fox diets were heavily skewed towards 0% in preliminary analyses (see Phillips and Gregg 2003).

I corrected fox samples for isotopic discrimination (i.e. change in isotope signature from diet to consumer) by using values calculated for captive red foxes (Roth & Hobson 2000); I subtracted 2.6‰ and 3.3‰ from δ^{15}N ratios of blood and fur, respectively, and 0.6‰ and 2.6‰ from δ^{13}C ratios of blood and fur, respectively. Fox tissues were, thus, normalised to their equivalent dietary values. Similarly, I corrected fur samples from seals for isotopic discrimination (i.e. difference in isotope signatures between fur and muscle) by using values calculated for 3 different species of seals – one of which was ringed seals (Hobson et al. 1996); I subtracted 0.6‰ from δ^{15}N ratios of fur and 1.5‰ from δ^{13}C ratios of fur.

I provide 1st to 99th percentiles of possible source contributions unless otherwise stated (Phillips and Gregg 2003).

4.3 Results

Small mammal abundance varied considerably among years (Figure 4.2). Annual variation in small mammal abundance was greater among collared lemmings than among red-backed voles. Collared lemming abundance peaked in 2000 and was followed by declining and low abundance during the rest of the study.

Arctic fox diets were heavily skewed towards collared lemmings and cached eggs (Table 4.2, Figure 4.3). Arctic fox diets also included large proportions of ptarmigan in the spring of 2000 and 2001. The contribution of cached eggs to arctic fox diets was inversely related to collared lemming abundance (Figure 4.4). Specifically, the contribution of cached eggs to overall *spring diets* increased from 0-28% in years when collared lemmings were abundant to 30-74% in years when collared lemmings were scarce. Similarly, the contribution of cached eggs to overall *fall diets* increased from 1-19% in years when collared lemmings were abundant to 44-65% in years when collared
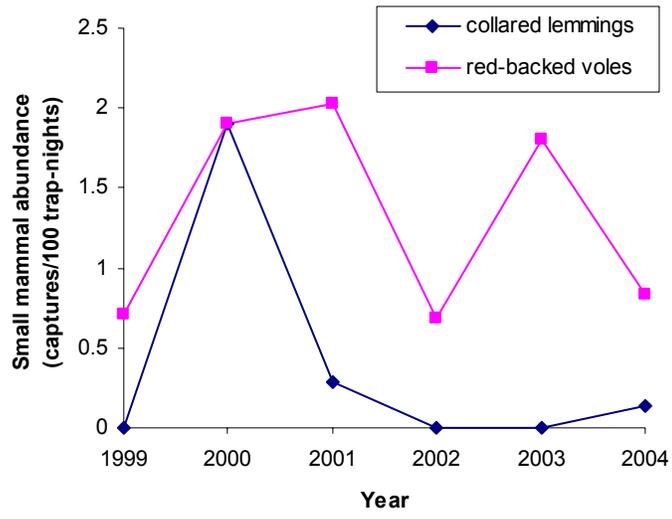
Figure 4.2. Small mammal abundance at Karrak Lake in 1999 to 2004. Brown lemmings were not captured or otherwise encountered at Karrak Lake during these years.

Table 4.2. Ranges of possible source contributions to spring and fall diets of arctic foxes at Karrak Lake in 2000 to 2004 (1st to 99th percentiles). Ranges of source contributions were calculated by using Program IsoSource (Phillips and Gregg 2003).

| | Foods | | | | | | | |
Year	Cached eggs, %	Collared lemmings, %	Red-backed voles, %	Caribou, %	Muskoxen, %	Ptarmigan, %	No. of foxes	Collared lemming abundance
Spring [a]								
2000	0–28	24-58	0-21	- [a]	0-28 [a]	12-47	1	high
2001	0–8	24-41	0-6	0-16	0-8	43-67	9	decreasing
2002	30–66	0-27	0-41	- [a]	0-29 [a]	0-20	4	low
2003	47–74	0-21	0-30 [a]	- [a]	0-24	0-15	5	low
2004	8–56	9-53	0-37	- [a]	0-26 [a]	0-32	4	low-medium
Fall [b, c]								
2000	1-19	69-85	0-12	0-9	0-10	0-11	7	high
2001	44-59	33-46	0-9	0-6	0-7	0-8	5	decreasing
2002	56-65	32-40	0-4	0-3	0-3	0-4	4	low
2003	51-62	34-43	0-6	0-4	0-5	0-5	4	low

[a] I used year specific signatures of caribou muscle in analyses of spring diets – these overlapped with red-backed vole signatures in 2003 and with muskox signatures in 2000, 2002, and 2004 so red-backed voles and caribou were pooled in 2003 and muskoxen and caribou were pooled in 2000, 2002, and 2004

[b] I pooled means of caribou muscle from all years in analyses of fall diets

[c] I have no data on fall diets in 2004 as winter fur of foxes captured in spring 2004 represented fall diets in 2003
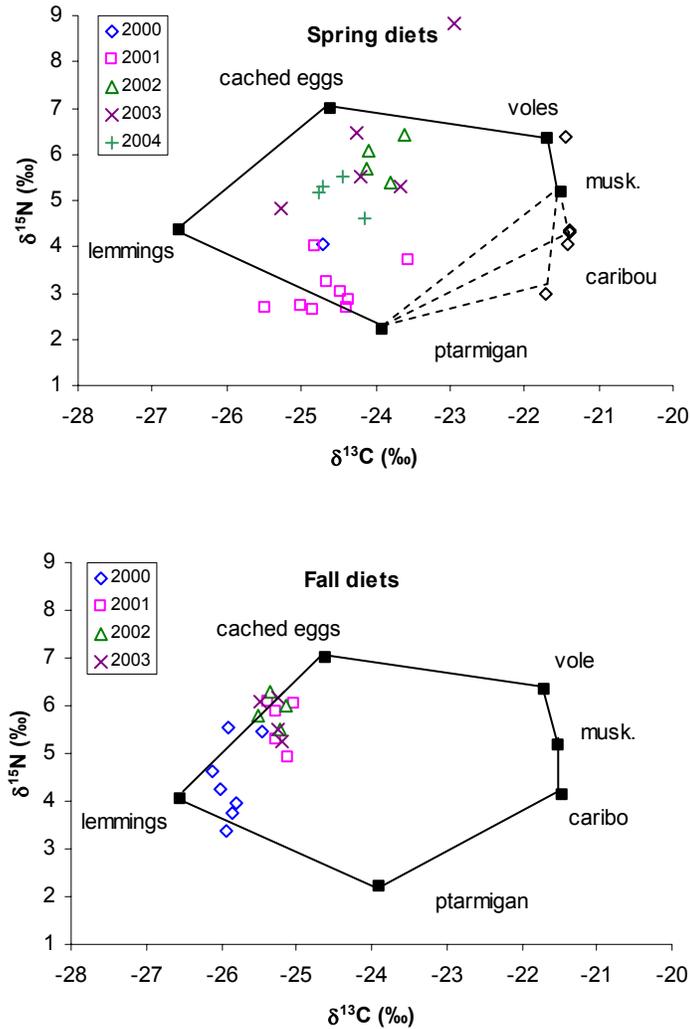
Figure 4.3. Isotopic signatures of arctic fox tissues at Karrak Lake in spring and fall in 2000 to 2004 where location in the source polygon is indicative of diet. Fox signatures were corrected for isotopic discrimination by using values calculated for red foxes (Roth and Hobson 2000). The source polygon differed somewhat among years in the spring (indicated by dashed lines) because spring signatures of caribou muscle differed isotopically among years.
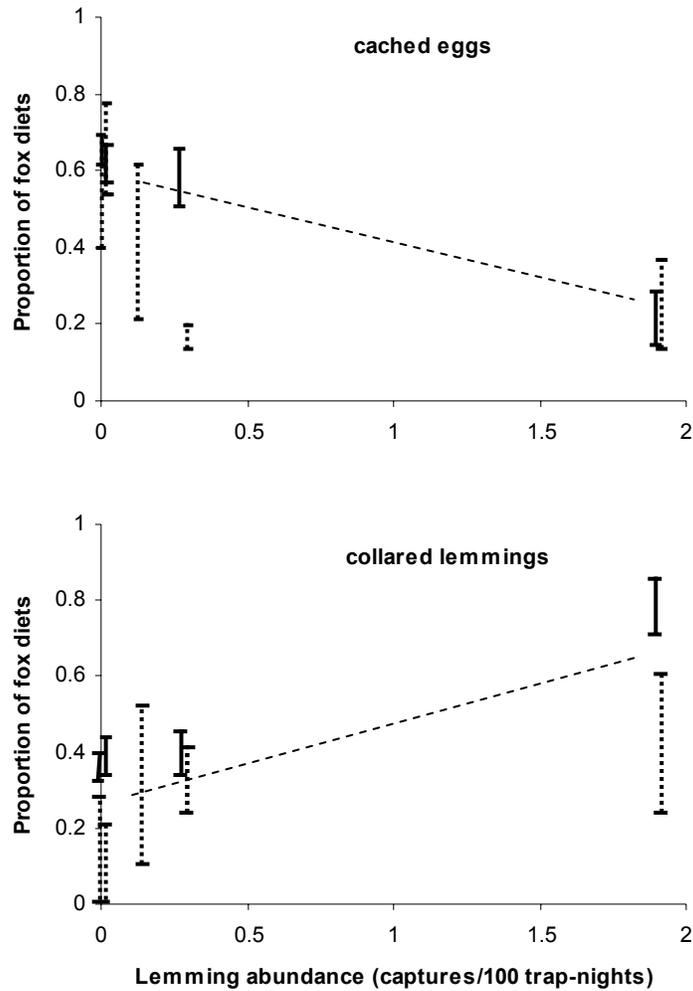
Figure 4.4. Contribution of cached eggs and collared lemmings to arctic fox diets at Karrak Lake in relation to collared lemming abundance. Brackets indicate 1st to 99th percentiles of source contributions for each year. Fall diets are indicated by solid brackets and spring diets by dashed brackets.

lemmings were scarce. The contribution of collared lemmings to arctic fox diets, in contrast, was positively related to collared lemming abundance (Figure 4.4). Body mass of arctic foxes in spring was unrelated to the contribution of cached eggs to their diets (Figure 4.5). I did not detect differences in isotope signatures between male and female foxes or between breeding and non-breeding foxes within years.

4.4 Discussion

The extent to which animals use cached foods is unknown for most species (Vander Wall 1990). However, this study showed that arctic foxes relied heavily on cached eggs in years when collared lemmings were scarce. Further, arctic foxes used cached eggs well into the following spring (almost 1 year after foods were acquired) which differs greatly from that of carnivores generally storing foods for only a few days (Vander Wall 1990). Carnivores in northern climates may, however, store foods for several months (e.g. Maccarone and Montevecchi 1981, Stickney 1991, Bantle and Alisauskas 1998) because decomposition rates are much lower than in more temperate or tropical environments (Vander Wall 1990). Further, the duration of storage may also vary among different foods depending on how well they keep. For example, eggs keep better than other foods because the shell, several protective membranes, and physio-chemical properties of albumen proteins prevent microbal activity (Freeman and Vince 1974). In fact, eggs keep for >1 year if properly cached (Stickney 1991, Bantle and Alisauskas 1998). My estimates of cached eggs contributing up to about 60% of arctic fox diets may, therefore, be on the extreme end of how much carnivores rely on cached foods as there may be few other situations where carnivores have access to foods that are equally suited for long-term storage.

The contribution of cached eggs to arctic fox diets was inversely related to collared lemming abundance whereas the contribution of collared lemmings followed that of their abundance. Further, arctic foxes cached similar number of eggs among years (Chapter 3) so there was no indication that foxes used cached eggs in proportion to the abundance of cached eggs. Arctic foxes, thus, switched from collared lemmings to cached eggs in years when collared lemmings were scarce which, in turn, suggests
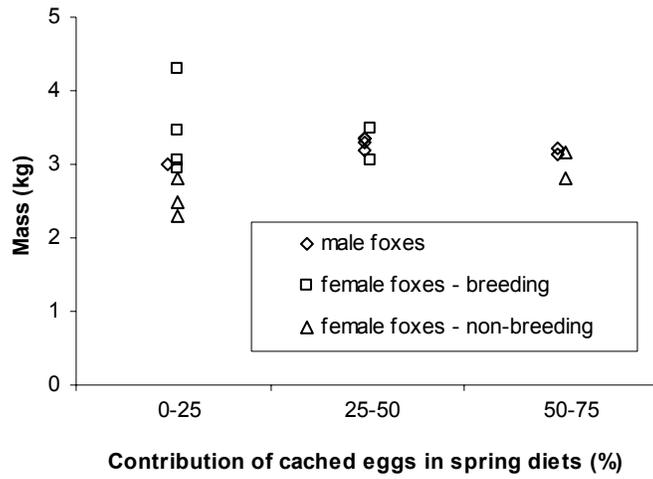
Figure 4.5. Body mass of arctic foxes in spring in relation to the contribution of cached eggs to their diets. Some breeding females did not appear to have given birth when weighed and were therefore heavier than expected.

that cached eggs functioned as a buffer when collared lemmings were scarce. Foxes may prefer collared lemmings over cached eggs because lemmings may be nutritionally more valuable to foxes or because large consumption of albumen can result in biotin deficiency (Klevay 1976). I did not, however, detect any signs of biotin deficiency (e.g. hair loss or impaired muscle coordination) even when cached eggs contributed 50-60% of their diets which suggests that arctic foxes were able to consume large amounts of albumen without suffering from biotin deficiency. Moreover, spring body mass of foxes was unrelated to the contribution of cached eggs to their diets which further suggests that large consumption of albumen did not appear to impede body condition of foxes. Arctic foxes at Karrak Lake switching to cached eggs when collared lemmings were scarce was similar to arctic foxes in costal areas switching to marine foods in years when lemmings were scarce (Roth 2002, 2003). However, switching to cached foods allowed foxes to remain in familiar areas with predictable food supplies and may be adaptive compared to dispersing to search for other foods (Samelius and Alisauskas 2000).

Arctic foxes at Karrak Lake switching to cached eggs in years when collared lemmings were scarce may explain why animals often store more foods than needed. Specifically, arctic foxes may cache eggs independent of small mammal abundance to compensate for unpredictable changes in future lemming abundance. In fact, arctic foxes cached similar number of eggs among years (Chapter 3) although they rarely fed on these eggs in years when collared lemmings were abundant. Animals may also store more foods than needed to compensate for losses to competitors and failure to locate caches (Vander Wall 1990).

5. SURVIVAL RATE OF EXPERIMENTAL FOOD CACHES: IMPLICATIONS FOR ARCTIC FOXES

Abstract: Avoiding cache loss is crucial to food hoarding animals. Arctic foxes scatter-hoard thousands of eggs annually at large goose colonies and I examined how survival rate of experimental caches were influenced by (*1*) nesting density by geese, (*2*) relative proportion of two sympatric goose species, (*3*) departure by ca 1 million geese and their young after hatch, and (*4*) age of cache sites. Known-fate models in Program MARK revealed that survival rate of experimental caches was related to age of cache sites in the first year of the study (e.g. 0.80 and 0.56 per 18-day period for caches from new and 1 month old cache sites, respectively) and departure by geese after hatch in the second year of the study (e.g. 0.98 and 0.74 per 18-day period during and after goose nesting, respectively). These results suggest that food abundance and deterioration of cache sites (e.g. loss of soil cover and partial exposure of caches) were important factors affecting cache loss at the study site. Further, annual variation in the importance of these factors suggests that strategies to prevent cache loss are not fixed in time but vary with existing conditions. Evolution of caching behaviours by arctic foxes may, thus, have been shaped by multiple selective pressures.

5.1 Introduction

Food storage (termed food hoarding or food caching) is common among birds and mammals and may be adaptive to avoid food shortage in environments where food availability fluctuates greatly (Smith and Reichman 1984, Vander Wall 1990). Food hoarding may also be adaptive to supplement diets of growing young or to reduce time spent foraging when other behaviours are more important (Smith and Reichman 1984, Vander Wall 1990). Animals generally cache foods either in many small caches scattered in space (scatter-hoarding) or in a few closely-spaced caches with many foods in each cache (larder-hoarding, Vander Wall 1990). The strategy of how foods are cached appears to be influenced by the ability to defend caches against competitors; scatter-hoarded foods are typically not defended whereas larder-hoarded foods are more

likely to be defended (Stapanian and Smith 1978, Vander Wall 1990). Further, scatter-hoarding animals generally rely on secretive behaviours and inconspicuous caches whereas larder-hoarding animals often devote considerable time and energy in defending larders (Vander Wall 1990).

Cache loss, either from theft or decomposition, can be detrimental to food-hoarding animals; strategies to reduce cache loss are, thus, critical to animals that hoard foods (Andersson and Krebs 1978, Vander Wall 1990). Strategies to reduce cache loss include selection of cache sites, secretive behaviours when caching foods, spatial arrangement of caches, aggressive defence of caches, and storing more food than needed (Smith and Reichman 1984, Vander Wall 1990). However, the relative importance of factors affecting cache loss is unknown in most animals (Vander Wall 1990). Further, most studies have examined cache loss of foods that are acquired from a central source whereas cache loss of foods that are acquired from multiple sources dispersed in space is poorly understood.

Cache loss is often difficult to study because the identity of animals retrieving caches is generally unknown (Vander Wall 1990). However, experimental caches provide a useful means of separating cache loss from retrieval as removal of experimental caches must be attributed to pilfers (Vander Wall and Jenkins 2003). In fact, experimental caches have provided indirect evidence of cache loss (e.g. Stapanian and Smith 1978, 1984, Clarkson et al. 1986, Tamura et al. 1999) and are useful for examining various aspects of cache loss (Vander Wall and Jenkins 2003).

Arctic foxes commonly cache foods when foods are abundant (Audet et al. 2002). Caching and use of stored foods appears to be especially common among arctic foxes at large bird colonies where food is often superabundant during the nesting-season (Stickney 1991, Samelius and Alisauskas 2000). Caching of foods at these colonies may be adaptive in comparison to dispersing to search for other foods because food caching allows foxes to remain in familiar areas with predictable food supplies (Samelius and Alisauskas 2000). However, the extent and implication of food caching by arctic foxes and other carnivores is poorly understood (Vander Wall 1990).

Arctic foxes scatter-hoard >1,000 eggs per fox during the nesting season at large goose colonies (Samelius and Alisauskas 2000, Chapter 3). Caching of eggs at these

colonies therefore provides an ideal system to study food hoarding by carnivores. The objective of this study was to examine spatial and temporal variation in survival rate of experimentally deployed caches. Specifically, I evaluated survival rate of experimental caches in relation to (*1*) nesting density by geese, (*2*) relative proportion of two sympatric goose species, (*3*) departure by geese away from the colony after hatch (i.e. goose presence vs. goose absence), and (4) age of cache sites (i.e. new vs. 1 month old cache sites).

5.2 Methods

5.2.1 Experimental Caches

Survival rate of experimental caches distributed systematically in a 500×500 m grid in the south-central part of the colony was monitored during two summers. Locations of cache sites were selected from the Universal Transverse Mercator (UTM) grid system on a 1:50,000 map. Sample sites were marked with a ca 0.5 m tall marker and an experimental cache was placed 15 m away from each marker at the first site that resembled those used by arctic foxes (e.g. avoiding elevated knolls and rocky material). Locations of cache sites relative to markers were altered randomly in the 4 cardinal directions to avoid potential association between cache marker and cache; caches were not placed in the same cardinal direction between the first and second part of the experiment (see below). Experimental caches were not placed on islands or in areas that were either flooded or snow covered.

Experimental caches consisted of 1 goose egg that was buried in the ground and was covered with 1-2 cm of soil in an attempt to simulate caches by arctic foxes (see Quinlan and Lehnhausen 1982, Samelius and Alisauskas 2000). Eggs for the experiment were salvaged by collecting eggs that were found outside nest bowls during the egg-laying period (i.e. none of the eggs were incubated). Latex gloves were used when handling eggs during all aspects of the experiment and eggs were stored cool until they were deployed (eggs were stored in a container that was placed in a snow bank - but see minor modification among years below).

The study was repeated twice within each year by deploying one set of caches (n = 50 in 2001 and 43 in 2003) during goose nesting and another set of caches (n = 50 in 2001 and 42 in 2003) after geese left the colony following hatch. The first part of the study was conducted 14 June - 3 July in 2001 and 17 June - 5 July in 2003, and the second part of the study was conducted 12 - 31 July in 2001 and 13 - 31 July in 2003. Caches that survived from the first part of the study to the start of the second part of the study (n = 40 in 2001 and 42 in 2003) were monitored also during the second part of the study (these cache sites were 1 month older than cache sites from the second part of the study whereas eggs of these caches were of the same age). There were, thus, three treatments; (*1*) new caches monitored during the nesting season, (*2*) new caches monitored after the nesting season, and (*3*) old caches monitored after the nesting season (but see correction for the transition from new to old caches occurring at the same time as the transition from presence to absence of geese below). Old caches during the nesting season could not be created as the ground was snow covered and frozen prior to goose nesting. Eggs from new caches from the second part of the study were 1 month older than eggs from new caches from the first part of the study. However, eggs keep >1 year if properly cached (Stickney 1991) so the main difference between new caches from the first and second part of the study was presence vs. absence of geese.

Experimental caches were revisited 3 times at 6-day intervals during each part of the study (the last visit of each part of the study in 2001 was made after 7 days but I corrected for this by setting the last interval in my analyses to 1.17). At each visit, it was determined whether caches were present or lost (i.e. missing or consumed at the site). Caches were considered to have been lost to foxes if the soil was pushed off in a neat pile on one side of the cache and lost to avian predators if the soil was scattered irregularly around the cache (based on independent field observations). Nesting density was determined by recording the number of nests within 20-m radius of each cache marker and species composition was determined by measuring length and width of all eggs and then separating species by using egg measurements following Alisauskas et al. (1998). Micro-habitat within 1 m of caches was determined based on soil and vegetation characteristics following McLandress (1983).

The experimental design was identical among years except for that eggs for the second part of the study were stored in the ground, covered with 1-2 cm of soil, in 2003 compared to in a container in a snow bank in 2001. However, I suggest that this had limited, if any, effect on the outcome of the experiment because eggs keep >1 year if properly cached (Stickney 1991) and eggs were kept cool and out of direct sunlight both when stored in the ground and the snow bank.

5.2.2 Data Analyses

I modelled survival rate per 18-day period for experimental caches as a function of (*1*) nesting density, (*2*) species composition (i.e. proportion of Ross's vs. lesser snow geese), (*3*) departure by geese after hatch (i.e. presence vs. absence of geese), and (*4*) age of cache sites (i.e. new vs. 1 month old cache sites) by using known-fate models in Program MARK (White and Burnham 1999). However, I could not separate the effect of age of cache sites from that of departure by geese for the set of caches that were monitored during both the first and second part of the study because the transition from new to old caches occurred concurrently with the transition from presence to absence by geese. I therefore performed analyses in two steps. Specifically, I examined (*1*) the effect of departure by geese by comparing new caches monitored during nesting with new caches monitored after nesting and (*2*) the effect of age of cache sites by comparing new caches monitored after nesting with old caches monitored after nesting. I derived 11 *a priori* candidate models for the first part of the analyses and 8 *a priori* candidate models for the second part of the analyses (see Tables 1 and 2 for suite of candidate models). Candidate models ranged from constant survival to all combinations of the variables above, plus interaction terms between (*1*) nesting density and departure by geese and (*2*) species composition and departure by geese as the influence of nesting density and species composition may vary between periods with and without geese. I selected the model with the lowest AIC_C value as the best approximating model and considered models within 2 AIC_C units to be of similar quality (Burnham and Anderson 1998).

Fate of caches was independent of that of neighbouring caches in both years ($\chi^2_{(1)}$ = 1.11 and 0.88, and P = 0.29 and 0.35 in 2001 and 2003, respectively) suggesting that cache loss was not clumped on the study area in either year. Further, cache loss was similar among habitats in both years (Fisher exact test, P = 0.414 and 0.653 in 2001 and 2003, respectively) so I pooled habitats within each year before performing final analyses. The proportion of Ross's geese increased with increasing nesting density in 2003 (r^2 = 0.19, P = 0.0031) whereas there was no correlation between these variables in 2001 (r^2 < 0.01, P = 0.61). I therefore used proportion of Ross's geese as an independent covariate in 2001 whereas I used the residual value of proportion of Ross's geese when controlling for nesting density in 2003.

5.3 Results

Thirty-eight of 100 experimental caches were lost in 2001 and 24 of 85 experimental caches were lost in 2003. Fifty-one caches were removed by arctic foxes, 4 by avian predators, and 7 by unknown pilferers. Nesting density ranged from 8 to 279 nests per ha ($\bar{x}$ = 79 and 69, and SD = 38 and 47 nests per ha in 2001 and 2003, respectively) and species composition ranged from 0 to 100% Ross's geese ($\bar{x}$ = 0.51 and 0.39, and SD = 0.36 and 0.35 in 2001 and 2003, respectively). Condition of cache sites deteriorated as the experiment progressed (e.g. soil cover was lost and eggs became partly visible); partial exposure of caches was greater in 2001 than in 2003 ($\chi^2_{(1)}$ = 5.85 and P = 0.016) with 18% and 6% of cached eggs partly visible in each year, respectively. There was, however, no correlation between partly visible eggs and cache loss in either year (Fisher exact test, P = 0.7784 and 0.3456 in 2001 and 2003, respectively).

Models {age of cache sites + species composition}, {age of cache sites}, and {age of cache sites + nesting density + species composition} fit the data considerably better than other models on age of cache sites and nesting distribution by geese in 2001 and accounted for 79% of the cumulative model weight (Table 5.1). Models on departure

Table 5.1. Model selection for spatial and temporal variation in survival rate of experimental caches at Karrak Lake in 2001. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), and model weights (w_i). Global models are underlined. I used *constant survival* as the null model of no effect of either of the variables examined. AIC_c values of the best models were 134.99 and 184.83 for the upper and lower comparison below.

Model [1]	K	Δ_i	w_i
Effects of departure by geese and nesting distribution by geese			
departure by geese	2	0	0.15
constant survival	1	0.16	0.14
departure by geese × species composition	3	0.28	0.13
species composition	2	0.52	0.12
departure by geese × species composition	4	0.68	0.11
departure by geese + species composition	3	1.27	0.08
nesting density	2	1.39	0.08
departure by geese + nesting density + species composition	4	1.60	0.07
nesting density + species composition	3	1.80	0.06
departure by geese × nesting density	4	3.04	0.03
departure by geese × (nesting density + species composition)	6	3.79	0.02
Effects of age of cache sites and nesting distribution by geese			
age of cache sites + species composition	3	0	0.38
age of cache sites	2	0.96	0.23
age of cache sites + nesting density + species composition	4	1.50	0.18
age of cache sites + nesting density	3	2.66	0.10
species composition	2	4.17	0.05
constant survival	1	5.38	0.03
nesting density + species composition	3	5.48	0.02
nesting density	2	6.90	0.01

[1] × indicates that both major effects and interactions between these major effects are included in the model

by geese, nesting density, and species composition, in contrast, did not fit data better than the null model of constant survival in 2001 (Table 5.1). Age of cache sites was common to all models that explained survival rate of caches in relation to age of cache sites, nesting density, and species composition whereas nesting density and species composition were present in only 1 and 2 models, respectively. More importantly, models that included nesting density and species composition improved the model fit only marginally (or not at all for nesting density) compared to the model where these parameters were not included (i.e. model {age of cache sites}), suggesting that these parameters had limited impact on survival rate of caches compared to age of cache sites. Age of cache sites was, thus, the main factor affecting survival rate of experimental caches in 2001.

Models {departure by geese}, {departure by geese × species composition}, and {departure by geese + species composition} fit the data considerably better than other models on departure by geese, nesting density, and species composition in 2003 and accounted for 73% of the cumulative model weight (Table 5.2). Models on age of cache sites, nesting density, and species composition, in contrast, fit data only marginally better than the null model of constant survival in 2003 (Table 5.2). Departure by geese was common to all models that explained survival rate of caches in relation to departure by geese, nesting density, and species composition whereas species composition was present in only 2 of these models. More importantly, models that included species composition did not improve the model fit compared to the model where species composition was not included (i.e. model {departure by geese}), suggesting that species composition had limited impact on survival rate of caches compared to departure by geese. Departure by geese was, thus, the main factor affecting survival rate of experimental caches in 2003.

Model averaged survival rate of experimental caches in 2001 was 0.87 (95% C.I. = 0.74-0.94), 0.80 (95% C.I. = 0.67-0.89), and 0.56 (95% C.I. = 0.39-0.70) per 18-day period for new caches during nesting, new caches after nesting, and old caches after nesting, respectively (Figure 5.1). Model averaged survival rate of experimental caches

Table 5.2. Model selection for spatial and temporal variation in survival rate of experimental caches at Karrak Lake in 2003. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), and model weights (w_i). Global models are underlined. I used *constant survival* as the null model of no effect of either of the variables examined. AIC_c values of the best models were 88.28 and 151.52 for the upper and lower comparison below.

Model [1]	K	Δ_i	w_i
Effects of departure by geese and nesting distribution by geese			
departure by geese	2	0	0.35
departure by geese × species composition	4	1.00	0.21
departure by geese + species composition	3	1.43	0.17
departure by geese + nesting density	3	2.05	0.13
departure by geese + nesting density + species composition	4	3.49	0.06
departure by geese × nesting density	4	3.96	0.05
<u>departure by geese × (nesting density + species composition)</u>	6	5.04	0.03
constant survival	1	9.23	<0.01
species composition	2	10.9	<0.01
nesting density	2	11.3	<0.01
nesting density + species composition	3	12.9	<0.01
Effects of age of cache sites and nesting distribution by geese			
species composition	2	0	0.26
nesting density + species composition	3	0.20	0.23
nesting density	2	1.43	0.13
constant survival	1	1.49	0.12
age of cache sites + species composition	3	2.05	0.09
<u>age of cache sites + nesting density + species composition</u>	4	2.27	0.08
age of cache sites + nesting density	3	3.47	0.05
age of cache sites	2	3.52	0.04

[1] × indicates that both major effects and interactions between these major effects are included in the model
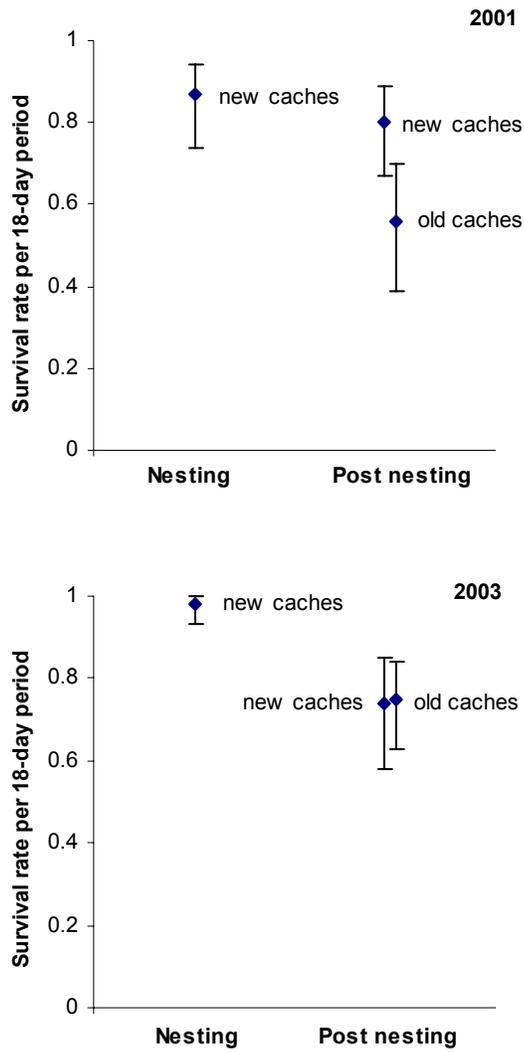
Figure 5.1. Survival rate of new and old experimental caches during and after the nesting season by geese at Karrak Lake in 2001 and 2003.

in 2003 was 0.98 (95% C.I. = 0.93-1.0), 0.74 (95% C.I. = 0.58-0.85), and 0.75 (95% C.I. = 0.63-0.84) per 18-day period for new caches during nesting, new caches after nesting, and old caches after nesting, respectively (Figure 5.1).

5.4 Discussion

Avoiding cache loss is critical to food hoarding animals (Andersson and Krebs 1978, Vander Wall 1990); this study showed that age of cache sites and departure by geese from the colony were important factors affecting cache loss at Karrak Lake and that the effects of these factors varied among years. These results suggest that food abundance and deterioration of cache sites (e.g. loss of soil cover and partial exposure of caches) were important factors affecting cache loss at Karrak Lake. Further, annual variation in the importance of these factors suggest that strategies to prevent cache loss may not be fixed in time but vary with existing conditions (see Vander Wall and Jenkins 2003 for similar suggestion).

Ageing of cache sites was the main factor affecting cache loss in the first year of the study which suggest that deterioration of cache sites was more important in affecting cache loss at Karrak Lake in that year than was nesting distribution by geese (i.e. nesting density and species composition) and departure by geese from the colony. Arctic foxes may reduce cache loss related to deterioration of cache sites by maintaining proper cache conditions; such strategies may involve relocation of foods from cache sites in poor condition and selection of cache sites that prevent deterioration of cache sites (see Vander Wall 1990). Arctic foxes may also reduce the need to maintain proper cache conditions by storing more foods than needed or by aggressively defending caches (see Smith and Reichman 1984, Vander Wall 1990). Arctic foxes often relocate eggs from existing caches (Samelius and Alisauskas 2000) which may, in part, be motivated by deterioration of cache sites. In fact, relocating eggs from cache sites in poor condition may be adaptive both to prevent detection of caches and to prevent decomposition of contents. However, foxes may also relocate eggs from existing caches to refresh cache memory or simply as a results from cache pilfering (see Vander Wall 1990, Vander Wall and Jenkins 2003). Benefits of redistributing caches

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may become greater in years with high fox abundance when the risk of pilfering appears to be greatest (Samelius and Alisauskas 2000).

Arctic foxes often appear undecided when caching foods (Quinlan and Lehnhausen 1982, Samelius and Alisauskas 2000) which may, in part, be related to searching for sites that prevent deterioration of cache sites. Wariness when caching foods may also be related to presence of competitors (Lathi and Rytkönen 1996) which, however, appears less influential among arctic foxes as they generally seem wary regardless of fox abundance (Samelius and Alisauskas 2000). I suggest that selection of cache site may have been important in reducing cache loss among arctic foxes at Karrak Lake despite the fact that survival rate of caches was similar among habitats because selection of cache sites may have operated on a different scale or on other criteria than what I examined. For example, soil structure and moisture can be important in affecting cache loss of foods that are stored in the ground (Vander Wall 1998, 2000, Briggs and Vander Wall 2004). Selection of cache sites may, similarly to above, become more important in years with high fox abundance when the risk of pilfering appears to be greatest (Samelius and Alisauskas 2000).

Arctic foxes at Karrak Lake may reduce the need to adjust cache sites in poor condition by storing more foods than needed (see Vander Wall 1990). For example, arctic foxes cache 1,000-3,000 eggs per fox during the nesting season at large goose colonies (Samelius and Alisauskas 2000, Chapter 3) which corresponds to 750,000-2,200,000 kjoules[2] (Robbins 1983, Slattery and Alisauskas 1995). This is 0.6-1.8 times annual *ad libitum* food intake for arctic foxes (Fuglei and Øritsland 1999) and, thus, suggests that arctic foxes cache more eggs than needed energetically by a single fox. Arctic foxes appear to cache similar number of eggs regardless of breeding status (Samelius and Alisauskas 2000, Chapter 3) which suggest that caching of more foods than needed is especially common among non-breeding foxes. Further, foxes may not be able to subsist solely on eggs as large consumption of albumen can cause biotin

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[2] energetic value of cached eggs were calculated as the average energetic content of [Ross's goose egg_{fresh}, lesser snow goose egg_{fresh}, Ross's goose $gosling_{hatch}$, lesser snow goose $gosling_{hatch}$] where lipid and protein content of eggs and goslings were from Slattery and Alisauskas (1995) and energetic value of lipid and protein were from Robbins (1983). The energetic value of eggs decrease with 30-35% during nesting because of metabolism of growing embryos.

deficiency (Klevay 1976), thus, further suggesting that foxes often cache more foods than they need or can consume.

Arctic foxes may also reduce the need to adjust cache sites in poor condition by aggressively defending caches (see Vander Wall 1990, Vander Wall and Jenkins 2003). Arctic foxes are territorial even though there may be considerable overlap in space use (Audet et al. 2002, Eide et al. 2004). There is, thus, potential for considerable intraspecific pilfering of caches. However, cache loss to conspecifics is less detrimental than cache loss to animals that do not cache foods because losses to conspecifics can be compensated by reciprocal pilfering (Vander Wall and Jenkins 2003). In fact, foxes may have benefited from allowing other foxes to cache foods in their territory during goose nesting and then switched to aggressively defending caches after hatch when food availability decreased dramatically (see Eide et al. 2004 for similar discussion on adjusting aggressiveness in relation to food abundance). However, aggressive defence of caches is generally associated with larder-hoarded foods and may not be important among arctic foxes because it is generally difficult to defend caches that are scattered over large areas (Vander Wall 1990).

Condition of cache sites deteriorated as the experiment progressed (e.g. loss of soil cover and partial exposure of eggs) and I suggest that this resulted largely from the caching process disturbing the soil structure and cached eggs preventing moisture from rising. Moreover, I suggest that the influence of ageing of cache sites in the first year of the study was related to such deterioration although cache loss was unrelated to visual exposure of caches because mammals generally use olfaction rather than vision when locating and pilfering caches (Thayer & Vander Wall 2005). Deterioration of cache sites may therefore have resulted in foxes detecting foods from older cache sites easier than they detected foods from new cache sites. The influence of deterioration of cache sites may vary among years in relation to soil moisture and weather conditions which, in turn, may affect the rate at which foxes detect cached eggs (see Vander Wall 2000 for influence of soil condition on cache loss).

Departure by geese after hatch was the main factor affecting cache loss in the second year of the study which suggest that the drastic drop in food abundance when ca 1 million geese and their young left the colony was more important in affecting cache

loss in that year than was nesting distribution by geese and age of cache sites. Similarly, increased cache loss after departure by geese in that year also suggest that strategies to prevent cache loss were more important after geese left the colony than they were during nesting by geese; foxes may therefore have maximised the number of foods they cached in that year by making temporary caches during goose nesting followed by rearrangement of caches after geese departed the colony. In fact, arctic foxes often move eggs from existing caches (Samelius and Alisauskas 2000) although the proportion of such movements that result from rearranging own caches versus pilfering those from others is unknown. Temporary caching and rearrangement of caches once foods are depleted is a common strategy among animals that cache foods from a single source (Jenkins et al. 1995, Jokinen and Suhonen 1995) and may also be important among animals that cache foods that are dispersed in space in some years (e.g. arctic foxes). However, this strategy may be adaptive only in years with low fox abundance as the cost associated with loss of temporary caches during goose nesting may be too great in years of high fox abundance. Other strategies to prevent cache loss after goose departure during the second year of this study may, similarly to above, have included storing of more foods than needed and exclusion of competitors (see Vander Wall 1990, Wander Wall and Jenkins 2003).

Cache loss in this study was largely unaffected by nesting distribution by geese which contrasts that of spatial arrangement of caches relative to their source often having large impact on cache loss in other studies (e.g. Stapanian and Smith 1978, Clarkson et al. 1986, Tamura et al. 1999). Foods in other studies were, however, acquired form a single source whereas foods in my study were dispersed over a large area. Factors affecting optimal arrangement of caches may therefore depend on whether foods are acquired from a single or multiple sources. My study is, to my knowledge, the first to examine factors affecting cache loss of foods that are dispersed in space and there is, thus, a need for further studies on optimal arrangement of caches from foods that are dispersed in space. My study, nevertheless, demonstrated that factors affecting cache loss of foods that are dispersed in space are not static but appear to vary with existing conditions and that evolution of caching behaviours may be shaped by multiple selective pressures (see Vander Wall and Jenkins 2003 for similar suggestion). There

may therefore be considerable flexibility in ultimate strategies to reduce cache loss of foods that are dispersed in space.

6. POPULATION DYNAMICS OF ARCTIC FOXES IN RELATION TO SEASONALLY ABUNDANT GEESE AND ANNUAL VARIATION IN SMALL MAMMAL ABUNDANCE

Abstract: Seasonal influxes of migratory animals provide predators with external subsidies that may elevate predator abundance above that which local foods can support. However, the influence of these influxes on population dynamics of predators is poorly understood. This is especially true for migratory animals whose movements are not tracked by their predators. I examined how large influxes of migratory geese influenced population dynamics of arctic foxes and how this varied with annual variation in small mammal abundance (the main prey of arctic foxes throughout most of their range). Specifically, I compared how arctic fox abundance, breeding density, and litter size varied inside and outside a large goose colony and in relation to annual variation in small mammal abundance. Information-theoretic model selection showed that (*i*) breeding density and fox abundance were 2-3 times higher inside the colony than they were outside the colony and (*ii*) litter size, breeding density, and annual variation in fox abundance followed that of small mammal abundance. Small mammal abundance was, thus, the main governor of population dynamics of arctic foxes whereas geese and their eggs elevated fox abundance and breeding density above that which small mammals could support. This study highlights the influence of seasonal and annual variation on population dynamics of consumers and the linkage between arctic environments and wintering areas by geese thousands of kilometres to the south.

6.1 Introduction

External subsidies and transfer of resources between ecosystems can have large impacts on abundance and distribution of organisms (Polis and Strong 1996, Polis et al. 1997). For example, marine subsidies often elevate animal abundance in coastal areas (Polis and Hurd 1996, Rose and Polis 1998). Similarly, transfer of resources such as windborne nutrients from Sahara can influence productivity of Amazonian rainforests (Swap et al. 1992). In fact, few ecosystems occur in isolation and transfer of resources

between ecosystems may be the norm rather than the exception (Polis and Strong 1996, Polis et al. 1997).

Large seasonal migrations are common among many vertebrates. Migratory animals, in turn, provide predators with seasonal pulses of external subsidies that may elevate predator abundance above that which local foods can support (Polis and Strong 1996, Polis et al. 1997). However, the influence of seasonal influxes of migratory animals on population dynamics of predators is poorly understood (but see Madsen and Shine 1996 and references therein for influence on predators that track migratory movements of their prey). This is especially true for migratory animals whose movements are not tracked by their predators (e.g. long-distance migrants such as birds and fishes). Further, the periodic nature of migratory movements may result in migratory prey being more important among generalist predators that switch between foods or predators that cache foods (see Vander Wall 1990, Ostfeld and Keesing 2000).

Arctic foxes are generalist predators and scavengers that rely heavily on lemmings and voles (small mammals hereafter) throughout most of their range (Audet et al. 2002). However, other foods such as birds and their eggs can be important in arctic fox diets in some years and parts of the arctic (Hersteinsson and MacDonald 1996, Bantle and Alisauskas 1998). Furthermore, the importance of birds and their eggs in arctic fox diets may be amplified by food caching which appears to be especially common among arctic foxes at large bird colonies where foxes cache >1,000 eggs each during the nesting season by birds (Stickney 1991, Samelius and Alisauskas 2000). Small mammal abundance often fluctuate dramatically over 3-5 year periods whereas migratory birds and their eggs provide arctic foxes with seasonal pulses of alternative and often superabundant foods. Areas with both migratory birds (e.g. geese) and small mammals therefore provide ideal settings to examine how population dynamics of arctic foxes are influenced by migratory birds and how this vary with fluctuations in other foods.

Reproductive output and abundance of arctic foxes often vary considerably among years (Audet et al. 2002). Variation in these parameters, in turn, appears to be closely related to food abundance and is especially pronounced among arctic foxes that feed predominantly on small mammals (Macpherson 1969, Angerbjörn et al. 1995). For

example, both litter size and breeding propensity by arctic foxes fluctuate widely in relation to food abundance (Angerbjörn et al. 1991, Tannerfeldt and Angerbjörn 1998, Strand et al. 1999). In fact, arctic foxes have the largest litter size in the order Carnivora and may have up to 18 pups when food is abundant (Tannerfeldt and Angerbjörn 1998). Similarly, abundance of arctic foxes is also closely related to abundance of their foods with peak fox abundance often occurring one year after that of their main foods (Angerbjörn et al. 1999, Samelius et al. *in press*) even though some studies (e.g. Angerbjörn et al. 1995, Kaikusalo and Angerbjörn 1995) did not find a delay in the numerical response by foxes. The latter studies, however, used breeding density as an estimate of fox abundance and therefore did not sample the non-breeding population which can be considerably larger than the breeding population in years when foods are scarce (Angerbjörn et al. 1991, Angerbjörn et al. 1995) – but see Angerbjörn et al. 1999 who found a delay of one year despite including only the breeding population.

The objective of this study was to examine how seasonal influxes of migratory geese and their eggs influenced population dynamics of arctic foxes and how this varied with annual variation in small mammal abundance. Specifically, I compared how arctic fox abundance, breeding density, and litter size varied inside and outside a large goose colony and in relation to annual variation in small mammal abundance.

6.2 Methods

Abundance and reproduction of arctic foxes was monitored in two 5×5 km areas at the colony at Karrak Lake and in two 5×5 km areas outside the colony (Figure 6.1). Study areas were distributed systematically around the southern and original part of the colony with study areas outside the colony located beyond the influence of nesting geese (>5 km from the edge of the colony) while assuring that they could be reached by foot. Locations of study areas were selected from the Universal Transverse Mercator (UTM) grid system on 1:50,000 maps; study areas in the colony were located 4 km apart and study areas outside the colony were located 8 km west and east of the southern study area in the colony. I suggest that foxes in study areas outside the colony did not have access to nesting geese based on home range sizes of arctic foxes in small
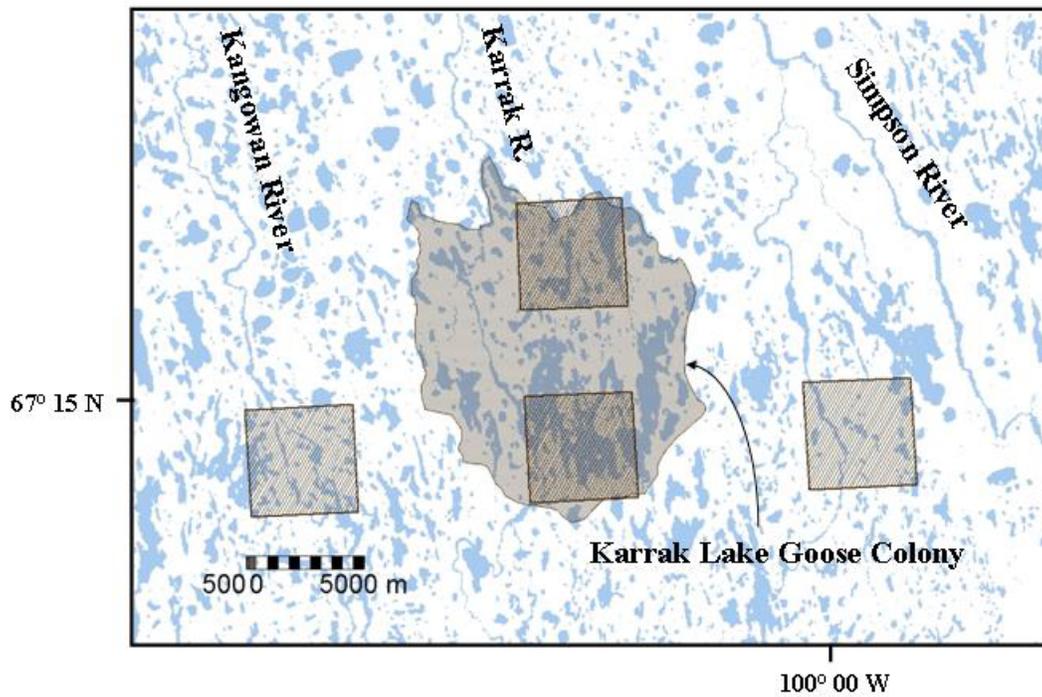
Figure 6.1. The goose colony at Karrak Lake and location of study areas inside and outside the colony in 2000 to 2004. The goose colony is outlined in grey and study areas by stippled rectangles.

mammal and goose nesting areas (see Audet et al. 2002). The main extent of the colony was similar among years even though there tended to be a northwest ward expansion of the colony during the study (Alisauskas, unpublished data). Average nesting density by geese in the two study areas in the colony ranged 35-49 nests/ha during this study (Alisauskas, unpublished data).

Study areas were similar in topography, geology, and plant communities except that heavy grazing by geese removed most graminoid plants (i.e. grasses and sedges) in lowland areas in the colony (Appendix A). Removal of graminoid plants was associated with a reduction in small mammal abundance of about one order of magnitude in lowland areas in the colony compared to those outside the colony (Appendix A). Abundance of both graminoid plants and small mammals in upland areas, in contrast, was similar inside and outside the colony (Appendix A).

6.2.1 Arctic Fox Abundance

Arctic fox abundance was monitored by recording number of adult foxes seen while walking transects that were distributed systematically throughout study areas ($n =$ 6 transects per study area). Transects were 5 km long (but see adjustments for water bodies below), spaced 1 km apart, and followed the Universal Transverse Mercator (UTM) grid system on 1:50,000 maps. Detours around smaller bodies of water (<1 km wide) were included as part of transects whereas detours around larger bodies of water (>1 km wide) were not included; I therefore corrected for distance travelled and used number of foxes seen per 30 km as an index of fox abundance for each study area. I estimated distance travelled by using Geographic Information System (GIS) (Intera Tydac 1991). Multiple observations of the same fox on the same transect were treated as one observation (foxes were identified by ear-tags or pelt-pattern).

Arctic fox abundance was monitored between 23:00 and 09:30 which corresponds to periods of continuous fox activity (Anthony 1997, Bantle 1998). Fox abundance was monitored only during days with clear sky or high thin clouds to minimise potential bias in detection rate of foxes caused by weather (see Nichols 1992). Similarly, fox abundance was monitored after geese departed the colony following

hatch to avoid potential bias in detection rate of foxes caused by nesting geese (foxes can be difficult to detect among nesting geese). Foxes were detected at similar distances inside and outside the colony (see Results) illustrating that detection rate of foxes was similar in both areas. Fox abundance could not be monitored in one study area outside the colony in 2004 because of grizzly bear activity.

6.2.2 Litter Size and Breeding Density

Litter size and breeding density was monitored by systematic den surveys where sites with fox-sized entrances >1 m deep were considered as potential den sites (see below for verification of whether dens were used for pup rearing). Dens were visited once in May and at least once in late June or early July when pups were ca 6-8 weeks old. Dens were located by systematic surveys in May and July 2000 during which dens were located from transects that were spaced 1 km apart. Study areas were travelled extensively throughout this study and arctic fox dens are generally easy to detect because repeated den use tend to result in lush vegetation (Audet et al. 2002); I therefore suggest that few, if any, potential den sites were missed.

Dens that showed evidence of reproduction in June or early July (i.e. fresh tracks in entrances, fresh diggings, pup-sized scats, or presence of foxes) were observed with spotting scopes to confirm pup rearing and to estimate litter size. Dens were monitored from distances of 300-800 m for 5 hours or more. Pup rearing was verified by visual confirmation of pups (14 litters), presence of pup-sized tracks and scats (1 litter outside the colony), and presence of a female with enlarged teats (1 litter inside the colony). Litter size estimated from unmarked litters is a minimum estimate as all pups may not be outside the den simultaneously (Angerbjörn et al. 1995); I therefore compared number of pups seen at the den survey to number of pups captured and marked in mid to late July (where pups were captured until no unmarked pups were seen). I used the highest number of pups encountered during either of these visits as an estimate of litter size at weaning for each den. However, pups could not be captured from all litters because pups died or were relocated before they could be capture (4 litters in the colony and 2 litters outside the colony). Similarly, litter size could not be

estimated by either method for 2 litters inside the colony and 1 litter outside the colony because pups died or were relocated before they could be either counted or captured.

I used number of breeding dens per study area as an estimate of breeding density. However, surface area of water bodies varied among study areas so I adjusted data to number of breeding dens per 25 km^2 terrestrial habitat for each study area before final analyses. I calculated the area of terrestrial habitat by using GIS (Intera Tydac 1991).

6.2.3 Small Mammal Abundance

Small mammal abundance was monitored at 3 permanent trap-lines established in 1994 following Shank (1993). Trap-lines consisted of 25 trap-stations with 1 snap-trap placed within 1 m of each trap-station. One trap-line was monitored during the second half of June and the other two were monitored during the second half of July. Small mammal abundance was monitored for 10 consecutive nights and I used number of captures per 100 trap-nights as sample unit for each year. I subtracted 0.5 trap-nights for each trap that was snapped without capture to correct for variation in sampling effort (Beauvais and Buskirk 1999). Trap-lines included habitats ranging from wet lowlands to dry upland hills.

6.2.4 Statistical Analyses

I examined how fox abundance, breeding density, and litter size varied inside and outside the colony and in relation to small mammal abundance by ANCOVA (Proc. GLM, SAS Institute Inc., 1990). I performed analyses separately for fox abundance, breeding density, and litter size ($n = 19$ indices of fox abundance, 20 estimates of breeding density, and 13 litters). I used small mammal abundance in the previous year for analyses on fox abundance and small mammal abundance in the current year for analyses on breeding density and litter size. I derived 5 *a priori* candidate models for each of these analyses that ranged from no variation inside and outside the colony or in relation to small mammal abundance, to models that included variation inside and outside the colony, small mammal abundance, and an interaction between these two

variables (see Table 6.1 for candidate models). I used variation around the grand mean as a null model (i.e. no effect of either of the variables examined). I used Akaike's information criterion (AIC = $n[\ln(\text{SSE}/n)]$ + 2K, where K = number of model parameters, including the intercept and σ^2) with small-sample adjustment (AIC_c = AIC + $[(2K(K + 1))/(n - K - 1)]$) to select the most parsimonious models that best explained variation in fox abundance, breeding density, and litter size (Burnham and Anderson 1998). I selected the model with the lowest AIC_C value as the best model and considered models within 2 AIC_C units to be of similar quality (Burnham and Anderson 1998).

6.3 Results

Twenty-eight foxes were encountered during 571 km travelled and 16 litters were encountered at 6 different dens from 2000 to 2004. Another 3 dens that showed signs of previous pup-rearing (i.e. numerous entrances and vegetation markedly different from the surrounding) but were not used for pup-rearing during this study were also encountered (located in 3 different study areas). Foxes moved pups to temporary dens among rocks on 4 occasions and to unknown sites on at least 1, but possibly 4, occasions (foxes may, alternatively, have failed their breeding attempts on 3 occasions). Temporary dens among rocks were never open in May and were, thus, not used for parturition. Foxes were detected at similar distances inside and outside the colony ($\bar{x}$ = 360 and 290 m in each area, respectively, range = 100-1,200 and 100-500 m in each area, respectively, although the range inside the colony was 100-500 m except for 1 fox that was detected at 1,200 m). My index of fox abundance inside the colony correlated with an independent estimate of fox abundance determined by the number of fox-fox interactions observed per hour and year during behavioural observations (r^2 = 0.48 and n = 10 estimates of fox abundance from 5 years). Small mammal abundance varied considerably among years with peak small mammal abundance in 2000 (Figure 6.2).
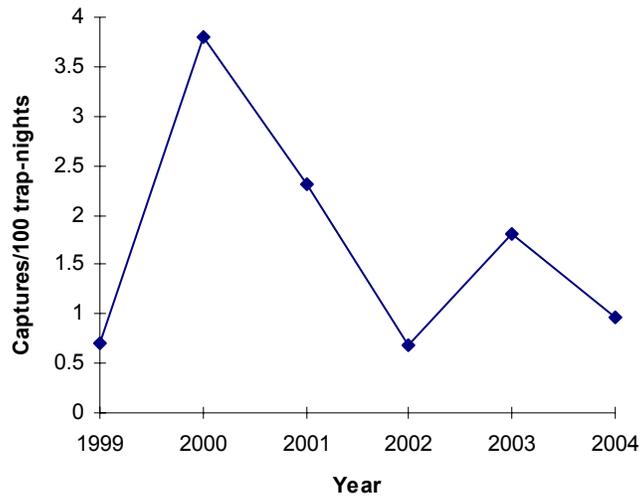
Figure 6.2. Small mammal abundance at the Karrak Lake area in 1999 to 2004.

6.3.1 Arctic Fox Abundance

Models {Goose Nesting × Small Mammals Previous Year}, {Goose Nesting}, and {No Effect} described variation in arctic fox abundance better than other models and accounted for 80% of the cumulative model weight (Table 6.1). Arctic fox abundance was, thus, related to both small mammal abundance in the previous year and seasonal influxes of geese and their eggs. However, factors other than goose nesting and small mammal abundance in the previous year may also have affected fox abundance as the null model (i.e. no relation between fox abundance and either nesting distribution by geese or small mammal abundance) accounted for 21% of the cumulative model weight. Nevertheless, arctic fox abundance was about 2 times higher in the colony than it was outside the colony with a mean of 2.1 (range = 0-5.4) and 0.9 (range = 0-3.9) foxes seen per 30 km in each area, respectively (Figure 6.3). Further, arctic fox abundance inside the colony followed that of small mammal abundance in the previous year ($r^2 = 0.45$) whereas fox abundance outside the colony was unrelated to small mammal abundance in the previous year ($r^2 = 0.07$). Fox abundance was unrelated to small mammal abundance in the current year both inside and outside the colony ($r^2 < 0.01$ for both areas). Fox abundance in the colony was correlated to nesting density by geese in the current year ($r^2 = 0.40$) whereas there was no correlation between fox abundance in the colony and nesting densities in the previous year ($r^2 = 0.01$). However, the correlation between fox abundance and nesting density by geese in the current year was driven by one data point so the relationship between these parameters was therefore unclear ($r^2 < 0.01$ when outlier was removed). Small mammal abundance in the previous year was, thus, the main factor affecting annual variation in fox abundance in the colony whereas seasonal influxes of geese and their eggs elevated fox abundance above that which small mammal could support.

6.3.2 Breeding Density

Models {Goose Nesting + Small Mammal} and {Goose Nesting × Small Mammal} described variation in breeding density by foxes better than other models and accounted for 93% of the cumulative model weight (Table 6.1). Breeding density by

Table 6.1. Model selection for variation in arctic fox abundance, breeding density, and litter size inside and outside the goose colony at Karrak Lake and in relation to small mammal abundance in 2000-2004. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), model weights (w_i), and coefficient of determination (r^2). I used variation around the grand mean as the null model (called 'no effect' in the table). AIC_c values for the best models were 18.13, 2.33, and - 19.07 for models on fox abundance, breeding density, and litter size, respectively.

Model [1]	K	Δ_i	w_i	r^2
Fox Abundance				
Goose Nesting × Small Mammal Previous Year	5	0	0.30	0.43
Goose Nesting	3	0.03	0.29	0.17
No Effect	2	0.66	0.21	na
Goose Nesting + Small Mammal Previous Year	4	1.97	0.11	0.22
Small Mammal Previous Year	3	2.44	0.09	0.05
Breeding density				
Goose Nesting + Small Mammal	4	0	0.66	0.54
Goose Nesting × Small Mammal	5	1.81	0.27	0.58
Goose Nesting	3	5.20	0.05	0.29
Small Mammal	3	6.61	0.02	0.24
No Effect	2	9.35	<0.01	na
Litter Size				
Small Mammal	3	0	0.55	0.30
No Effect	2	1.13	0.31	na
Goose Nesting + Small Mammal	4	4.06	0.07	0.31
Goose Nesting	3	4.11	0.07	0.04
Goose Nesting × Small Mammal	5	9.78	<0.01	0.30

[1] × indicates that both major effects and the interaction between major effects were included in the model
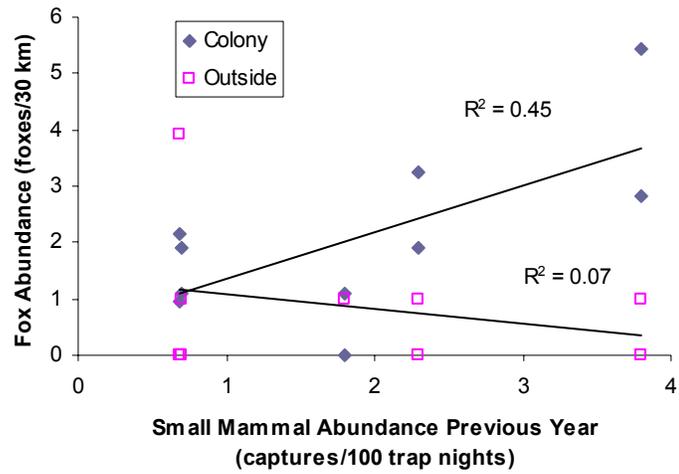
Figure 6.3. Arctic fox abundance inside and outside the goose colony at Karrak Lake and in relation to small mammal abundance in the previous year in 2000 to 2004.

foxes was, thus, related to both small mammal abundance and seasonal influxes of geese and their eggs. Breeding density by foxes was about 3 times higher in the colony than it was outside the colony with a mean of 1.9 (range = 0-3.9) and 0.6 (range = 0-2.3) breeding dens per 25 km^2 in each area, respectively (Figure 6.4)[3]. Further, breeding density by foxes was highly correlated with small mammal abundance both inside and outside the colony. In fact, foxes did not breed in any study area or in the colony as a whole in 2002 when small mammal abundance was at its lowest. The influence of small mammal abundance on breeding density of foxes was especially pronounced in the colony in years when small mammals were abundant – thus, the interaction between small mammal abundance and nesting distribution by geese. Breeding density of foxes in the colony was unrelated to nesting density by geese in both the current (r^2 <0.01) and the previous year (r^2 <0.01). Small mammal abundance was, thus, the main factor affecting whether foxes bred whereas seasonal influxes of geese and their eggs elevated breeding density of foxes above that which small mammals could support.

6.3.3 Litter Size

Models {Small Mammal} and {No Effect} described variation in litter size better than other models and accounted for 85% of the cumulative model weight (Table 6.1). Litter size was, thus, related mainly to small mammal abundance whereas seasonal influxes of geese and their eggs had limited, if any, impact on litter size. However, factors other than small mammal abundance may also have affected litter size by foxes as the null model accounted for 31% of the cumulative model weight. Litter size, nevertheless, increased with increasing small mammal abundance (Figure 6.5). Mean litter size at weaning was 7.4 pups (range = 4-11 pups) from 2000 to 2004.

6.4 Discussion

The influence of migratory animals on population dynamics of predators is poorly understood. However, this study showed that population dynamics of arctic

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[3] mean breeding density before water bodies were excluded was 1.1 and 0.5 breeding dens per 25 km^2 inside and outside the colony, respectively (range = 0-2 dens per 25 km^2 for both areas).
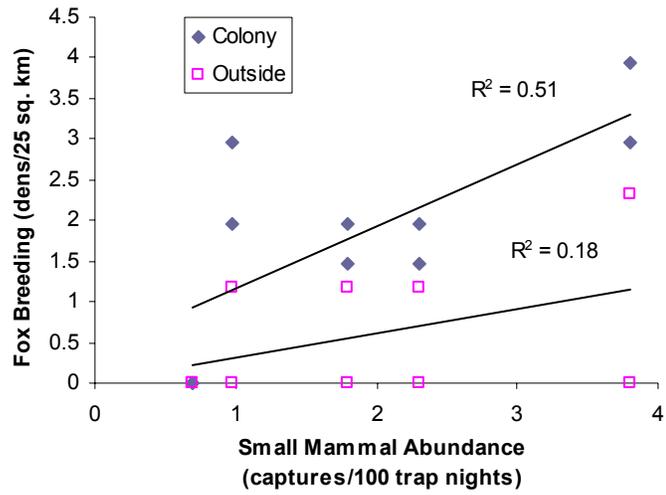
Figure 6.4. Breeding density by arctic foxes inside and outside the goose colony at Karrak Lake and in relation to small mammal abundance in 2000 to 2004.
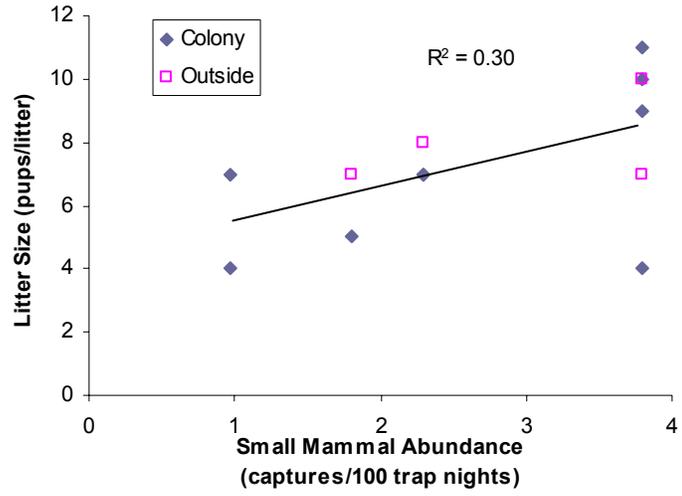
Figure 6.5. Litter size of arctic foxes at weaning inside and outside the goose colony at Karrak Lake and in relation to small mammal abundance in 2000 to 2004.

foxes was influenced by both seasonal influxes of migratory geese and annual variation in small mammal abundance. Specifically, small mammal abundance was the main factor affecting reproductive output and annual variation in fox abundance whereas geese and their eggs provided foxes with external subsidies that elevated breeding density and fox abundance above that outside the colony. Small mammal abundance was, thus, the main factor governing population dynamics of arctic foxes whereas geese and their eggs elevated breeding density and fox abundance above that which small mammals could support. Furthermore, the influence of geese and their eggs extended well into the following spring as breeding density by foxes at Karrak Lake was elevated above that outside the colony even though geese left the colony 8-9 months before foxes started to breed. This was consistent with arctic foxes using similar areas throughout the year at a large waterfowl-nesting area in Alaska (Anthony 1997).

Geese and their eggs elevating fox abundance at Karrak Lake above that which small mammal could support was similar to that of predators often congregating in areas with migratory prey (Madsen and Shine 1996, Willson et al. 1998). However, predators seldom remain in these areas after migratory animals leave (Madsen and Shine 1996, Willson et al. 1998) whereas fox abundance at Karrak Lake remained elevated well into the following spring (i.e. at least 10 months after geese left the colony). Differences in the way predators respond to migratory prey may largely be related to behavioural differences in how they exploit temporarily abundant foods and how these behaviours link predators in space. Specifically, caching and use of stored foods allows predators to remain in familiar areas with predictable foods (Vander Wall 1990, Samelius and Alisauskas 2000) whereas strategies such as fat storage, tracking movements of migratory prey, and switching among foods do not link predators in space. Limited influence of geese and their eggs on annual variation in fox abundance at Karrak Lake was similar to arctic foxes at Cape Churchill in Manitoba, Canada, not responding numerically when lesser snow geese at the nearby colony at La Pérouse Bay increased from 4,000 to 40,000 nesting geese (Roth 2002). In fact, a lack of a numerical response of predators (other than seasonal congregations) allows migratory animals to escape predator regulation and appears to be the ultimate reason why migratory animals are often numerous (Fryxell et al. 1988).

Annual variation in fox abundance at Karrak Lake was driven largely by small mammal abundance in the previous year which follows that of a close link between arctic foxes and small mammals in other areas where they coexist (Tannerfeldt and Angerbjörn 1998, Angerbjörn et al. 1999, Strand et al. 1999). Further, this also shows that small mammals are key determinants of population dynamics of arctic foxes even in areas where they have access to seasonally superabundant foods (see Samelius et al. *in press* for similar results). The link between fox abundance and small mammal abundance in the previous year appeared to reflect reproductive output in previous year and follows that of recruitment of young appearing to be a key determinant of arctic fox abundance throughout their range (Macphearson 1969, Angerbjörn et al. 1991, Angerbjörn et al. 1999). Fluctuations in fox abundance may also reflect variation in survival and dispersal rates (see O'Donoghue et al. 1997). I suggest that differences in the influence of small mammals and geese in this study were largely related to differences in the length of time that these foods were present at the colony and the extent of time that they overlapped with the breeding season by foxes. Specifically, small mammal abundance remained high for several months in years when they were abundant (Samelius, personal observation) and therefore overlapped the entire breading season by foxes (i.e. March to August). Geese and their eggs, in contrast, were abundant for only 1 month of the year and therefore overlapped only part of the breeding season by foxes. Limited influence of geese and their eggs on reproductive output by foxes in this study, thus, suggest that foxes were not caching sufficient number of eggs to meet nutritional demands of reproduction the following spring. Eggs may, alternatively, be poor in meeting nutritional demands of reproduction because large consumption of albumen can cause biotin deficiency (Klevay 1976) and thereby limit the number of eggs foxes can consume.

I was surprised that arctic fox abundance outside the colony was unrelated to small mammal abundance. In fact, I predicted that the influence of small mammals would be stronger outside the colony than it was inside the colony because foxes outside the colony did not have access to seasonally abundant geese and their eggs. However, I suspect that the lack of a linkage between small mammals and fox numbers

outside the colony was an artefact of low fox densities making it difficult to detect this relationship.

Arctic foxes never used more than two thirds of the dens available for pup-rearing which suggest that reproductive output by foxes was not limited by availability of den sites. However, the proportion of dens used for pup-rearing may not be a reliable index of whether reproductive output by foxes was limited by den sites because territorial behaviour may reduce the number of dens available for pup-rearing (Gordon 1997). For example, foxes were often seen visiting dens other than those in which they reared their young (Samelius, unpublished data) which suggest that foxes may have claimed or attempted to claim more than one den site. So, although territorial behaviours tend to be relaxed when foods are abundant (Tsukada 1997, Eide et al. 2004), there was only a limited number of suitable dens sites available to foxes. Availability of den sites may, thus, limit reproductive output by foxes in years when small mammals are abundant and would otherwise allow more foxes to breed (see Smits et al. 1988 for suggestion that availability of den sites may limit reproductive output by arctic foxes in areas where suitable dens sites are scarce).

In summary, arctic foxes are closely linked to small mammals throughout most of their range (Audet et al. 2002) and this study showed that small mammal abundance was the main factor governing population dynamics of arctic foxes even in areas where they have access to seasonally superabundant foods. However, seasonal influxes of geese and their eggs provided foxes with external subsidies that elevated breeding density and fox abundance above that which small mammals could support. This study highlights the influence of seasonal and annual variation on population dynamics of consumers and the linkage between arctic environments and wintering areas by geese thousands of kilometres to the south (see Alisauskas 2002). This study also suggests that the influence of migratory animals on population dynamics of predators may largely be related to the extent of time that influxes of migratory animals overlap with the breeding season by predators.

7. SYNTHESIS

7.1 Food Caching and Superabundant Foods

Food caching may be adaptive to avoid food shortage in stochastic environments; use of stored foods allows animals to remain in familiar areas and is an alternative strategy to migration, torpor, hibernation, and fat storage (Smith and Reichman 1984, Vander Wall 1990). However, the extent to which animals cache and use stored foods is unknown for most species (Vander Wall 1990). This is especially true for members of the order Carnivora for which few studies have examined caching behaviours in detail (but see Tinbergen 1965, Macdonald 1976, Harrington 1981, Henry 1986, Samelius and Alisauskas 2000). This study showed that arctic foxes cached 2,000-3,000 eggs per fox each year and that the rate at which eggs were cached was independent of sex, size, breeding status, and age of foxes (Chapter 3). Food caching was, thus, not limited to a certain portion of the population. Further, this study showed that arctic foxes used cached eggs almost 1 year after foods were cached (Chapter 4). This differs greatly from that of carnivores generally storing foods for only a few days before consumption (Vander Wall 1990). Long-term storage of eggs may largely be related to cold temperatures and physio-chemical properties of eggs impairing microbial activity (Stickney 1991, Bantle and Alisauskas 1998).

Arctic foxes at Karrak Lake cached similar numbers of eggs among years (Chapter 3) although they rarely used cached eggs in years when collared lemmings were abundant (Chapter 4). Instead, foxes appeared to cache as many eggs as possible during the nesting season by geese which may be an adaptive strategy to ensure a buffer against unpredictable changes in lemming abundance. Similarly, arctic foxes caching eggs independently of availability of alternative foods and current energetic demands (Chapter 3) may help to explain why predators occasionally kill more prey than they can consume (termed surplus killing by Kruuk 1972). Specifically, surplus killing may provide predators with a buffer against unpredictable changes in prey abundance or failure to capture prey. The adaptiveness of such buffers may, however, depend on the rate at which prey decompose.

7.2 Migratory Prey and Linkages of Ecosystems

Migratory animals provide predators with seasonal pulses of external subsidies that may elevate predator abundance above that which local foods can support (Polis and Strong 1996, Polis et al. 1997). However, the influence of seasonal influxes of migratory animals on population dynamics of predators is poorly understood (but see Madsen and Shine 1996 and references therein for effects on predators that track migratory movements of their prey). This is especially true for migratory animals whose movements are not tracked by their predators (e.g. long-distance migrants such as birds and fishes). This study showed that seasonal influxes of geese and their eggs elevated both fox abundance and breeding density above that which small mammals could support but that overall population dynamics of arctic foxes were driven largely by small mammals (Chapter 6). However, geese and their eggs provided arctic foxes with seasonally superabundant foods on which foxes relied heavily in years when small mammals were scarce (Chapter 4). The periodic nature of migration may result in the influence of migratory prey being more important among generalist predators that switch between foods or predators that cache foods (see Vander Wall 1990, Ostfeld and Keesing 2000).

Geese and their eggs elevating fox abundance and breeding density above that which small mammals could support (Chapter 6) highlights the linkage between arctic environments and wintering and staging areas of geese thousands of kilometres to the south (see Alisauskas 2002). Further, anthropogenic subsidies in goose diets outside of the arctic (see Abraham et al. 2005) may, thus, have had indirect effects on local population dynamics of arctic foxes (but see Roth 2002 for lack of large-scale effects of geese on arctic fox population dynamics). In fact, few systems occur in isolation and most ecosystems are linked to other system in some way or another (Polis and Strong 1996, Polis et al. 1997).

8. LITERATURE CITED

Abraham K.F., Jefferies R.L. and Alisauskas R.T. 2005. The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biol. 11: 841-855.

Alisauskas R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. J. Wildl. Manage. 66: 181-193.

Alisauskas R.T., Slattery S.M., Ryder J.P., Gloutney M.L., Afton A.D., Kerbes R.H. and McLandress M.R. 1998. Discrimination of Ross's and lesser snow goose eggs. J. Field Ornithol. 69: 647-653.

Andersson M. and Erlinge S. 1977. Influence of predation on rodent populations. Oikos 29: 591-597.

Andersson M. and Krebs J. 1978. On the evolution of hoarding behaviour. Anim. Behav. 26: 707-711.

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

Angerbjörn A., Tannerfeldt M. and Erlinge S. 1999. Predator-prey relationships: arctic foxes and lemmings. J. Anim. Ecol. 68: 34-49.

Angerbjörn A., Tannerfeldt M., Bjärvall A., Ericson M., From J. and Norén E. 1995. Dynamics of the arctic fox population in Sweden. Ann. Zool. Fennici 32: 55-68.

Anthony R.M. 1997. Home range and movements of arctic fox (*Alopex lagopus*) in Western Alaska. Arctic 50: 147-157.

Audet A.M., Robbins C.B. and Larivière S. 2002. *Alopex lagopus*. Mammal. Species 713: 1-10.

Bantle J.L. 1998. Arctic fox predation on Ross's and lesser snow geese. MSc thesis, University of Saskatchewan, Saskatoon, Canada.

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

Barnett B.A. 1994. Carbon and nitrogen isotope ratios of caribou tissues, vascular plants, and lichens. M.Sc. Thesis. University of Alaska, Fairbanks.

Beauvais G.P. and Buskirk S.W. 1999. Modifying estimates of sampling effort to account for sprung traps. Wildl. Soc. Bull. 27: 39-43.

Begon M., Harper J.L. and Townsend C.R. 1996. Ecology: individuals, populations and communities. 3rd ed. Blackwell Scientific Publications, Boston.

Bêty J., Gauthier G., Korpimäki E. and Giroux J.F. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J. Anim. Ecol. 71: 88-98.

Bolnick D.I., Svanbäck R., Fordyce J.A., Yang L.H., Davis J.M., Hulsey C.D. and Forister M.L. 2003. The ecology of individuals: Incidence and implications of individual specialization. Am. Nat. 161: 1-28.

Briggs J.S. and Vander Wall S.B. 2004. Substrate type affects caching and pilferage of pine seeds by chipmunks. Behav. Ecol. 15: 666-672.

Bronson F.H. 1989. Mammalian reproductive biology. Chicago University Press, Chicago.

Bugnyar T. and Kotrschal K. 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*. Anim. Behav. 64: 185-195.

Burnham K.P. and Anderson D.R. 1998. Model selection and inference: a practical information- theoretic approach. Springer, New York.

Clarkson K., Eden S.F., Sutherland W.J. and Houston A.I. 1986. Density dependence and magpie food hoarding. J. Anim. Ecol. 55: 111-121.

Drucker D., Bocherens H., Pike-Tay A. and Mariotti A. 2001. Isotopic tracking of seasonal dietary change in dentine collagen: preliminary data from modern caribou. Earth Plan. Sci. 333: 303-309.

Eide N.E., Jepsen J.U. and Prestrud P. 2004. Spatial organization of reproductive arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. J. Anim. Ecol. 73: 1056-1068.

Fay F.H. and Stephenson R.O. 1989. Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bearing Sea. Can. J. Zool. 67: 1986-1994.

Freeman B.M. and Vince M.A. 1974. Development of the avian embryo. Chapman and Hall, London, England.

Fryxell J.M., Greever J. and Sinclair A.R.E. 1988. Why are migratory ungulates so abundant? Am. Nat. 131: 781-798.

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

Gendron R.P. and Reichman O.J. 1995. Food perishability and inventory management: a comparison of three caching strategies. Am. Nat. 145: 948-968.

Gese E.M., Ruff R.L. and Crabtree R.L. 1996. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. Can. J. Zool. 74: 784-797.

Gordon D.M. 1997. The population consequences of territorial behavior. Trends Ecol. Evol. 12: 63-66.

Grier J.W. and Burk T. 1992. Biology of animal behavior. 2nd ed. Mosby Year Book, St. Louis.

Gunn A. and Adamczewski J. 2003. Muskox – *Ovibos moschatus*. In Feldhamer G.A., Thompson B.C. and Chapman J.A. Wild mammals of North America: biology, management, and conservation. 2nd ed. The John Hopkins University Press, Baltimore.

Gunn A., Fournier B. and Nishi J. 2000. Abundance and distribution of the Queen Maud Gulf caribou heard, 1986-98. Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories, File Report No. 126.

Hadj-Chikh L.Z., Steele M.A. and Smallwood P.D. 1996. Caching decisions by grey squirrels: a test of the handling time and perishability hypothesis. Anim. Behav. 52: 941-948.

Hanski I., Hansson L. and Henttonen H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. J. Anim. Ecol. 60: 353-367.

Hansson L. 1986. Geographic differences in the sociability of voles in relation to cyclicity. Anim. Behav. 34: 1215-1221.

Harrington F.H. 1981. Urine-marking and caching behavior in the wolf. Behaviour 76: 280-288.

Heinrich B. and Pepper J.W. 1998. Influence of competitors on caching behaviour in the common raven, *Corvus corax*. Anim. Behav. 56: 1083-1090.

Henry J.D. 1986. Red fox: the catlike canine. Smithsonian Institution Press, Washington D.C.

Hersteinsson P. and MacDonald D.W. 1996. Diet of arctic fox (*Alopex lagopus*) in Iceland. J. Zool. (London) 240: 457-474.

Hobson K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314-326.

Hobson K.A., Schell D.M., Renouf D. and Noseworthy E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions. Can. J. Fish Aquat. Sci. 53: 528-533.

Holder K. and Montgomerie R. 1993. Rock Ptarmigan (*Lagopus mutus*). *In* The Birds of North America, No. 51 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union

Holmgren M., Scheffer M., Ezcurra E., Gutierrez J.R. and Mohren G.M.J. 2001. El Nino effects on the dynamics of terrestrial ecosystems. Trends Ecol. Evol. 16: 89-94.

Holt R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theor. Pop. Biol. 12: 197-229.

Intera Tydac. 1991. Spans GIS. Nepean, Ontario, Canada.

Jenkins, S.H., Rothstein, A. and Green, W.C.H. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. - Ecology 76: 2470-2481.

Jokinen S. and Suhonen J. 1995. Food caching by willow and crested tits: a test of scatterhoarding models. Ecology 76: 892-898.

Kaikusalo A. and Angerbjörn A. 1995. The arctic fox population in Finnish Lapland during 30 years, 1964-93. Ann. Zool. Fennici 32: 69-77.

Kelly J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78: 1-27.

Kerbes R.H. 1994. Colonies and numbers of Ross' and lesser snow geese in the Queen Maud Gulf Migratory Bird Sanctuary. Occasional Paper No. 81. Canadian Wildlife Service, Ottawa, Canada. 47 pp.

Klevay L.M. 1976. The biotin requirements of rats fed 20% egg white. J. Nutr. 106: 1643-1646.

Krebs C.J., Boutin S., Boonstra R., Sinclair A.R.E., Smith J.N.M., Dale M.R.T., Martin K. and Turkington R. 1995. Impact of food and predation on the snowshoe hare cycle. Science 269: 1112-1115.

Krebs C.J., Boonstra R., Boutin S. and Sinclair A.R.E. 2001. What drives the 10-year cycle of snowshoe hares? Bioscience 51: 25-35.

Kruuk H. 1972. Surplus killing by carnivores. J. Zool. 166: 233-244

Landa A., Strand O., Linnell J.D.C. and Skogland T. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in alpine environment. Can. J. Zool. 76: 448-457.

Lathi K. and Rytkönen S. 1996. Presence of conspecifics, time of day and age affect willow tot food hoarding. Anim. Behav. 52: 631-636.

Lawton J.H. 1999. Are there general laws in ecology? Oikos 84: 177-192.

Lima S.L. and Dill L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619-640.

Maccarone A.D. and Montevecchi W.A. 1981. Predation and caching of seabirds by red foxes (*Vulpes vulpes*) on Baccalieu Island, Newfoundland. Can. Field-Nat. 95: 352-353.

MacDonald D.W. 1976. Food cahing by red foxes and some other carnivores. J. Tierpsychol. 42: 170-185.

Macpherson A.M. 1969. The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series No. 8. Canadian Wildlife Service, Ottawa, Canada. 52 pp.

Madsen T. and Shine R. 1996. Seasonal migration of predators and prey - a case study of phytons and rats in tropical Australia. Ecology 77: 149-156.

McLandress M.R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and lesser snow geese. Auk 100:335-343.

McNamara J.H. and Houston A.I. 1987. Starvation and predation as factors limiting population size. Ecology 68: 1515-1519.

Miller F.L. 2003. Caribou – *Rangifer tarandus*. In Feldhamer G.A., Thompson B.C. and Chapman J.A. Wild mammals of North America: biology, management, and conservation. 2nd ed. The John Hopkins University Press, Baltimore.

Nichols J.D. 1992. Capture-recapture models: Using marked animals to study population dynamics. Bioscience 42: 94-102.

O'Donoghue M., Boutin S., Krebs C.J. and Hofer E.J. 1997. Numerical response of coyotes and lynx to the showshoe hare cycle. Oikos 80: 150-162.

Ostfeld R.S. and Keesing F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol. Evol. 15: 232-237.

Pasitschniak-Arts. M. 1993. Ursus arctos. Mammalian Species 439: 1-10.

Perry G. and Pianka E.R. 1997. Animal foraging: past, present and future. Trends Ecol. Evol. 12: 360-364.

Phillips D.L. and Gregg J.W. 2003. Source partitioning using stable isotopes: coping with to many sources. Oecologia 136: 261-269.

Polis G.A. and Hurd S.D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147: 396-423.

Polis G.A. and Strong D.R. 1996. Food web complexity and community dynamics. Am. Nat. 147: 813-846.

Polis G.A., Hurd S.D., Jackson C.T. and Sánchez-Piñero F. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78: 1884-1897.

Post D.M., Conners, M.E. and Goldberg D.S. 2000. Prey preference by a top predator and the stability of linked food chains. Ecology 81: 8-14

Preston S.D. and Jacobs L.F. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Behav. Ecol 12: 517-523.

Quinlan S.E. and Lehnhausen W.A. 1982. Arctic fox, *Alopex lagopus*, predation on nesting common eiders, *Somateria mollissma*, at Icy Cape, Alaska. Can. Field Nat. 96: 462-466.

Raveling D.G. 1989. Nest-predation rates in relation to colony size of black brant. J. Wildl. Manage. 53: 87-90.

Robbins C.T. 1993. Wildlife feeding and nutrition. 2nd ed. Academic Press.

Rodgers A.R. and Lewis M.C. 1986. Diet selection in arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): demography, home range, and habitat use. Can. J. Zool. 64: 2717-2727.

Rose M.D. and Polis G.A. 1998. The distribution and abundance of coyotes: the effect of allochtonous food subsidies from the sea. Ecology 79: 998-1007.

Roth J.D. 2002. Temporal variability in arctic fox diets as reflected in stable-carbon isotopes; the importance of sea ice. Oecologia 133: 70-77.

Roth J.D. 2003. Variability in marine resources affects arctic fox population dynamics. J. Anim. Ecol. 72: 668-676.

Roth J.D. and Hobson K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. Can. J. Zool. 78: 848-852.

Ryder J.P. 1972. Biology of nesting Ross's geese. Ardea 60: 185-215.

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

Samelius G., Alisauskas R.T. and Hines J.E. Productivity of lesser snow geese on Banks Island in 1995 to 1998. Occasional Paper, Canadian Wildlife Service, Ottawa, Canada. *in press*.

Samelius G., Larivière S. and Alisauskas R.T. 2003. Immobilization of arctic foxes with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®). Wildl. Soc. Bull. 31: 192-196.

SAS. 1990. SAS user's guide. Version 6. SAS Institute Inc. Cary, North Carolina.

Shank C.C. 1993. The Northwest Territories small mammal survey: 1990-1992. Department of Renewable Resources, Government of Northwest Territories, Yellowknife, NWT, Manuscript Report No. 72.

Sinclair A.R.E. and Arcese P. 1995. Population consequences of predation-sensitive foraging: the serengeti wildebeest. Ecology 76: 882-891.

Slattery S.M. 1994. Neonate reserves, growth rate and survival of Ross' and lesser snow geese goslings. MSc thesis, University of Saskatchewan, Saskatoon, Canada.

Slattery S.M. and Alisauskas R.T. 1995. Egg characteristics and body reserves of neonate Ross' and lesser snow geese. Condor 97: 970-984.

Smith C.C. and Reichman O.J. 1984. The evolution of food caching by birds and mammals. Ann. Rev. Ecol. Syst. 15: 329-351.

Smits C.M.M, SmithC.A.S. and Slough B.G. 1988. Physical charecteristics of arctic fox (*Alopex lagopus*) dens in northern Yukon Territory, Canada. Arctic 41: 12-16.

Stapanian M.A. and Smith C.C. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59: 884-896.

Stapanian M.A. and Smith C.C. 1984. Density-dependent survival of scatterhoarded nuts: an experimental approach. Ecology 65: 1387-1396.

Stearns. S.C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford, UK.

Stephens D.W. and Krebs J.R. 1986. Foraging theory. Princeton Univ. Press, Princeton, New Jersey.

Stickney A. 1991. Seasonal patterns of prey availability and foraging behaviour of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Can. J. Zool. 69: 2853-2859.

Strand O., Landa A., Linnell J.D.C., Zimmermann B. and Skogland T. 2000. Social organisation and parental behavior in the arctic fox. J. Mammal. 81: 223-233.

Swap R., Garstang M., Greco S., Talbot R. and Kallberg P. 1992. Saharan dust in the Amazon basin. Tellus B Chem. Phys. Meteorol. 44: 133-149.

Tamura N., Hashimoto Y. and Hayashi F. 1999. Optimal distances for squirrels to transport and hoard walnuts. Anim. Behav. 58: 635-642.

Tannerfeldt M. and Angerbjörn A. 1996. Life history strategies in fluctuating environment: establishment and reproductive success in the arctic fox. Ecography 19: 209-220.

Tannerfeldt M. and Angerbjörn A. 1998. Fluctuating resources and the evolution of litter size in the arctic fox. Oikos 83: 545-559.

Taylor R.J. 1984. Predation. Chapman and Hall. NY.

Temple S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68: 669-674.

Thompson W.L., White G.C. and Gowan C. 1998. Monitoring vertebrate populations. Academic Press, San Diego, CA.

Tinbergen N. 1965. Von den vorratskammern des rotfuchses (*Vulpes vulpes*). Z. Tierpsychol. 22: 119-149.

Tsukada H. 1997. A division between foraging range and territory related to food distribution in the red fox. J. Ethol. 15: 27-37.

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

Vander Wall S.B. 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. Oikos 74: 533-537.

Vander Wall S.B. 1998. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. Ecology 79: 233-241.

Vander Wall S.B. and Jenkins S.H. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behav. Ecol. 14: 656-667.

Vander Wall, S.B. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). - Behav. Ecol. 11: 544-549.

Warburton K., Retif S. and Hume D. 1998. Generalist as a sequential specialist: diets and prey switching in juvenile silverperch. Environ. Biol. Fishes 51: 445-454.

White G.C. and Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study (Suppl.) 46: 120-139.

Williams B.K., Nichols J.D. and Conroy M.J. 2002. Analysis and management of animal populations. Academic Press, SanDiego.

Willson M.F., Gende S.M. and Bisson P.A. 2004. Anadromous fishes as ecological links between ocean, fresh water, and land. In Polis G.A., Power M.E. and Huxel G.R. (eds). Food webs at the landscape level. University of Chicago Press.

APPENDIX A: HABITAT ALTERATION BY GEESE AT A LARGE ARCTIC GOOSE COLONY – CONSEQUENCES FOR LEMMINGS AND VOLES

A.1 Introduction

Heavy grazing by herbivores can have dramatic impact on distribution and abundance of plants (Crawley 1983). For example, recent increases in populations of arctic-nesting geese have resulted in considerable habitat alterations in some parts of the arctic (Ganter 1996, Jefferies et al. 2004, Abraham et al. 2005, Alisauskas et al. *in press*). However, the influence of these habitat alterations on other animals is poorly understood (but see Rockwell et al. 2003 for negative effects on savannah sparrows). Ross's and lesser snow geese nest at large arctic colonies where they feed predominantly on graminoid plants such as grasses and sedges (Ryder and Alisauskas 1995, Mowbray et al. 2000). There is often considerable niche overlap between geese and small mammals such as lemmings and voles (Gauthier et al 1996). There is, thus, potential for resource competition among these herbivores (see Bêty et al. 2002 for apparent competition among geese and small mammals). In this study I examined how grazing by Ross's and lesser snow geese at a large goose colony affected abundance and distribution of small mammals and plants.

A.2 Methods

Small mammal abundance and aboveground biomass of plants was monitored in two 1×1 km study areas in the goose colony at Karrak Lake and in two 1×1 km study areas outside the colony. Study areas were distributed systematically around the southern and original part of the colony with outside areas located outside the influence of nesting geese (>5 km from the edge of the colony) while assuring that these areas could be reached by foot. Location of study areas were selected from the Universal Transverse Mercator (UTM) grid system on a 1:50,000 map; the northern study area in the colony was located 9 km north of the southern study area in the colony and the two study areas outside the colony were located 13 km west and east of the southern study area in the colony. The main extent of the colony was similar among years even though

there tended to be a north and westward expansion of the colony during the study (Alisauskas, unpublished data). Study areas inside and outside the colony were similar in topography and geography.

A.2.1 Monitoring of Small Mammal Abundance

Small mammal abundance was monitored at three trap-lines of snap-traps in each study area in early to mid July. Trap-lines were established in habitats preferred by small mammals following Banfield (1974); two trap-lines in each study were established on high dry ground (called upland hereafter) and one trap-line in each study area was established in wet lowland tundra (called lowland hereafter). Trap-lines in uplands were established on the two hills closest to the center of each study area (selected from 1:50,000 maps) whereas trap-lines in lowlands were established at the wet lowland closest to the center of each study area (wet lowland areas were not indicated on 1:50,000 maps so these were identified in the field).

Trap-lines consisted of 25 trap-stations, spaced 10 m apart, and with one snap-trap within 1 m of each trap-station following Shank (1993). Trap-lines ran for two consecutive nights and I converted data to number of captures per 100 trap-nights for each trap-line. I subtracted 0.5 trap-nights for each trap that was snapped without capture to account for variation in sampling effort following Beauvais and Buskirk (1999). Microhabitat for each trap-station was determined following McLandress (1983). Small mammal abundance could not be monitored in one study area outside the colony in 2004 because of grizzly bear activity.

A.2.2 Sampling of Aboveground Biomass of Plants

Aboveground biomass of plants (called plant biomass hereafter) was sampled by taking core samples (75 mm in diameter) following Jefferies and Abraham (1994). Three core samples were taken at each trap-line in lowland areas and 2 core samples at each trap-line in upland areas; sample-sites were standardised as mossy tussocks in lowland areas and mixed habitat in upland areas following habitat classifications by McLandress (1983). Sample sites were spaced evenly along trap-lines and core samples

were taken at the center of the first tussock north of selected trap-stations in lowland areas and 0.4 m north of selected trap-stations in upland areas (core samples were taken south of sample sites if there was bedrock in the northerly direction). Lowland areas were sampled in 2001 and upland areas were sampled in 2002 to allow for processing of samples within 24 hours (processing of samples was very time consuming under primitive field-conditions). I was interested in differences in aboveground biomass inside and outside the colony, not between lowland and upland areas, so sampling in different years did not affect analyses.

Vegetation samples were processed within 24 hours of collection following Jefferies and Abraham (1994). Vegetation was cut at soil level for upland samples and at moss level for lowland samples. Plants were sorted into live and dead material of graminoid plants, lichen, moss (phylum Bryophyta), and species level for shrubs and herbaceous plants. Vegetation samples were dried in the field and then re-dried to constant mass (±0.001 g) at $70^{o}C$ in the laboratory.

A.2.3 Community Similarity

I calculated proportional similarity (PS) of plant communities based on aboveground biomass by [PS = $1-(\Sigma|p_i - q_i|)/2$] where p_i = the proportion of aboveground biomass of species i in the first sample and q_i = the proportion of aboveground biomass of species i in the second sample (Brower et al. 1997:189). I calculated proportional similarity both among and within study areas inside and outside the colony. I also calculated proportional similarity with and without graminoid plants to examine how grazing by geese affected community similarity.

A.2.4 Statistical Analyses

I examined how small mammal abundance varied inside and outside the colony and among years by two-way ANOVA where data were arranged by capture data per trap-line, type of area (i.e. inside versus outside the colony), and year (Proc. GLM, SAS Institute Inc., 1990). I performed analyses separately for upland and lowland areas ($n =$ 38 trap-lines from upland and 19 trap-lines from lowland areas). There was

considerable heterogeneity in the variance for captures of small mammals so I log-transformed data as this provided the best approximation of equal variance (Zar 1999). I derived 4 candidate models for small mammal abundance where we, *a priori*, included models that ranged from no variation among areas and years to including both these variables. I used variation around the grand mean as the null model (i.e. no effect of the variables examined). I used Akaike's information criterion (AIC) with small-sample adjustment (AIC_C) to select the model that best explain variation in small mammal abundance (Burnham and Anderson 1998). Further, I selected the model with the lowest AIC_C value as the best model and considered models within 2 AIC_C units to be of similar quality (Burnham and Anderson 1998).

I examined how plant biomass varied inside and outside the colony by ANOVA where data were arranged by biomass and type of area (i.e. inside versus outside the colony) (Proc GLM, SAS Institute Inc. 1990). I performed analyses separately for upland ($n = 16$) and lowland areas ($n = 12$). Further, I performed these analyses with and without graminoid plants to examine how grazing by geese affected plant biomass. I derived 2 candidate models for plant biomass where we, *a priori*, included one model with variation among areas and one model without variation among areas. I used variation around the grand mean as the null model (i.e. no effect of nesting geese). I used Akaike's information criterion with small-sample adjustment (AIC_C) to select the model that best explain variation in small mammal abundance as above.

A.3 Results

Twenty-three red-backed voles, 15 collared lemmings, and 3 brown lemmings were captured in 2744.5 trap-nights during this study ($\bar{x} = 1.5$ captures per 100 trap-nights, range = 0-11 captures per 100 trap-nights). Capture rates were 1.1 red-backed voles, 0.5 collared lemmings, and 0 brown lemmings per 100 trap-nights in upland areas and 0.2 red-backed voles, 0.7 collared lemmings, and 0.3 brown lemmings per 100 trap-nights in lowland areas. Further, brown lemmings were captured only outside the colony. In fact, only 1 brown lemming has been capture in the colony in 7,091 trap-nights from 1994 to 2004 (Alisauskas, unpublished data).

Model {Inside vs. Outside Colony} described variation in small mammal abundance in lowland areas better than other models and accounted for 81% of the cumulative model weight (Table A.1). Specifically, small mammal abundance was higher in lowland areas outside the colony than in lowland areas inside the colony; mean small mammal abundance was 2.6 and 0.2 captures per 100 trap-nights in each area, respectively (range = 0-11 and 0-2.0 captures per 100 trap-nights in each area, respectively). Model *no effect*, in contrast, described variation in small mammal abundance in upland areas better than other models and accounted for 67% of the cumulative model weight (Table A.1). Specifically, small mammal abundance was similar in upland areas inside and outside the colony; mean small mammal abundance was 1.6 and 2.4 captures per 100 trap-nights in each area, respectively (range = 0-10 and 0-10 captures per 100 trap-nights in each area, respectively).

Model {Inside vs. Outside Colony} described variation in plant biomass in lowland areas better than the *no effect* model and accounted for 95% of the cumulative model weight (Table A.2). Specifically, plant biomass was higher in lowland areas outside the colony than in lowland areas inside the colony (Table A.3); mean biomass of plants was 380 and 83 g/m^2 in each area, respectively (range = 190-640 and 10-210 g/m^2 in each area, respectively). This was driven by virtually complete removal of graminoid plants inside the colony. Biomass of plants other than graminoids, in contrast, was similar in lowland areas inside and outside the colony and was illustrated by the *no effect* model described variation in plant biomass better than model {Inside vs. Outside Colony} when graminoid plants were not included (model weight = 0.79, Table A.2). Model {Inside vs. Outside Colony} described variation in plant biomass in upland areas better than the *no effect* model and accounted for 85% of the cumulative model weight (Table A.2). Specifically, plant biomass was greater in upland areas outside the colony than in upland areas inside the colony (Table A.3); mean biomass of plants was 300 and 130 g/m^2 in each area, respectively (range = 30-510 and 10-350 g/m^2 in each area, respectively). This was largely the result of greater abundance of lichens and mountain avens outside the colony. Graminoid plants were rare in upland areas both inside and

Table A.1. Model selection for variation in small mammal abundance in lowland and upland areas inside and outside the goose colony at Karrak Lake in 2000 to 2004. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), model weights (w_i), and coefficient of determination (r^2). I used variation around the grand mean as the null model (i.e. no effects of the variables examined). AIC_c values for the top model was 40.31 and 84.92 in lowland and upland areas, respectively.

	K	Δ_i	w_i	r^2
Lowland areas:				
goose effect[1]	3	0	0.81	0.26
no effect	2	2.99	0.18	na
year effect	6	11.54	<0.01	0.26
year & goose effect	8	15.70	<0.01	0.49
Upland areas:				
no effect	2	0	0.67	na
goose effect[1]	3	1.66	0.29	0.02
year effect	6	6.01	0.03	0.11
year & goose effect	8	11.71	<0.01	0.12

[1] goose effect refers to inside versus outside the colony

Table A.2. Model selection for variation in aboveground biomass of plants in lowland and upland areas inside and outside the goose colony at Karrak Lake in 2000 to 2004. Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K), model weights (w_i), and coefficient of determination (r^2). I used variation around the grand mean as the null model (i.e. no effects of the variables examined). AIC_c values for the top model was -3.63, -27.14, -12.67, and -12.79 for analyses with and without graminoid plants in lowland and upland areas, respectively.

Model	K	Δ_i	w_i	r^2
Lowland areas:				
All plants:				
goose effect[1]	3	0	0.95	0.55
no effect	2	5.94	0.05	na
No graminoid plants:				
no effect	2	0	0.79	na
goose effect[1]	3	2.64	0.21	0.08
Upland areas:				
All plants:				
goose effect[1]	3	0	0.85	0.34
no effect	2	3.52	0.15	na
No graminoid plants:				
goose effect[1]	3	0	0.85	0.34
no effect	2	3.47	0.15	na

[1] goose effect refers to inside versus outside the colony

Table A.3. Aboveground biomass of plants inside and outside the large goose colony at Karrak Lake in the summers of 2001 and 2002. I standardised sample sites as mossy tussocks in lowland areas and mixed habitat in upland areas where habitat classification followed those by McLandress (1983). Plants were sampled 8-15 July in 2001 and 12-21 July in 2002.

Habitat & Location	Type of plant (dry weight in g/m^2 ± 95% C.I.)													
		Woody plants							**Annual herbs**			**Non-vasc. plants**		
	graminoid plants	cran-berry	crow-berry	arctic heather	Labrador tea	bill-berry	willow	mountain aven	bog Rose-Mary	ragwort	unknown herb	lichen	moss	total biomass
Lowland Area														
outside	330[1] ± 230	17 ± 34	1.1 ± 2.9	0 ± 0	4.5 ± 12	11 ± 29	3.0 ± 6.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	13 ± 25	na	380 ± 200
colony	0[2] ± 0[2]	34 ± 29	0 ± 0	1.5 ± 1.5	33 ± 61	0 ± 0	0 ± 0	0 ± 0	1.5 ± 3.9	0 ± 0	0.8 ± 1.9	13 ± 12	na	83 ± 74
Upland Area														
outside	1.4[1] ± 2.7	8.5 ± 9.0	0 ± 0	16 ± 10	41 ± 58	0 ± 0	0 ± 0	53 ± 85	0 ± 0	0 ± 0	1.7 ± 4.0	140 ± 110	32 ± 70	300 ± 120
colony	0 ± 0	45 ± 36	0 ± 0	1.1 ± 1.1	23 ± 29	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.1 ± 2.7	0 ± 0	50 ± 51	8.8 ± 14	130 ± 90

[1] 68 and 80% of the graminoid plants were brown/dead graminoid plants in lowland and upland areas outside the colony, respectively

[2] trace amounts to small to register on the scale

outside the colony and omission of graminoid plants from the analyses did not alter the results for plant biomass in upland areas (Tables 2 and 3).

Proportional community similarity inside and outside the colony was 0.09 and 0.63 for lowland and upland areas, respectively (Table A.4). However, proportional community similarity of lowland areas inside and outside the colony increased to 0.58 when graminoid plants were not included (i.e. 58% similarity among other plants in lowland areas inside and outside the colony). Proportional community similarity was generally greater between than within study areas inside and outside the colony when graminoid plants were not included (Table A.4); plant communities were, thus, similar among study areas inside and outside the colony for plants other than graminoids.

A.4 Discussion

Heavy grazing by geese has resulted in substantial habitat alteration in some parts of the arctic (Ganter 1996, Jefferies et al. 2004, Abraham et al. 2005). However, the influence of these habitat alterations on other animals is poorly understood. This study showed that heavy grazing by geese had a negative impact on distribution and abundance of small mammals in the colony at Karrak Lake. In fact, geese removed virtually all graminoid plants in lowland areas in the colony (see Alisauskas et al. *in press* for similar results) which, in turn, coincided with a dramatic reduction in small mammal abundance in lowland areas in the colony. A similar reduction in small mammal abundance could, alternatively, have resulted from apparent competition where geese elevated predator abundance above that outside the colony (see Chapter 6 for such effect on arctic foxes) and thereby increased their predation pressure on small mammals (see Bêty et al. 2002 for apparent competition among geese and small mammals). However, I suggest that the reduction in small mammal abundance was driven primarily by habitat alteration rather than apparent competition as small mammal abundance in the colony was reduced only in lowland areas and not in upland areas.

Small mammals can have a large indirect impact on nesting performance of birds in that predators often switch from small mammals to bird prey in years when small mammals are scarce (Summers 1986, Bêty et al. 2001). This study, in contrast,

Table A.4. Proportional community similarity in aboveground biomass of plants with and without graminoid plants inside and outside the goose colony at Karrak Lake in 2001 and 2002.

Community comparisons	Proportional Community Similarity		Sample size
	incl. graminoids	excl. graminoids	
Among goose and non-goose nesting areas:			
lowland areas inside and outside the colony	0.09	0.58	12
upland areas inside and outside the colony	0.63	0.63	16
within goose and non-goose nesting areas:			
lowland areas outside the colony	0.71	0.84	6
lowland areas inside the colony	0.40	0.40	6
upland areas outside the colony	0.44	0.45	8
upland areas inside the colony	0.46	0.46	8

showed that grazing by geese can have strong impact on small mammal abundance through resource consumption and habitat alteration. There is, thus, evidence for complex interactions among these herbivores even in a relatively simple ecosystem dominated by geese, small mammals, and arctic foxes. Part of this complexity may be related to colony size and the relative abundance of these herbivores. Specifically, small mammal abundance and predator switching appears to influence nesting performance only at small colonies (Raveling 1989) whereas heavy grazing by geese and reduction in small mammal abundance appears to occur only at large colonies (e.g. this study). The dominating process may, thus, switch from top-down to bottom-up effects as colony size increases.

A.5 Literature Cited

Abraham K.F., Jefferies R.L. and Alisauskas R.T. 2005. The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biol. 11: 841-855.

Alisauskas R.T., Charlwood J.W. and Kellett D.K. Vegetation correlates of nesting history and density by Ross's and lesser snow geese at Karrak Lake, Nunavut. Arctic: *in press*.

Banfield A.W.F. 1974. The mammals of Canada. National Museum of Natural Sciences, National Museums of Canada, Canada.

Beauvais G.P. and Buskirk S.W. 1999. Modifying estimates of sampling effort to account for sprung traps. Wildl. Soc. Bull. 27: 39-43.

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

Bêty J., Gauthier G., Korpimäki E. and Giroux J.F. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J. Anim. Ecol. 71: 88-98.

Brower J.E., Zar J.H. and von Ende C.N. 1997. Field and laboratory methods for general ecology. 4th Ed. WCB McGraw-Hill, Boston. 273 p.

Burnham K.P. and Anderson D.R. 1998. Model selection and inference: a practical information- theoretic approach. Springer, New York.

Crawley M.J. 1983. Herbivory: the dynamics of animal-plant interactions. University of California Press, Berkeley, CA.

Ganter B., Cooke F. and Mineau P. 1996. Long-term vegetation changes in a snow goose nesting habitat. Can. J. Zool. 74: 965-969.

Gauthier G., Rochefort L. and Reed A. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. Geosci. Can. 23: 253-259.

Jefferies R.L. and Abraham K.F. 1994. Goose foraging and its effects on plant communities: observations and recording procedures. University of Toronto, Ontario Ministry of Natural Resources, and Canadian Wildlife Service, Toronto, Ontario. 20 pp.

Jefferies R.L., Henry H.A. and Abraham K.F. 2004. Agricultural nutrient subsidies to migratory geese and change in arctic coastal habitats. *In* Polis G.A., Power M.E. and Huxel G.R. (eds). Food webs at the landscape level. University of Chicago Press.

McLandress M.R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and lesser snow geese. Auk 100:335-343.

Mowbray T.B., Cooke F. and Ganter B. 2000. Snow goose (*Chen caerulescens*). *In* the Birds of North America 514 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Raveling D.G. 1989. Nest-predation rates in relation to colony size of black brant. J. Wildl. Manage. 53: 87-90.

Rockwell R.F., Witte C.R., Jefferies R.L. and Weatherhead P.J. 2003. Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony. Ecoscience 10: 33-37.

Ryder J.P. and Alisauskas R.T. 1995. Ross' goose (*Chen rossi*). *In* the Birds of North America 162 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

SAS. 1990. SAS user's guide. Version 6. SAS Institute Inc. Cary, North Carolina.

Shank C.C. 1993. The Northwest Territories small mammal survey: 1990-1992. Department of Renewable Resources, Government of Northwest Territories, Yellowknife, NWT, Manuscript Report No. 72.

Summers R.W. 1986. Breeding production of dark-bellied brent geese Branta bernicla bernicla in relation to lemming cycles. Bird Study 33: 105-108.

Zar J.H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Inc., NJ.