

FOODS OF ARCTIC FOXES (*ALOPEX LAGOPUS*) DURING WINTER AND SPRING IN WESTERN ALASKA

R. MICHAEL ANTHONY,* NEIL L. BARTEN, AND PAMELA E. SEISER

Alaska Biological Science Center, United States Geological Survey, 1011 East Tudor Road,
Anchorage, AK 99503

Present address of NLB: Alaska Department of Fish and Game, P.O. Box 240020,
Douglas, AK 99824-0020

Present address of PES: Alaska Cooperative Fish and Wildlife Research Unit,
University of Alaska, 209 Irving I, Fairbanks, AK 99775-7020

During 1986–1991, carcasses of 619 arctic foxes (*Alopex lagopus*) collected from local trappers and at biological field camps on the Yukon-Kuskokwim Delta in western Alaska from November through May were analyzed to determine gastrointestinal contents, age, sex, and body condition. Prey in declining order of importance were small mammals (95% tundra voles, *Microtus oeconomus*), birds, marine mammals, and fishes. Foxes with small mammal remains in their stomachs were captured farther from the Bering Sea coast (\bar{X} = 5.2 km) than those without small-mammal remains (2.8 km); foxes consuming remains of marine mammals were closer to the coast (1.9 km) than others (4.9 km). Although eggshells had a poor likelihood of occurrence in stomachs, they were found in all months and years. In 1986 and 1987, foxes consumed fewer small mammals than in other years. Mean ages of foxes captured in 1986 (3.7 years) and 1987 (3.2) were greater than in all other years (1.5). Capture of adults was more common as winter progressed. Indexes of subcutaneous fat decreased annually in April–May and were highest in 1991, when occurrence of carrion of marine mammals was highest.

Key words: Alaska, *Alopex lagopus*, arctic foxes, food habits, stomach contents

Arctic foxes (*Alopex lagopus*), which occupy varied northern, circumpolar habitats, are opportunistic predators but generally prefer arvicoline rodents (Bantle and Alisauskas 1998; Burgess 1984; Chesemore 1968; Fay and Stephenson 1989; Fine 1980; Garrott et al. 1983; Hall 1989; Kennedy 1980; Macpherson 1969; Smits et al. 1989; Speller 1972). Studies of diets of arctic foxes in regions not having small mammals describe consumption of birds and eggs, marine mammals, marine and freshwater fishes, marine and terrestrial invertebrates, reindeer (*Rangifer tarandus*), and domestic lambs (Frafjord 1995; Hersteinsson and Macdonald 1996). Prey available to arctic foxes in the

coastal, wet tundra of western Alaska are varied and abundant, especially in summer (Anthony 1997). High densities of nesting birds and fluctuating populations of rodents occurred in home ranges of foxes studied in this region in the mid-1980s (Anthony 1997). Concurrent with those studies, arctic foxes were trapped and hunted in areas near biological field camps in an attempt to improve nesting success of geese (Anthony et al. 1991), which had declined greatly in this region (Raveling 1984). From 1986 to 1991, specimens of arctic foxes were collected at those biological camps in late spring and also from local trappers during winter and spring. We used those specimens to determine important foods, body condition, and ages of arctic foxes.

* Correspondent: mike_anthony@usgs.gov

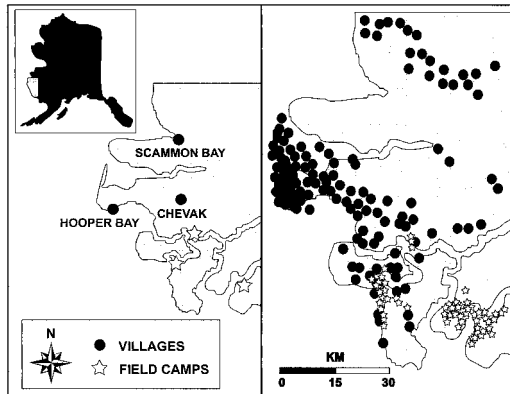


FIG. 1.—Location of study area and capture locations of arctic foxes collected by local trappers (●) and at biological camps (☆) along the coast of the Yukon-Kuskokwim Delta in western Alaska, 1986–1991.

MATERIALS AND METHODS

Study area.—The study area was located on the Bering Sea coast of the Yukon-Kuskokwim Delta in western Alaska between 61° and 62°N (Fig. 1). Plant communities and environmental factors were described elsewhere (Babcock and Ely 1994; Kincheloe and Stehn 1991; G. F. Tande and T. W. Jennings, in litt.). Foxes were collected near 3 biological field camps in April–May. Local trappers from the villages of Chevak, Hooper Bay, and Scammon Bay provided skinned carcasses of foxes taken in November–April.

Available prey.—Birds and their eggs are an important prey of arctic foxes in the coastal region of the Yukon-Kuskokwim Delta (Stickney 1991). Minimum mean density for all ducks, loons, grebes, geese, gulls, and terns for all coastal habitats combined was 10.62 nests/km² (Flint and Grand 1996; R. A. Stehn, pers. comm.). The most abundant species in descending abundance were cackling Canada geese (*Branta canadensis minima*), Pacific white-fronted geese (*Anser albifrons frontalis*), emperor geese (*Chen canagica*), northern pintail (*Anas acuta*), black brant (*Branta bernicla nigricans*), glaucous gulls (*Larus hyperboreus*), Pacific loon (*Gavia pacifica*), red-throated loon (*Gavia stellata*), mew gull (*Larus canus*), greater scaup (*Aythya marila*), arctic tern (*Sterna paradisaea*), Sabine's gull (*Xema sabini*), oldsquaw (*Clangula hyemalis*), and northern shoveler (*Anas cly-*

peata). Density estimates of 2.5 breeding pairs of shorebirds/ha—mainly sandpipers (*Calidris*), black turnstones (*Arenaria melanocephala*), and red-necked phalaropes (*Phalaropus lobatus*)—were reported by Gill and Handel (1990). Other species commonly nesting within the study area included parasitic jaegers (*Stercorarius parasiticus*), lapland longspurs (*Calcarius lapponicus*), savannah sparrows (*Passerculus sandwichensis*), and willow ptarmigans (*Lagopus lagopus*—Holmes and Black 1973; K. Kertell, in litt.). Terrestrial mammals in the area included red fox (*Vulpes vulpes*), mink (*Mustella vison*), river otters (*Lutra canadensis*), tundra hares (*Lepus timidus*), beavers (*Castor canadensis*), muskrats (*Ondatra zibethicus*), tundra voles (*Microtus oeconomus*), meadow jumping mice (*Zapus hudsonicus*), masked shrews (*Sorex cinereus*), collared lemmings (*Discrotonyx torquatus*), and brown lemmings (*Lemmus sibiricus*). Carrion of marine mammals was available from local hunting of walrus (*Odobenus rosmarus*) and spotted seals (*Phoca largha*).

Collection of specimens.—Beginning in 1986, arctic foxes were hunted and trapped in the vicinity of biological camps at which studies of nesting geese were being conducted. Locations of captures were recorded on maps (1:63,360). Harvested foxes were processed at camps to obtain teeth for aging and gastrointestinal tracts (hereafter stomachs), which were preserved in ethanol for analysis later in the laboratory. Qualitative indexes of abundance of subcutaneous and visceral fat were used to assess general condition of arctic foxes. Abundance of subcutaneous fat was placed in 6 categories similar to those used by Prestrud and Nilssen (1991). Visceral fat was independently scored in 6 categories based on amounts of fat along the spine, in the mesentery, and around the kidneys.

During 1987–1991, skinned arctic foxes were collected from trappers by village agents and shipped frozen to our laboratory for analysis. Forms completed by trappers and agents identified date of capture and location of capture marked on a map of the area. Similar to processing of specimens from camps, we assigned fat-index values and removed stomach contents from each fox. Age of foxes ≥ 1 year was estimated by examination of annual lines in the cementum of canine teeth that had been sectioned and stained (Grue and Jensen 1976); foxes < 1 year of age were identified by date of capture

and radiographic measurements of the pulp cavity of canine teeth (Bradley et al. 1981).

Locations of captures of foxes from camps and villages (Fig. 1) were converted to Universal Transverse Mercator (UTM) coordinates by overlaying maps on a digitizing tablet. Distances from capture locations to the nearest point on the coast and to the nearest village were computed to assess relations between capture location and diet, especially human refuse, marine mammals, and fishes.

Laboratory analysis.—Stomach contents were rinsed under running water in a sieve, placed in petri dishes, and air-dried in a fume hood. Dried contents were weighed on an electronic balance. All stomachs with identifiable food items were included in the analysis of food habits. Contents were identified to species based on hair, feather, or dental patterns and compared with reference samples when possible (Day 1966; Moore et al. 1974; Williamson 1951). In the analyses, we used 7 general categories: small mammals, birds, fishes, marine mammals, eggshells, human refuse, and other (insects, bone fragments, cartilage, and mollusks). Dried items were spread on a 2-cm grid to estimate proportion of each category in individual samples. Aggregate percentage (average of volumetric percentages for a given food item—Swanson et al. 1974) and percentage occurrence (proportion of all stomachs containing a given food item) were computed for analysis. We used aggregate percentage because that method, compared with aggregate volume, minimized overall importance of a large quantity of a food item in a single stomach.

Statistical analyses.—Aggregate percentages of food categories were normalized by arcsine transformation (Manly 1992) and compared for significance and interaction of variables with analysis of variance using the general linear model for unbalanced designs (GLM—SAS Institute Inc. 1988); differences among data classes were determined with Duncan's multiple-range test. Juvenile foxes were assigned an age of 1 year for purposes of computing mean ages. Linear regression analysis (SAS Institute Inc. 1988) was used to compare age classes and distance to seacoast, subcutaneous and visceral fat indexes, subcutaneous fat indexes and capture date, subcutaneous fat indexes and stomach contents, and age of foxes and capture date. Frequencies of sexes and age classes, stomachs with

or without food, and adults or juveniles trapped monthly and annually were compared with chi-square contingency tables. Scores of subcutaneous fat were compared between sexes and between age classes with the Kruskal–Wallis test (NPARIWAY—SAS Institute Inc. 1988). For all comparisons, $P < 0.05$ was considered significant.

RESULTS

Only arctic foxes collected from November through May were used in the analysis because of small samples in other months. During the 6-year collection period, 619 foxes were processed; 153 of those had empty stomachs or had nonfood items (e.g., vegetation, fox hair, wood, and soil) in their stomachs. There was no difference in frequencies of empty stomachs among years ($P = 0.84$; Table 1), sexes ($P = 0.76$; Table 2), or age classes ($P = 0.44$; Table 2), but frequencies among months were different ($\chi^2 = 20.17$, $d.f. = 6$, $P = 0.002$; Table 3). The sample of foxes with stomachs containing food items had a sex ratio of 53:47 ($n = 449$) and a juvenile:adult ratio of 62:38 ($n = 442$). Capture of adults increased ($\chi^2 = 116.5$, $d.f. = 6$, $P < 0.001$) as winter progressed (Table 3). Mean age ($\pm SE$) of foxes captured in 1986 (3.7 ± 0.3 years) and 1987 (3.2 ± 0.2) was greater ($F = 30.3$, $d.f. = 5$, $P < 0.001$) than in 1988 (2.0 ± 0.1), 1989 (1.8 ± 0.1), 1990 (1.9 ± 0.3), and 1991 (1.4 ± 0.1).

Mean distance from capture location to the nearest point on the coast was 4.5 ± 0.4 km; 74% of foxes were captured ≤ 6 km from the coast. Foxes captured in 1986 and 1987 were closer to the coast (2.1 ± 0.1 km) than other years (5.0 ± 0.1 km; $F = 9.4$, $d.f. = 1$, $P = 0.002$). There were no differences in that distance among age classes or sexes. Among food categories, foxes consuming remains of marine mammals were closer to the coast (1.9 ± 0.3 km) than those without (4.9 ± 0.4 km; $F = 6.4$, $d.f. = 1$, $P = 0.01$); samples with the other food category also were closer to the coast (2.3 ± 0.5 km) than those without (5.0 ± 0.4

TABLE 1.—Number (proportion) of stomachs with and without foods by age classes from foxes collected during 1986–1991 on the Yukon-Kuskokwim Delta, Alaska, and percentages of stomachs from collected foxes with specific food items. Different superscripts denote significance ($P \leq 0.05$) within a single type of food.

Variable	Years					
	1986	1987	1988	1989	1990	1991
Number of						
Juveniles	8 (24)	12 (22)	59 (82)	66 (73)	37 (66)	94 (70)
Adults	25 (76)	43 (78)	13 (18)	25 (27)	19 (34)	41 (30)
Empty stomachs	5 (13)	24 (29)	27 (26)	29 (24)	21 (26)	47 (24)
Food items in stomachs	33 (87)	58 (71)	75 (74)	94 (76)	60 (74)	146 (76)
Aggregate percentage (frequency of occurrence)						
Small mammals	15 ^c (26)	36 ^b (50)	65 ^a (77)	54 ^a (69)	57 ^a (68)	51 ^a (66)
Birds	18 ^{a,b} (37)	27 ^a (47)	16 ^{a,b} (28)	22 ^a (34)	7 ^b (26)	6 ^b (15)
Marine mammals	0 ^c (3)	4 ^{b,c} (7)	2 ^c (3)	9 ^{b,c} (13)	13 ^{a,b} (21)	20 ^a (26)
Fishes	8 ^a (20)	5 ^a (17)	3 ^a (12)	10 ^a (14)	5 ^a (13)	8 ^a (17)
Other	30 ^a (66)	12 ^b (25)	0 ^c (3)	8 ^{b,c} (14)	8 ^{b,c} (23)	9 ^{b,c} (17)
Human refuse	4 ^a (9)	3 ^a (8)	0 ^a (0)	4 ^a (7)	2 ^a (11)	1 ^a (8)
Eggshells	1 ^a (6)	2 ^a (10)	3 ^a (13)	3 ^a (4)	1 ^a (10)	2 ^a (6)

km; $F = 8.4$, $d.f. = 1$, $P = 0.004$). Foxes with small-mammal remains in their stomachs were captured farther from the coast (5.0 ± 0.5 km) than those without (2.3 ± 0.5 km; $F = 8.9$, $d.f. = 1$, $P = 0.003$). Mean distance from capture location to the nearest village was 20.2 ± 0.8 km. Stomachs with fishes (15.4 ± 1.4 km; $F = 8.5$, $d.f. = 1$, $P = 0.004$) and marine mammals (12.3 ± 1.7 km; $F = 15.1$, $d.f. = 1$, $P <$

0.001) were closer to villages compared with those without these foods (21.0 ± 0.9 km and 21.0 ± 0.8 km, respectively).

Small mammals (identified as tundra voles in >95% of the stomachs) were the most common food item by proportion of stomach samples and frequency of occurrence in all months (Table 3) and all years, except 1986 (Table 1). Aggregate percentage of small mammals was lower in 1986

TABLE 2.—Number (proportion) of foxes collected during 1986–1991 on the Yukon-Kuskokwim Delta, Alaska, with and without food items in stomach and aggregate percentage of foods in stomachs (frequency of occurrence) by sex and age classes.

	Sex		Age	
	Male	Female	Juvenile	Adult
Number of				
Empty stomachs	81 (24)	66 (24)	97 (26)	49 (23)
Food items in stomachs	239 (76)	210 (76)	276 (74)	166 (77)
Aggregate percentage (frequency of occurrence)				
Small mammals	52 (64)	51 (64)	50 (63)	54 (64)
Birds	15 (27)	13 (27)	15 (29)	11 (24)
Marine mammals	12 (14)	9 (15)	14 (18)	6 (9)
Fishes	10 (18)	4 ^a (14)	9 (16)	4 (16)
Other	12 (22)	8 (19)	10 (20)	10 (21)
Human refuse	2 (6)	2 (7)	2 (8)	2 (4)
Eggshells	3 (7)	1 (7)	7 (6)	2 (8)

^a Different ($P \leq 0.01$) from paired value.

TABLE 3.—Number (proportion) of foxes collected by age class, presence of food items in stomachs, and aggregate percentage of foods (frequency of occurrence) by month in 1986–1991 on the Yukon-Kuskokwim Delta, Alaska. Different superscripts denote significance ($P \leq 0.05$) within a single type of food.

	November	December	January	February	March	April	May
Number of							
Juveniles	16 (100)	56 (95)	32 (73)	82 (78)	17 (40)	14 (19)	59 (57)
Adults	0 (0)	3 (5)	12 (27)	23 (22)	26 (60)	58 (81)	44 (43)
Empty stomachs	4 (20)	7 (11)	16 (25)	27 (20)	13 (19)	25 (28)	61 (35)
Food items in stomachs	16 (80)	59 (89)	49 (75)	109 (80)	54 (81)	65 (72)	114 (65)
Aggregate percentage (frequency of occurrence)							
Small mammals	62 ^a (69)	48 ^a (96)	53 ^a (65)	6 ^a (62)	51 ^a (63)	53 ^a (68)	48 ^a (60)
Birds	48 ^a (62)	23 ^b (41)	4 ^c (12)	6 ^c (13)	14 ^{b,c} (32)	15 ^{b,c} (31)	14 ^{b,c} (33)
Marine mammals	10 ^b (13)	10 ^b (15)	7 ^b (10)	25 ^a (35)	11 ^b (17)	0 ^b (5)	2 ^b (4)
Fishes	6 ^{b,c} (6)	14 ^{a,b} (24)	21 ^a (39)	4 ^c (11)	2 ^c (7)	6 ^{b,c} (20)	2 ^c (8)
Other	0 ^a (0)	11 ^a (20)	8 ^a (14)	11 ^a (22)	8 ^a (17)	5 ^a (18)	11 ^a (25)
Human refuse	0 ^b (0)	5 ^a (14)	0 ^b (4)	1 ^{a,b} (8)	1 ^b (6)	0 ^b (5)	3 ^{a,b} (7)
Eggshells	9 ^a (13)	2 ^a (5)	1 ^a (10)	2 ^a (4)	2 ^a (20)	2 ^a (5)	2 ^a (7)

than 1987, and both years were lower than all others ($F = 7.8$, $d.f. = 5$, $P < 0.001$). Mean ranks of aggregate percentage of foods for all years occurred in the following descending order: small mammals, birds, marine mammals, fishes, other, eggshells, and human refuse. Although eggshells had a low probability of occurrence, they were found in all months and had a maximum frequency of occurrence of 20% (Table 3). Occurrence of remains of marine mammals increased during the study peaking in 1991 ($F = 3.7$, $d.f. = 5$, $P = 0.003$; Table 1). Remains of marine mammals were more common ($F = 8.5$, $d.f. = 1$, $P = 0.004$) in the stomachs of foxes captured in November–March ($\bar{X} = 16.7\%$) than those captured in April–May (1.6%). Although remains of marine mammals were more common in the stomachs of juvenile foxes (13.9%; Table 2) than those of adults (5.9%), there was no difference in consumption of marine mammals between juveniles and adults when time of capture was taken into account ($P = 0.18$). Food items in the other category were more abundant in 1986 ($F = 13.6$, $d.f. = 5$, $P < 0.001$) than in subsequent years (Table 1).

Subcutaneous fat indexes were correlated

with visceral fat indexes ($r = 0.75$; $d.f. = 1$, $P < 0.001$), but there was no relationship ($P = 0.67$) between fat indexes and total weight of stomach contents. Subcutaneous fat indexes were similar from December through March ($\bar{X} = 3.1 \pm 0.1$) and then declined in April–May (1.4 ± 0.1 ; $\chi^2 = 97.0$, $d.f. = 6$, $P < 0.001$). Subcutaneous fat indexes were the same for males and females for all months combined (2.5 ± 0.1 ; $P = 0.86$) and were similar for April and May (1.4 versus 1.3 ± 0.1 ; $P = 0.86$). Indexes were similar for reproducing females and nonreproducing females ($P \geq 0.08$) and for juveniles and adults ($P \geq 0.57$) when analyzed by time of capture. Subcutaneous fat indexes and amount of remains of marine mammals in stomachs were correlated positively ($r = 0.16$; $d.f. = 1$, $P < 0.001$).

DISCUSSION

Most studies of food habits of arctic foxes have relied on scat analysis during summer (Frafjord 1995). Our research was based on stomach contents collected during winter–spring for 6 consecutive years. Four other studies also used stomach contents to determine food habits of foxes (Fay and

Stephenson 1989; Kapel 1999; Macpherson 1969; Prestrud 1992). Although analysis of stomach contents is more representative of actual food habits than analysis of scats (Lockie 1959; Scott 1941), differences in digestion rates, methods of ingestion, biomass of individual food items, and densities of food items plus different methods of collecting foxes in this study (shooting or trapping by local inhabitants or by biologists in field camps) also result in biases in estimates of relative consumption of foods.

The proportion of empty stomachs in this study (25%) was lower than that observed in other studies of stomach contents ($\geq 40\%$ —Fay and Stephenson 1989; Prestrud 1992), which may represent our more liberal definition of stomachs with food, a more productive environment (Anthony 1997), or a higher proportion of sampled foxes taken by shooting, a common harvest method in the region of this study, rather than trapping. The high proportion of young foxes collected in early winter is consistent with the hypothesis that juveniles are more vulnerable to harvest than adults (Bradley et al. 1981; Garrott and Eberhardt 1987; Hammill 1983). This interaction of age classes and time of capture confounded interpretations of the effect of age class on diet.

Distance from capture locations to the coast for foxes with small mammals and remains of marine mammals in their stomachs is consistent with the distribution of these food items. Although some foxes may have scavenged remains of marine mammals and fishes from villages, based on the rare occurrence of human refuse in stomachs and poor relationship between refuse consumption and distance to nearest village, this population of arctic foxes was less likely to rely on anthropogenic foods than those in oil-development areas of northern Alaska (Fine 1980; Garrott et al. 1983).

Fat indexes that we estimated showed depletion of fat in April–May, similar to that quantified and discussed by Prestrud and

Nilssen (1991), indicating populations with adequate availability of food in winter and depletion of fat in spring with breeding activities. The relationship of remains of marine mammals and fat indexes, although weak, suggests the importance of these foods in maintaining condition in winter. There was no difference between fat indexes for any population of males and females, as observed by Hammill (1983) and Prestrud and Nilssen (1991). However, our qualitative estimates of fat may not have been sensitive enough to change to detect differences observed by Prestrud and Nilssen (1991). Furthermore, our results may have been influenced by low productivity in 1986 and 1987, resulting in a population of females whose fat stores were not depleted by reproduction, followed by abundant small mammals and other foods in years with more breeding females.

The high proportion of foods from the other category (largely scavenged items and invertebrates) in 1986, when small-mammal consumption was lowest, demonstrated adaptation by an opportunistic feeder like the arctic fox (Angerbjorn et al. 1994; Kapel 1999). Birks and Penford (1990) documented high occurrence of insects in the diet of foxes in Greenland in an environment with limited foods and no small mammals. Garrott et al. (1983) also observed increased occurrence of invertebrates in scats of juvenile foxes in a year with diminished numbers of small mammals. Unexpectedly, birds were not the most abundant food item in 1986; generally, birds are the 2nd most common food item after small mammals (Bantle and Alisauskas 1998; Fine 1980; Frafjord 1995; Hersteinsson and Macdonald 1996; Macpherson 1969; Smits et al. 1989). Furthermore, high rates of predation on nests in 1986 (Anthony et al. 1991; Stickney 1991) supported an expectation that consumption of birds by arctic foxes would be great at this time. However, most foxes from 1986 were collected in late spring, when availability of live birds was limited

and caches probably were depleted from use in winter.

Occurrence of eggshells in all months and all years is noteworthy because of their low probability of ingestion. Based on our observations of recovered cached eggs, foxes consuming large eggs usually break a hole in the side and eat the contents. Consequently, only a few shell fragments are consumed with the contents of each egg. Nevertheless, Bantle and Alisauskas (1998), Frafjord (1993), Garrott et al. (1983), and Kennedy (1980) documented ingestion of eggshells by arctic foxes in summer. Others have observed high rates of egg caching (Burgess 1984; Stickney 1991; Syroechkovskii 1972), but recovery of cached eggs was unknown. Our results indicate that eggs are used throughout the year and may be an important source of energy to maintain body condition in winter.

As with other populations of arctic foxes that have abundant numbers of arvicolines available (Fay and Stephenson 1989; Frafjord 1995; Kennedy 1980; Smits et al. 1989), rodents (in this case, tundra voles) made up a high proportion of the diet throughout the winter and spring. Stomach contents of foxes on St. Lawrence Island, Alaska, had high proportions of small mammals in June–October but decreased occurrence in November–April (Fay and Stephenson 1989). Our research and the impressive ability of arctic foxes to locate rodents under snow (Mullen and Pitelka 1972) weaken the hypothesis by Fay and Stephenson (1989) that foxes were unable to penetrate snow quickly enough to capture small mammals. However, differences in snow conditions and access to abundant marine-based food caches may have made capture of rodents less profitable for the island population of arctic foxes that they studied. Low proportions of small mammals in stomachs collected in 1986 and 1987 reflect low availability of tundra voles. Fay and Stephenson (1989) found a significant correlation between frequency of occurrence of voles in fox stomachs in

December and vole trapping indexes the previous summer. Furthermore, geographically limited trapping of small mammals on the Yukon-Kuskokwim Delta indicated low numbers in the mid-1980s (Anthony 1997). This low abundance of small mammals plus the greater ages of foxes and closer capture distances from the coast in 1986 and 1987 support the explanation (Anthony et al. 1991) of high predation by arctic foxes on a colony of black brant about this time. This explanation was based on poor reproduction of arctic foxes during a period of low populations of tundra voles, which resulted in increased fox activity along the coast, where black brant nested. Therefore, the influence of populations of small mammals on nest predation by arctic foxes may be more than a simple case of prey switching.

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