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Spatial and Temporal Patterns in Arctic Fox Diets at a Large Goose Colony

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ABSTRACT. We studied diets of arctic foxes (*Alopex lagopus*) associated with a large nesting colony of lesser snow and Ross's geese in the central Canadian Arctic. From 15 May to 5 August 1994 and from 18 May to 7 August 1995, we examined arctic fox diets using frequency of occurrence of prey remains in faeces. Most scats (n = 791 of 817, or 97%) were collected from den sites. Scats from foxes with dens inside the goose colony contained eggs more frequently than those of foxes that depended more on small mammals outside the colony. Foxes were opportunistic in their feeding habits, as prey use was linked to the nesting cycle of geese, coinciding to periods of egg, goose, and gosling abundance. However, diets in spring, i.e., before geese arrive, reflected the importance to arctic foxes of caching geese and eggs from the previous summer at Karrak Lake. We suggest that large increases in nesting populations of lesser snow and Ross's geese may have beneficial implications for arctic fox populations over a large area.

Key words: arctic fox, *Alopex lagopus*, diet, food caching, Queen Maud Gulf Bird Sanctuary, Ross's goose, *Chen rossii,* lesser snow goose, *Chen caerulescens*

RÉSUMÉ. On a étudié le régime alimentaire du renard arctique (*Alopex lagopus*) associé à une vaste colonie nicheuse de petites oies blanches et d'oies de Ross dans le centre de l'Arctique canadien. Du 15 mai au 5 août 1994, et du 18 mai au 7 août 1995, on a examiné le régime alimentaire du renard arctique en utilisant la fréquence de l'occurrence de restes de proies dans les crottes. La plupart (n = 792 sur 817, ou 97 p. cent) ont été recueillies sur les sites des terriers. Les crottes des renards dont le terrier se trouvait à l'intérieur de la colonie d'oies contenaient plus souvent des oeufs que celles des renards dont le terrier était situé en dehors de la colonie et qui dépendaient plus des petits mammifères. Les renards se montraient opportunistes dans leurs habitudes alimentaires, l'utilisation des proies étant liée au cycle nicheur des oies et coïncidant avec des périodes d'abondance d'oeufs, d'oies et d'oisons. Toutefois, les régimes alimentaires au printemps, c'est-à-dire avant l'arrivée des oies, reflétaient l'importance pour les renards de Karrak Lake des réserves d'oies et d'oeufs de l'été précédent. On suggère que de fortes augmentations dans les populations nicheuses de la petite oie blanche et de l'oie de Ross pourraient avoir des retombées bénéfiques à grande échelle sur les populations de renards arctiques.

Mots clés: renard arctique, *Alopex lagopus,* régime alimentaire, mise en réserve de nourriture, refuge d'oiseaux du golfe Reine-Maud, oie de Ross, *Chen rossi,* petite oie des neiges, *Chen caerulescens*

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INTRODUCTION

The ability to use a variety of foods, learn new hunting skills, and exploit local variation in prey availability is crucial to survival of arctic fox (*Alopex lagopus)* in the circumpolar Arctic (Prestrud, 1992). Arctic foxes are generalist carnivores that feed opportunistically and scavenge (Braestrup, 1941; Elton, 1942; Shibanoff, 1958; Macpherson, 1969; Prestrud, 1992). They depend heavily on small mammals, such as lemmings (*Lemmus* and *Dicrostonyx*) (Braestrup, 1941; Elton, 1942; Shibanoff, 1958; Chesemore, 1968; Macpherson, 1969; Speller, 1972; Kennedy, 1980; Smits et al., 1989), in areas where such prey are abundant. However, when lemming numbers are low, nesting avian migrants (waterfowl and seabirds), and their eggs and young may constitute a large proportion of arctic fox diets (Larson, 1960; Chesemore, 1968; Macpherson, 1969; Stephenson, 1970; Speller, 1972; Eberhardt, 1977; Garrott, 1980; Burgess, 1984; Fay and Stephenson, 1989). Stickney (1991) found that arctic foxes switched from microtines to goose eggs when migratory birds began to nest. Most eggs taken (80%; Stickney, 1991) are cached for future consumption (Macdonald, 1976; Smith and Reichman, 1984). Arctic foxes may use prey cached during the previous summer (Braestrup, 1941; Fay and Stephenson, 1989; Prestrud, 1991; Frafjord, 1993), and this extra food can enhance their chances of winter survival (Fay and Stephenson, 1989).

Our objectives in studying food habits of this population from scat remains were to determine 1) the composite diets of foxes with dens inside and outside a large mixed colony of

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Ross's (*Chen rossii*) and lesser snow geese (*Chen caerulescens*), 2) how fox diets change from phase to phase of the nesting cycle of geese, and 3) the importance of cached avian prey remains in the spring diets of foxes.

STUDY AREA

Karrak Lake, Northwest Territories (67°14′N, 100°15′W) is located within the Queen Maud Gulf Bird Sanctuary (QMGBS). The goose colony at Karrak Lake is the largest known colony in the QMGBS, consisting of 396 000 nesting Ross's and lesser snow geese in 1994 and 495 000 in 1995 (Alisauskas et al., 1997). In those years, the colony included 48.6 and 62.6 km^2, respectively, of terrestrial habitat, in a heterogeneous environment with rock outcrops, sedge meadows, and tundra ponds, as described by Ryder (1972). Terrestrial mammals seen at the study area included small mammals (*Lemmus sibiricus, Dicrostonyx torquatus,* and *Clethrionomys rutilus*), barren-ground caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), arctic wolf (*Canis lupus*), barren-ground grizzly bear (*Ursus arctos*), and wolverine (*Gulo gulo*). In addition, various numbers of avian migrants, including arctic tern (*Sterna paradisaea*), glaucous (*Larus hyperboreus*) and herring gulls (*L. argentatus*), oldsquaw (*Clangula hyemalis*), and king eider (*Somateria spectabilis*) ducks, Canada geese (*Branta canadensis*), sandhill crane (*Grus canadensis*), jaegers (*Stercorarius* species), rock ptarmigan (*Lagopus mutus*), and passerine species nest in the Karrak Lake region.

METHODS

Fox scats were collected from 15 May to 5 August 1994 and from 18 May to 7 August 1995. Fresh scats, dark and glossy in appearance (Macpherson, 1969), were collected opportunistically from captured fox (Bantle, unpubl. data 1994) and during regular weekly visits to den sites (Fig. 1) both inside and outside the colony. The boundary of the colony was estimated from aerial surveys; densities of nesting birds were lower at the boundary than at the centre (Alisauskas, unpubl. data 1994, 1995). A scat was considered to be either the entire excrement or a portion thereof defecated by any arctic fox (Chesemore, 1968). In 1994, 762 scats were collected during regular visits to seven active dens (three outside and four inside the goose colony), with most visits in July. In 1995, fewer dens contained fox families, and only 26 scats were collected opportunistically or from trap sites (Bantle, unpubl. data 1995) and 29 from visits to dens with nonbreeding foxes (Bantle, unpubl. data 1995). Scats were placed in plastic bags, labelled by date and location, and coded according to one of four periods of collection corresponding to phases of goose nesting chronology: 1) before arrival of geese (23–31 May); 2) laying and incubation of eggs (21 June–10 July); 3) gosling hatch and exodus from the colony (11–20 July); and 4) brood rearing after exodus of geese from the colony (21 July–10 August). Although dens were searched regularly, and scats were collected opportunistically, no scats were recovered during nest initiation and laying (1–20 June). Goose nesting at Karrak Lake is quite synchronous, with 50% of geese initiating nests within a 5-day period, and all nest initiation being complete within a 14-day range (Ryder, 1972; R. Alisauskas, unpubl. data 1994, 1995).

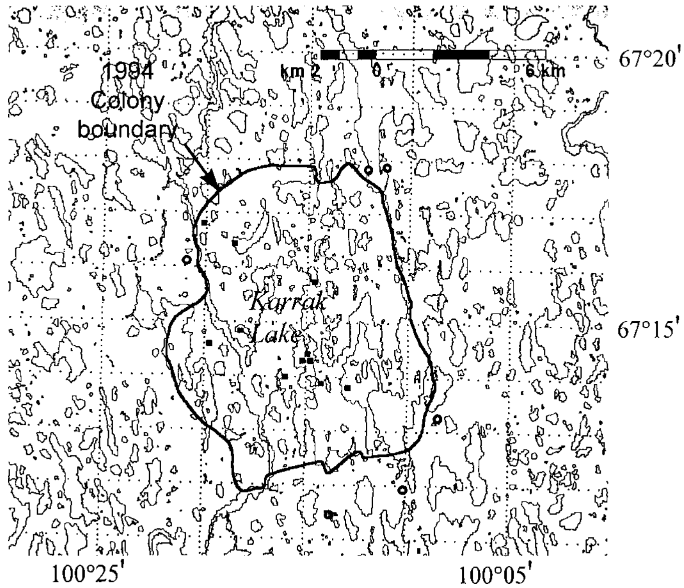

FIG. 1. Map showing arctic fox den locations inside (■) and outside (❍) the Karrak Lake goose colony, Northwest Territories (1994).

In the laboratory, scats were dried in an oven for a minimum of three hours at 90°C, to prevent human exposure to eggs of the tapeworm *Echinococcus multilocularis.* Scats were broken apart by hand, and the frequencies of occurrence of small mammal (hair, teeth, and jaws), egg (eggshell fragments), goose (feathers, bones, and gosling down), and other prey (caribou, muskox, and insect) remains were calculated. No attempt was made to distinguish between scats of adult and young fox. Plant remains and gravel were rare in scats and so were excluded from analysis. The frequency of occurrence of each prey type was calculated for each den during each period of collection corresponding to goose-nesting chronology.

STATISTICAL ANALYSES

Frafjord (1993) found statistical dependencies in the composition of scats from the same dens and large differences in diets between different fox families (litters) denning near each other. Therefore, we treated each den, rather than each scat, as a sampling unit for diet analysis. Frequencies of occurrence for each prey type were calculated for each den site, partitioned by location and period, and assigned ranks. A two-way ANOVA using ranked data (Conover and Iman, 1981; PROC GLM, SAS Institute Inc., 1990) was used to test if percent occurrence of small mammal, egg, goose, or other prey remains in scats was independent of period (before arrival of geese, laying and incubation of the eggs, gosling hatch and exodus, and brood rearing after exodus of geese) or location (outside vs. inside the colony, Fig. 1). We were interested in composite diets of foxes, so the number of scats collected at each den site was used to weight the importance of each den. Composite diets weighted by number of scats are more relevant to assessing impacts on nesting geese than fox diets simply averaged per den, because by weighting diets, we can represent dens with variable numbers of pups in the correct proportion to their total consumption of prey. The number of pups per den was unknown, but the number of scats found near dens was assumed to be proportional to the number of foxes occupying each den. Failure to weight average den diets by number of scats causes the analysis to underrepresent dens with many pups and overestimate the importance of dens with few pups. Student-Newman-Keuls *a posteriori* contrasts were done for diets where spatial, temporal, or interaction effects were significant. A comparison of diets between 1995 and 1994 (dens pooled) failed to show significant differences (PROC CATMOD, SAS Institute Inc., 1990); therefore data for the two years were pooled.

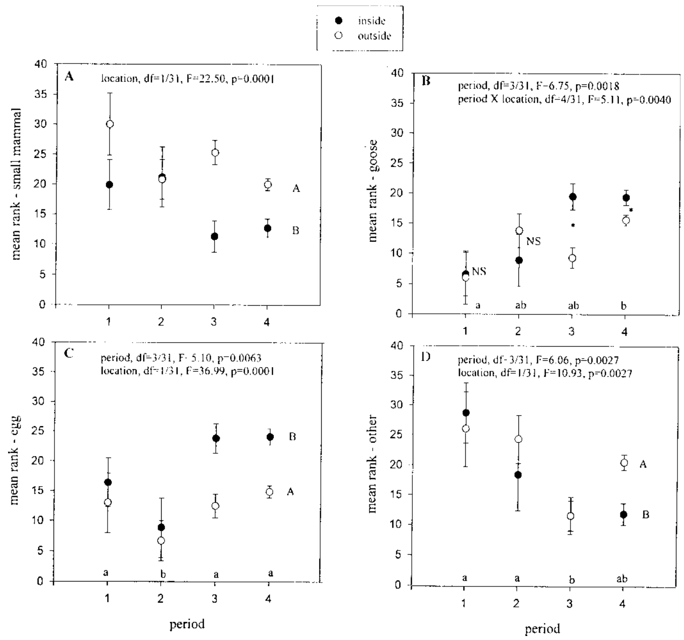

FIG. 2. Mean percent of arctic fox scats collected at dens that contained A) small mammal, B) goose, C) egg, and D) other remains, inside and outside the colony, during four periods: 1) before the arrival of the geese; 2) laying and incubation; 3) gosling hatch and exodus; and 4) brood rearing after the exodus of geese at Karrak Lake, Northwest Territories. A two-way ANOVA was done on ranked data using dens visited at each period as sampling units, weighted by the number of scats collected at each den site per period (See Methods). Letters along the x-axis correspond to periods during which fox diets were different (Student-Newman-Keuls test, $p < 0.05$); different upper case letters along the right side of each graph correspond to differences ($p < 0.05$) in diets inside and outside the colony. For interaction effects between period and location, asterisks denote significant and NS denote nonsignificant (Student-Newman-Keuls test, $p < 0.05$) spatial differences by goose chronology.

RESULTS

Arctic fox diets showed significant spatial and temporal variation during the study (Fig. 2). Outside the colony, geese and small mammals formed the major food of arctic foxes throughout all periods (Table 1). Geese became consistently more important components of arctic fox diets from the time of laying and incubation until the brood-rearing geese left the colony, while small mammals were most important before the arrival of the geese. Occurrence of eggs was low and stable during the study. Caribou and insect remains were found in only 4% of scats, most of which were collected before the geese arrived.

Inside the colony, goose carcasses and goose eggs were major foods of arctic foxes throughout all periods (Table 1, Fig. 2). Geese and eggs were most prevalent from gosling hatch and exodus until brood rearing. Small mammals, the next most important prey item in arctic fox diets inside the colony, were prominent in scat remains only before the arrival of the geese. Other prey remains, including caribou and muskox, were most common then as well.

The occurrence of small mammal, egg, and other prey items varied significantly between scats collected inside and outside the colony (Fig. 2). Small mammals occurred more often in fox scats outside the colony, while eggs occurred more often in scats found inside the colony (Table 1, Fig. 2). There was no difference in occurrence of geese in scats found inside or outside the colony (Table 1, Fig. 2).

Goose prey varied significantly with the interaction of period and location in arctic fox diets (Table 1). In general, goose items became more prevalent in scats as goose nesting progressed, but compared to arctic foxes inside the colony, those outside relied less on geese during gosling hatch and exodus (df = 1/7, F = 15.2, $p = 0.008$) and brood rearing (df = 1/10, F = 5.27, $p = 0.047$; Fig. 2).

DISCUSSION

Arctic foxes at Karrak Lake are opportunistic foragers, judging from their diet shift during the nesting cycle of geese. This conclusion generally agrees with earlier studies on arctic fox food habits (e.g., Chesemore, 1968; Frafjord, 1993). The importance of geese in fox diets has been noted in various studies (e.g., Thompson and Raveling, 1987; Stickney, 1991; Syroechkovskiy et al., 1991; Prestrud, 1992). Availability of geese, their eggs, and their young caused a significant shift in the diet of arctic foxes at Kokechik Bay, in Alaska (Stickney, 1991), regardless of the state of small mammal populations (Anthony et al., 1991) or the breeding status of foxes (Stickney, 1989). Thus, birds, their eggs, and their young may be preferentially chosen over small mammals (Stickney, 1991).

Before geese arrived to nest, arctic fox diets consisted primarily of small mammals outside the colony and small mammals and other prey (most importantly caribou) within the colony. However, the presence of egg and goose remains in scats during this period may suggest the importance of these prey items to arctic foxes during the period before goose arrival. In addition, the fact that eggs and geese contain a smaller proportion of indigestible material than small mammals (Garrott and Eberhardt, 1987) may result in underestimates of their frequency of occurrence in faecal remains.

TABLE 1. Number (#) and frequency of occurrence (%) of prey remains in arctic fox faeces from dens outside and inside the colony at Karrak Lake, Northwest Territories.

Period* (date)	# Scats	Small mammal #	Small mammal %	Egg #	Egg %	Goose #	Goose %	Other #	Other %
Dens Outside the Colony:									
Before arrival of geese (23–31 May)	18	17	94	2	11	3	17	2	11
Laying and incubation of eggs (21 June–10 July)	36	16	44	2	6	26	72	1	3
Gosling hatch and exodus (11–20 July)	94	56	60	10	11	59	63	0	0
Brood rearing after exodus (21 July–10 August)	364	154	42	69	19	285	78	1	0
Total	512	243	47	83	16	373	73	4	1
Dens Inside the Colony:									
Before arrival of geese (23–31 May)	43	16	37	9	21	9	21	22	51
Laying and incubation of eggs (21 June–10 July)	23	13	57	4	17	10	43	2	9
Gosling hatch and exodus (11–20 July)	62	7	11	31	50	55	89	0	0
Brood rearing after exodus (21 July–10 August)	177	23	13	87	49	158	89	1	0
Total	305	59	19	131	43	232	76	25	8

* no scats were found at dens or opportunistically during the period of nest initiation and laying (1–20 June).

Once geese began to nest, they became predominant arctic fox prey; during hatch, the diet breadth of foxes expanded to include eggs and goslings. However, arctic fox diets outside the colony, predictably, did not reflect as strong an increase in egg use. An adult arctic fox can carry only one egg or one goose carcass in its mouth at a time. A single adult or growing/grown gosling carcass offers considerably more nutrition than does an egg. Therefore, for adult foxes foraging outside the colony, energy returns would be greater per foraging trip if they chose larger prey items to carry back to young foxes at dens. In contrast, arctic foxes within the colony should not have incurred as great travel costs, and thus may have realized equal benefits whether returning to dens with eggs or with goose carcasses. Since adult arctic foxes defecate infrequently at dens (Speller, 1972), most scats collected from den sites were probably from young of the year. Therefore, adults denning outside the colony may have used the abundance of eggs for their own meals, but optimized foraging strategies by carrying entire gosling carcasses instead of eggs back to young foxes at dens.

Stickney's (1991) study of arctic fox foraging behaviour concluded that eggs were the most important prey items to arctic foxes when geese were present. Arctic foxes with dens near colonial-nesting geese may prefer goose eggs because shorter, more successful searches increase the rate of prey acquisition and reduce the costs of foraging (Stickney, 1991). Such individuals may improve their survival probability and fitness, particularly during years when small mammal density is low. Although arctic foxes may switch to more available prey during summer, small mammals are believed to be the main influence on their survival and breeding (Macpherson, 1969; Smits et. al., 1989). However, small mammals appear to be very difficult for arctic foxes to catch in winter, when voles and lemmings are protected by a covering of dense, hard snow (Fay and Stephenson, 1989). As found in this study and others (e.g., Braestrup, 1941; Stickney, 1991), eggshell fragments and goose feathers in scats during late May, before the geese arrive, suggest that the caching and scavenging done by arctic foxes may also contribute to their survival and successful breeding. Late May is the most critical time of year for arctic fox survival (Braestrup, 1941; Fay and Stephenson, 1989). Recovery of eggs from caches before geese arrive to nest and after nesting coincides with periods of low or declining prey availability (Stickney, 1991). Thus, eggs appear to be valuable resources stored for future consumption (Macdonald, 1976; Smith and Reichman, 1984), as they remain palatable after being stored for at least one winter (Stickney, 1991).

Fay and Stephenson (1989) and Prestrud (1991, 1992) concluded that caching behaviour is important to the survival of arctic foxes throughout their range. Quinlan and Lehnhausen (1982) reported the destruction of a common eider (*Somateria mollissima)* colony by a single fox estimated to have cached 500 eggs at Icy Cape, Alaska, a barrier island. Ryder (1969) suspected that abandonment of some nesting islands was a direct result of fox predation; in one instance, he documented the destruction of more than 100 nests in less than 5 hours by a single fox. Anthony et al. (1991) reported egg losses of 3000 and 11 750, respectively, from black brant (*Branta bernicla nigricans*) located at Tutakoke River and Kokechik Bay on the Yukon-Kuskokwim Delta, Alaska. Observations by Stickney (1991) indicated that most of these eggs were cached. Presumably, this strategy is selected because of extreme seasonal shifts in food at high latitudes (Braestrup, 1941; Fay and Stephenson, 1989), to create a nutritional bridge through periods of low (winter and spring) to abundant (summer) prey densities. Foxes may leave their breeding grounds in winter to search for scarce food and not return until the following denning season, when food caches may allow survival during the most critical time of year (Braestrup, 1941; Fay and Stephenson, 1989). Following winter, a certain amount of body fat is probably necessary as an energy/nutrient resource for successful reproduction in arctic foxes (Prestrud, 1991). During especially severe winters, fat content at onset of reproduction in March might be too low; hence, caches may be an important supplement to fat reserves (Prestrud, 1991), thereby influencing arctic fox reproduction. Prestrud (1991) found that a cache of 10 adult little auks (*Alle alle*) and 4 adult Brunnich's guillemots (*Uria lomvia*) contained fat comparable to the mean fat content of arctic fox in late autumn. Storage of prey during summer months for use in winter is assumed to be a common and widespread attribute of arctic fox food habits throughout their range, although it is poorly documented (Fay and Stephenson, 1989).

A comparison of arctic fox diets associated with dens inside and outside the colony at Karrak Lake revealed differences in frequencies of occurrence of small mammal, egg, and other prey remains in scats. Low prevalence of eggs in scats outside the colony was compensated for by a higher prevalence of small mammals, compared to scats within the colony. Inside the colony, arctic foxes may be affected by large-scale alteration of vegetation cover due to overgrazing by geese (Alisauskas et al., 1997), which may have reduced available forage and suitable habitat for small mammals. Other prey remains, primarily caribou, were found to be more prevalent in diets of arctic foxes denning within the colony during late May. Caribou have been noted in arctic fox diets in previous studies (e.g., Kennedy, 1980; Prestrud, 1992), but spatial variation of this food at Karrak Lake may have resulted from scavenging of the nearby carcass of a caribou that happened by chance to die within the goose colony perimeter. Goose consumption did not differ significantly between arctic foxes denning outside and inside the colony. Therefore, arctic foxes denning outside the colony must have travelled a greater distance to capture geese (see above) rather than using more available small mammal prey (as shown in spring diets). This supports Stickney's (1991) suggestion that arctic foxes preferentially choose geese over small mammals.

In summary, arctic foxes denning at or near Karrak Lake rely heavily on geese, their eggs, and their young in addition to small mammals. When goose prey items were available, arctic foxes apparently chose them preferentially over small mammals. This preference may be due to reduced foraging costs (Stickney, 1991). Furthermore, our results suggest that arctic foxes denning at or near high concentrations of nesting avian migrants cache goose prey items not needed by their young in summer and that such cached items may enhance winter survival and spring breeding. Although we studied only one goose colony in the region south of the Queen Maud Gulf, the number and size of goose colonies are growing (Alisauskas and Boyd, 1994; Alisauskas et al., 1997). Consequently, such reliance on geese may have large-scale implications for arctic fox populations in this region.

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REFERENCES

ALISAUSKAS, R.T., and BOYD, H. 1994. Previously unrecorded colonies of Ross' and lesser snow geese in the Queen Maud Gulf Bird Sanctuary. Arctic 47:69–73.

ALISAUSKAS, R.T., SLATTERY, S.M., and DIDIUK, A.B. 1997. Growth in populations of Ross' and lesser snow geese with habitat consequences at Karrak Lake. Unpubl. progress report. Available at Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Rd., Saskatoon, Saskatchewan S7N 0X4, Canada.

ANTHONY, R.M., FLINT, P.L., and SEDINGER, J.S. 1991. Arctic fox removal improves nest success of black brant. Wildlife Society Bulletin 19:176–184.

BRAESTRUP, F.W. 1941. A study on the arctic fox in Greenland (immigration, fluctuations in numbers based on trading statistics). Meddelelser øm Gronland 131. 101 p.

BURGESS, R.M. 1984. Investigations of patterns of vegetation, distribution and abundance of small mammals and nesting birds, and behavioural ecology of arctic foxes at Demarcation Bay, Alaska. M.Sc. thesis, University of Alaska Fairbanks.

CHESEMORE, D.L. 1968. Notes on the food habits of arctic foxes in northern Alaska. Canadian Journal of Zoology 46:1127–1130.

CONOVER, W.J., and IMAN, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. The American Statistician 35:124–129.

EBERHARDT, W.L. 1977. The biology of arctic and red foxes on the North Slope. M.Sc. thesis, University of Alaska Fairbanks.

ELTON, C. 1942. Voles, mice and lemmings: Problems in population dynamics. Oxford: Clarendon Press.

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, Bering Sea. Canadian Journal of Zoology 67:1986–1994.

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

GARROTT, R.A. 1980. Den characteristics, productivity, food habits and behaviour of arctic foxes in northern Alaska. M.Sc. thesis, Pennsylvania State University, University Park.

GARROTT, R.A., and EBERHARDT, L.E. 1987. Arctic fox. In: Novak, M., Baker, J.A., Obbard, M.E., and Malloch, M., eds. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, and the Ontario Ministry of Natural Resources. 394–406.

KENNEDY, A.J. 1980. Site variation in summer foods of arctic fox, Prince of Wales Island, NWT. Arctic 33:366–368.

LARSON, S. 1960. On the influence of the arctic fox, *Alopex lagopus*, on the distribution of arctic birds. Oikos 11:276–305.

MACDONALD, D.W. 1976. Food caching by red foxes and some other carnivores. Journal of Comparative Ethology 42:170–185.

MACPHERSON, A.H. 1969. The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series Number 8. 52 p.

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

———. 1992. Food habits and observations of the hunting behaviour of arctic foxes, *Alopex lagopus*, in Svalbard. Canadian Field-Naturalist 106(2):225–236.

QUINLAN, S.E., and LEHNHAUSEN, W.A. 1982. Arctic fox, *Alopex lagopus*, predation on nesting common eiders, *Somateria mollissima*, at Icy Cape, Alaska. Canadian Field-Naturalist 96:462–466.

RYDER, J.P. 1969. Nesting colonies of Ross' goose. Auk 86:282–292.

———. 1972. Biology of nesting Ross' geese. Ardea 60:185–213.

SAS INSTITUTE INC. 1990. SAS user's guide, version 6. 2 vols. Cary, North Carolina.

SHIBANOFF, S.V. 1958. Dynamics of arctic fox numbers in relation to breeding, food and migration conditions. Translation of Russian Game Reports 3. Ottawa: Department of Northern Affairs and Natural Resources. 5–28.

SMITH, C.C., and REICHMAN, O.J. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329–351.

SMITS, C.M., SLOUGH, B.G., and YASUI, C.A. 1989. Summer food habits of sympatric arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*, in the northern Yukon Territory. Canadian Field-Naturalist 103:363–367.

SPELLER, S.W. 1972. Food ecology and hunting behaviour of denning arctic foxes at Aberdeen Lake, NWT. Ph.D. thesis, University of Saskatchewan, Saskatoon.

STEPHENSON, R.O. 1970. A study of the summer food habits of the arctic fox on St. Lawrence Island, Alaska. M.Sc. thesis, University of Alaska Fairbanks.

STICKNEY, A. 1989. The foraging behaviour, habitat use and diet of arctic foxes (*Alopex lagopus*) in a goose nesting area near Kokechik Bay, Alaska. M.S. thesis, University of Alaska Fairbanks.

———. 1991. Seasonal patterns of prey availability and the foraging behaviour of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Canadian Journal of Zoology 69:2853–2859.

SYROECHKOVSKIY, Y.V., LITVIN, K.Y., and EBBINGE, B.S. 1991. Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988: Interplay of weather and arctic fox predation. Ardea 79:373–382.

THOMPSON, S.C., and RAVELING, D.G. 1987. Incubation behaviour of emperor geese compared with other geese: Interactions of predation, body size and energetics. Auk 104:707–716.