Home Ranges and Movements of Arctic Fox (*Alopex lagopus*) in Western Alaska

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ABSTRACT. During the period from 1985 to 1990, radio collars were attached to 61 arctic foxes (*Alopex lagopus*) in the coastal region of the Yukon-Kuskokwim Delta in western Alaska. Radio tracking using hand-held receivers from aircraft and from fixed towers was conducted to determine daily and seasonal movements of foxes. Intensive radio tracking of 18 foxes from May through July indicated that males used larger areas ($\bar{x} = 10.22 \pm 6.18$ km^2) than females ($\bar{x} = 4.57 \pm 1.94$ km^2) regardless of breeding status. Generally foxes were relocated near ($\bar{x} = 3.4 \pm 2.4$ km) their summer home ranges during other seasons of the year. There were no complex social groups of foxes among the marked population. Foxes did not have a definitive preference for any plant community, probably because of the even distribution and abundance of prey throughout all communities. Thirty foxes were relocated repeatedly during a period of at least 10 months, which included the denning season of one year and the breeding season of the next. Of 24 confirmed deaths of collared foxes, 16 were caused by shooting or trapping by local residents and 8 had unidentified causes. Maximum distance moved between relocations was 48.4 km. Males moved farther from initial capture sites in the winter following capture than did females, largely because of greater than 20 km movements by two foxes. There were no seasonal differences in movements between males and females.

Key words: Alaska, arctic fox, *Alopex lagopus*, home range, telemetry

RÉSUMÉ. Au cours de la période allant de 1985 à 1990, des colliers émetteurs ont été posés à 61 renards arctiques (*Alopex lagopus*) dans la région côtière du delta du Yukon-Kuskokwim dans l'Alaska occidental. On a utilisé le pistage radioélectrique effectué à l'aide de receveurs portatifs, depuis des aéronefs et des tours stationnaires pour déterminer les déplacements quotidiens et saisonniers des renards. Un pistage radioélectrique intensif de 18 renards effectué de mai à fin juillet a révélé que les mâles utilisaient une superficie plus vaste ($\bar{x} = 10,22 \pm 6,18$ km^2) que les femelles ($\bar{x} = 4,57 \pm 1,94$ km^2) indépendamment de leur statut de reproducteur. En général, durant les autres saisons de l'année, on retraçait les renards près de leurs territoires estivaux ($\bar{x} = 3,4 \pm 2,4$ km). La population identifiée ne contenait pas de groupes sociaux complexes. Les renards ne manifestaient pas de préférence marquée pour une communauté végétale, à cause probablement de la répartition égale et de l'abondance de proies dans toutes les communautés. On a retracé 30 renards de façon répétée durant une période d'au moins 10 mois incluant la saison de mise bas d'une année et la saison d'accouplement de la suivante. Sur les 24 renards munis de colliers émetteurs dont la mort a été confirmée, 16 ont été tués par des résidents locaux, au fusil ou par des pièges, et 8 sont morts de cause non identifiée. La distance maximale parcourue entre des relevés était de 48,4 km. Durant l'hiver qui a suivi leur capture, les mâles se sont plus éloignés de leur site initial que les femelles, et ceci en grande partie à cause de déplacements supérieurs à 20 km effectués par deux renards. On n'a remarqué aucune différence saisonnière entre les mâles et les femelles en ce qui concernait leurs déplacements.

Mots clés: Alaska, renard arctique, *Alopex lagopus*, domaine vital, télémétrie

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INTRODUCTION

Throughout much of their range, arctic foxes (*Alopex lagopus*) are dependent on a limited number of prey species, particularly arvicoline rodents (Macpherson, 1969; Kennedy, 1980; Summers, 1986; Summers and Underhill, 1987; Hersteinsson et al., 1989; Angerbjorn et al., 1995; Frafjord, 1995a). The distribution and group size of arctic foxes and other carnivores are strongly influenced by the distribution and density of prey (Hersteinsson and Macdonald, 1982; Macdonald, 1983; Sandell, 1989). Depending on the habitat that they occupy, arctic foxes have been described as seasonally nomadic and solitary (Shibanoff, 1958; Chesemore, 1968; Northcott, 1975; Wrigley and Hatch, 1976; Eberhardt and Hanson, 1978; Eberhardt et al., 1983a) or as territorial and social (Hersteinsson and Macdonald, 1982; Ovsyannikov, 1988; Frafjord, 1992; Frafjord and Prestrud, 1992). My interest in the distribution and abundance of arctic foxes was related to their predation on diminished populations of geese nesting near the Bering Sea coast of the Yukon-Kuskokwim Delta of western Alaska (Pamplin, 1986; Anthony et al., 1991). Foxes had been identified as a significant predator of goose eggs (Larson, 1960; MacInnes and Misra, 1972; Raveling, 1989), but the relationship of fox density to egg

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losses was unknown. My goal was to determine how foxes use areas with high densities of bird nests, their seasonal movements relative to summer territories, and the interactions of foxes in these important nesting areas.

STUDY AREAS

Kokechik Bay, the primary study area in which foxes were intensively radio-tracked during 1985–87, is located near the westernmost point of the Yukon-Kuskokwim Delta, Alaska (Fig. 1). The 59 km² study area was bounded on the north by Kokechik Bay and on the south by a 26 m high bluff that marked the transition from wet tundra to drier upland tundra plant communities. The diversity of geomorphic features in the study area was reflected by six major plant communities (Jackson, 1981) that occurred between the bluff and the bay shore, about 4 km away. About 39% of the area was covered with lakes and ponds varying in depth from less than 0.5 to 2.0 m. Lowland tundra was less than 0.5 m above mean high tide and dominated by sedges and grasses. High pingos, islands of drier areas with elevations up to 2 m, were characterized by prostrate willows (*Salix* spp.), Labrador tea (*Ledum palustre*), and dwarf birch (*Betula nana*). Lichens were the most abundant vegetation in the upland, with ericads and mosses comprising the majority of other plants (Jackson, 1981). The relatively high diversity of plant communities in the study area was indicated by the abundance and diversity of fauna found there, which included one of the largest colonies of nesting black brant (Byrd, 1981), with an estimated population of 6000 nests (Stehn, 1986), and the highest

density of nesting emperor geese (*Chen canagica*) in the region (Eisenhauer and Kirkpatrick, 1977; Petersen, 1985). Large numbers of cackling Canada geese (*Branta canadensis minima*) and greater white-fronted geese (*Anser albifrons frontalis*) also nested in the area, as well as many species of other waterfowl, passerines, and shorebirds (Holmes and Black, 1973). Willow ptarmigan (*Lagopus lagopus*) nested in the drier sites in the study area. Mammals in the area included red fox (*Vulpes vulpes*), mink (*Mustella vison*), tundra hares (*Lepus othus*), beavers (*Castor canadensis*), muskrats (*Ondatra zibethicus*), tundra voles (*Microtus oeconomus*), meadow jumping mice (*Zapus hudsonicus*), masked shrews (*Sorex cinereus*), and collared lemmings (*Discrostonyx torquatus*).

In a secondary study area near Hazen Bay (61°03′ N latitude, Fig. 1), where an associated study on arctic fox predation was conducted, radio-collared foxes were located with hand-held receivers and from aircraft in the summers and winters of 1988–90 to determine their fidelity to territories. Although this coastal, wet tundra study site was similar to Kokechik Bay, it was larger (about 107 km²) with less complex vegetation. Large sedge-grass meadows occupied most of the area, interspersed with islands of uplands (Tande and Jennings, 1986). As at Kokechik Bay, densities of nesting geese and other birds were high, and small mammal populations were similarly diverse.

METHODS

Marking Foxes

Unlike many other populations of arctic foxes, animals in this region were very wary of humans and difficult to observe or capture. Consequently, I set padded foothold traps beneath snow and soil to capture foxes. A nylon string from each trap was attached to a magnet that controlled the on-off switch of a radio transmitter concealed 2–3 m from the trap. Movement of the trap activated the transmitter. Trap transmitters were monitored regularly throughout the day to allow quick removal of foxes from traps, minimizing trap-induced trauma. Trapping began in late April and early May and continued at varying intensities through July. In 1985, captured foxes were equipped with 80 g radio transmitters, built at the Denver Wildlife Research Center, with a 15 cm antenna. In 1986–90, each captured fox was fitted with a 150 g radio collar (Model L2B5 or Model MOD-300, Telonics, Inc., Mesa, Arizona; use of manufacturers' names does not imply U.S. government endorsement of commercial products) from which a 40 cm antenna exited (midway on the collar) and extended along the side or back of the fox. Expected life of the Denver and Telonics transmitters was 6 months and 15 months, respectively. Before attachment of radios, foxes were weighed, classified by sex, examined for reproductive condition, ear-tagged, and marked on both sides with a unique code using livestock dye. Foxes were released at their capture site after handling.
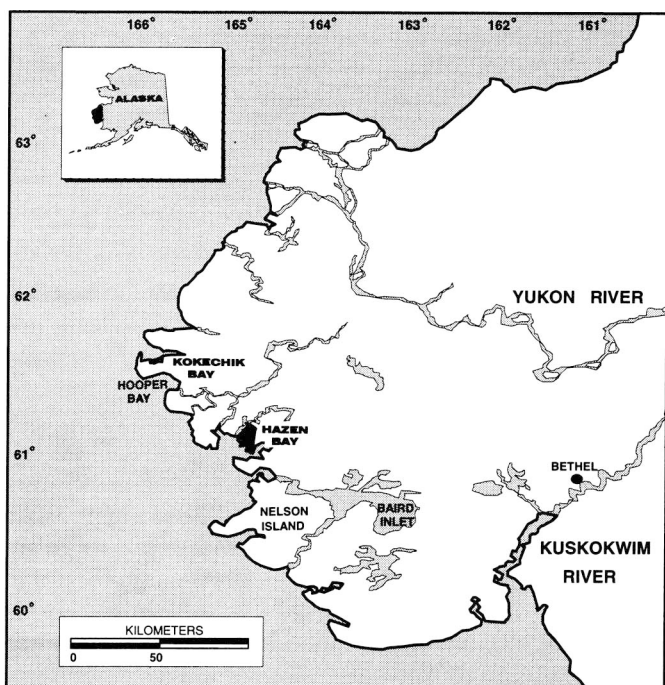

FIG. 1. Arctic foxes were fitted with radio collars in study areas at Kokechik Bay and Hazen Bay on the Yukon-Kuskokwim Delta in western Alaska during 1985–90.

Distribution of Prey

In 1986 and 1987, the distribution and abundance of small mammals in plant communities was estimated by signs of subnivean rodent activity (runways, feces, nests, and caches of clipped vegetation) in May after snowmelt and by capture rates with snap traps in July. Ten 200 m transects were randomly located in each plant community. Along each line, 20 circular plots with 2 m radius were spaced at 10 m intervals. Presence of mice was indexed using a scale from one to five based on abundance, freshness, and type of sign at each subplot.

Estimates of abundance and distribution of bird nests were compiled from nest surveys conducted during this study and from nest studies by others (Holmes and Black, 1973; Stehn, 1986). Various sampling methods were used during 1985–87 to estimate the number of nests in the brant colony in the wet sedge community (Anthony et al., 1991). To estimate distribution of nests of other species, in 1986 and 1987 I calculated proportions of total nests found in each plant community (N = 491) during systematic nest searches of randomly located 0.5 km² plots and nests found coincidental to other activities in the study area. Nest density within plant communities was calculated using these estimates of distribution and the nest density estimates used by Stickney (1991) for black brant, emperor geese, cackling Canada geese, greater white-fronted geese, spectacled eiders (*Somateria fischeri*), common eiders (*Somateria mollissima*), dunlin (*Calidris alpina*), and western sandpipers (*Calidris mauri*).

Home Ranges

In 1985, I relocated foxes with hand-held, two-element Yagi antennas from the ground and also from small, fixed-winged aircraft. At Kokechik Bay in 1986 and 1987, locations of radio-collared foxes were determined by simultaneous triangulation of azimuths from three or four fixed tracking stations that had paired five-element Yagi antennas (Telonics Model RA-4A) mounted on poles 5 m high and connected to a null combiner. To ensure that all crew members were using similar techniques for obtaining bearings to transmitters, before tracking began each member of the crew independently determined the direction to 10 transmitters from the same tracking station. Later, during a fox-tracking session, precision of radio locations by the crew was estimated by triangulating on a transmitter carried by a person to 10 undisclosed sites. The differences between radio-derived azimuths and actual azimuths were used to determine the mean error of stations. Differences in azimuths among trackers were compared with analysis of variance at α = 0.05.

Before each fox-tracking session antennas were calibrated with transmitters at three known locations. Because of the flat topography of the area and the elevation of the receiving antennas, radio-collared foxes were usually within line of sight of receiving antennas. Estimates and errors of locations from azimuths were determined using a laptop computer program (White and Garrott, 1984) during tracking sessions.

Locations with areal error estimates of more than five hectares were eliminated from analysis during recording or processing of data.

Using triangulation from tracking stations, I monitored movements of foxes at regular intervals during tracking sessions of 3–23 hours. Tracking was conducted during the months from April through July, when foxes were denning and birds were nesting. Mean length of 16 tracking sessions in 1986 was 12.1 hours, and that of 19 sessions in 1987 was 6.3 hours. Independence between successive locations was tested per Swihart and Slade (1985a, b).

Home Range Analysis

In 1986 and 1987, home ranges were estimated with the Map and Image Processing System (MIPS) geographical information processing software (MicroImages, Inc., Lincoln, Nebraska), using the harmonic mean method with 95% of the radio locations (Dixon and Chapman, 1980). Minimum convex polygons were also constructed using MIPS for 1985, 1986, and 1987 locations to compare home ranges among years and among other studies. Overlap of home ranges among neighbouring foxes was estimated from independent locations using weighted values based on frequency of use (Smith and Dobson, 1994). To determine whether territorial defense by foxes increased when goose nests were available, five home ranges with significant overlap (≥ 10%) were reanalyzed using only relocations during the period from peak nest initiation to peak hatch by geese. Home range overlap among neighboring foxes and pairs of foxes was compared by analysis of variance of arcsine transformed proportions (Snedecor and Cochran, 1980).

Plant communities at Kokechik Bay were mapped from digitized colour infrared aerial photographs and verified with ground plots (Anthony, 1996). Use of plant communities by foxes within individual territories was determined with MIPS by overlay of radio locations and home range polygons on the digitized map of plant communities in the study area. For these analyses, I used locations taken from 2100 to 0500 hours, when foxes were consistently active (Fig. 2). I used Bonferroni simultaneous confidence intervals (Byers et al., 1984) to compare estimated proportions of plant community use according to Neu et al. (1974), with consideration for telemetry location errors as described by Samuels and Kenow (1992). To determine the effect of prey abundance on use of plant communities, availability of plant communities was weighted by associated nest densities and by small mammal indices for reanalysis of use by foxes.

Concurrent with this radio-telemetry study, arctic foxes at Kokechik Bay were observed regularly in studies of den use by foxes (Anthony, 1996), the nesting ecology of geese (Laing, 1991; Petersen, 1991) and the foraging behaviour of foxes (Stickney, 1991). In addition, direct observations of foxes were made during trapping for foxes and regular observations for fox activity with spotting scopes from blinds in towers 3 m high. Therefore, during all three years of radio-tracking arctic foxes at Kokechik Bay, supplemental information on
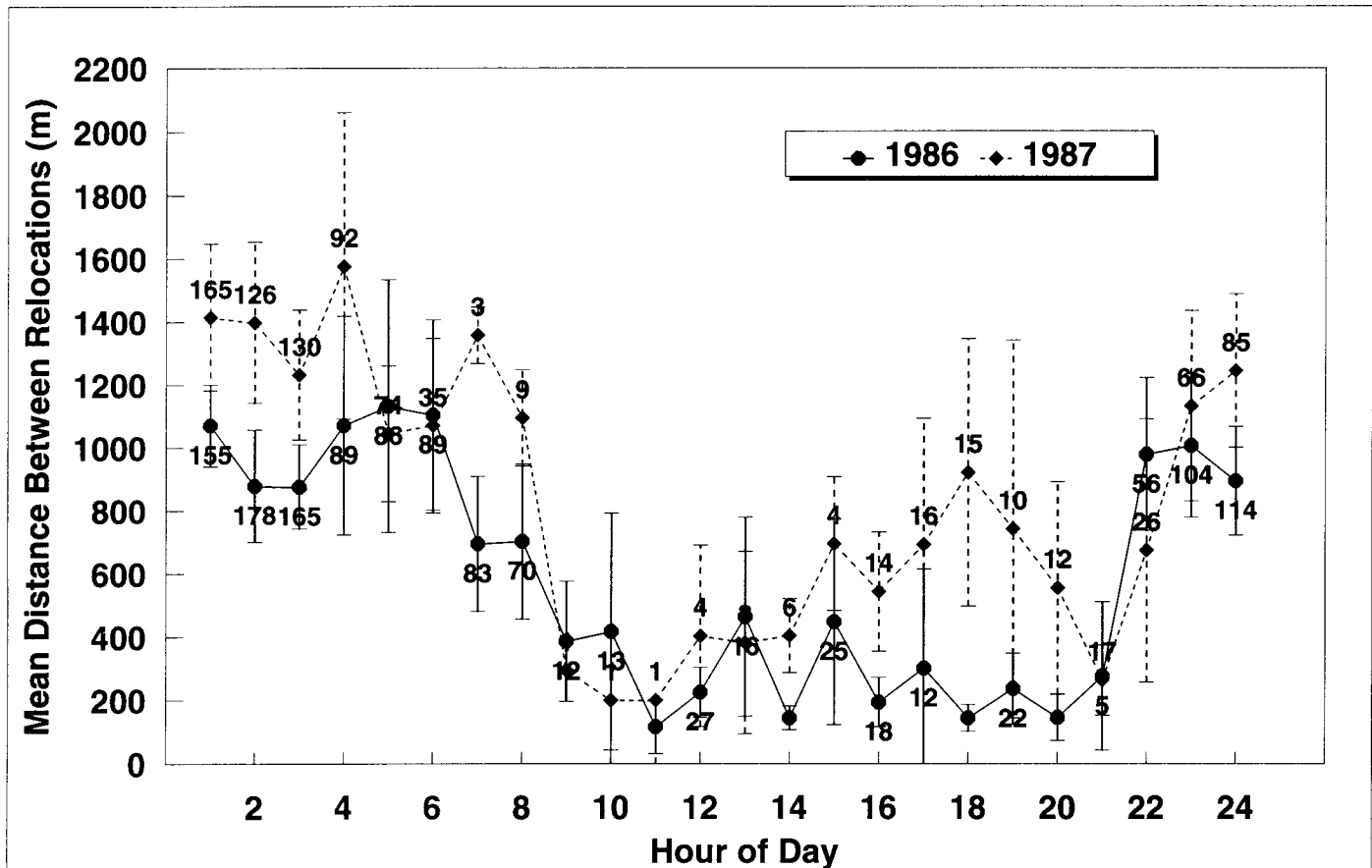
FIG. 2. Mean hourly rate of movement of radio-collared arctic foxes at Kokechik Bay, Alaska in summer 1986 and 1987. Number of locations by hour are shown below (1986) and above (1987) plotted rates; 95% confidence levels also are shown.

movements and associations among foxes from direct observation was collected.

Aerial Radio-tracking

During the period from 1985 to 1990, I conducted aerial telemetry surveys for radio-collared foxes in the Kokechik Bay and Hazen Bay study areas intermittently during the breeding season (May–August) and from October to April, as weather permitted. The study areas were traversed systematically at 2–4 km spacing with a single-engine aircraft equipped with a two-element Yagi antenna on each wing strut and flying at an altitude of 400–600 m. The coastal region between the two study areas was searched for radio signals along two transects paralleling the coastline at about 5 km and 10 km from shore. Locations of foxes were estimated with LORAN-C (White and Garrott, 1990) and by observers from landmarks on 1:63 360 scale topographic maps. As a measure of fidelity to summer home ranges, I used analysis of variance (PROC GLM, SAS Institute Inc., SAS Circle, Box 8000, Cary, North Carolina) to compare distances between capture location and relocations, both by sex and by the two aerial tracking periods (May–August and October–April). As a measure of seasonal movements, I also analyzed the distance between consecutive relocations by sex and by aerial tracking period. To observe directional trends in fox movements,

particularly toward the coast where marine mammal carcasses potentially provided a winter food source (Anthony et al., 1991), I calculated the x and y components of movement vectors between fox relocations. I assigned negative values to southward and westward components and positive values to northward and eastward components. Finally, I plotted these vector components as Cartesian coordinates to observe distribution of direction and distance of movements between relocations. I compared the absolute values of the vectors with analysis of variance and the number of vectors per quadrant with Chi-square analysis at $\alpha = 0.05$.

RESULTS

Marked Foxes

Sixty-one arctic foxes, 26 males and 35 females, were radio-collared at the two study sites from 1985 to 1990 (Table 1). Four female red foxes also were radio-collared between 1985 and 1987. All foxes radio-collared during 1985–87 (Table 2) were tracked intensively from May through July. Aircraft and occasional ground tracking were used to relocate foxes at Kokechik Bay and Hazen Bay during other months and years of the study. Thirty foxes were relocated 10 months or more after their capture, which allowed

TABLE 1. Arctic foxes captured and radio-collared on Yukon-Kuskokwim Delta, Alaska during 1985–90.

	Males	Breeding females	Nonbreeding females	Total
Kokechik Bay				
1985	1	3	2	6
1986	5	0	3	8
1987	4	2	0	6
1988–90	3	2	4	9
Hazen Bay				
1988–90	13	8	11	32
Total	26	15	20	61

comparison of movements during the breeding season to the remainder of the year. Of 24 confirmed deaths of collared foxes, 16 were caused by shooting or trapping by local residents and eight had unidentified causes.

Distribution of Prey

Frequency of sign of subnivean activity by small mammals (mean number of stations with sign per transect) increased from the bay shore south to the base of the bluff (Fig. 3). Trapping success in July suggested a similar distribution of small mammals in these same communities. Tundra voles were most abundant, accounting for 87.6% of all captures, and were captured in all communities but wet sedge. Masked shrews were captured in low pingo, high pingo, and tall sedge communities. Meadow jumping mice were found only in tall sedge.

A colony of black brant at Kokechik Bay, which was estimated to contain more than 6000 nests in 1985, 1986, and 1987, was located in the wet sedge plant community. Estimates of densities of brant and other species (Stickney, 1991) plus distributions based on my searches indicated that the mean number of nests ($\pm$ SD) per fox territory was 1058 $\pm$ 538 (Fig. 4). Densities for wet sedge meadow, sedge-grass meadow, low pingo, high pingo, and tall sedge communities were 368, 188, 145, 61, and 10 nests per km^2, respectively. Nest density by plant community was negatively correlated (r = -0.93, $p = 0.01$) to small mammal abundance.

Home Ranges

The difference between observers' estimates and true azimuths ($\bar{x} = 0.43 \pm 0.34°$) to transmitters at known locations was not significant ($F = 1.01$, $p = 0.40$). Mean error of azimuths to transmitters at known locations for all tracking stations was 2.03 $\pm$ 1.39. Mean area of error ellipses for valid locations from all towers in 1986 and 1987 was 1.85 $\pm$ 1.49 hectares (range 0.10–5.00).

In 1985, the mean home range of six arctic foxes was 4.07 $\pm$ 0.92 km^2. The female red fox was not relocated in the study area after capture. Home ranges of foxes occupied 37.2% of the Kokechik Bay study area (Fig. 5). In 1986, one radio-collared female from 1985 remained at Kokechik Bay; another female was trapped and killed in her 1985 home range, but the fate of all others was unknown. No foxes denned in the study area in 1986, but the distribution of eight fox home ranges throughout the study area was similar to the 1985 distribution (Fig. 5). Mean area of home ranges was

TABLE 2. Arctic foxes intensively radio-tracked at Kokechik Bay, Alaska during 1985–87.

Year	Map ID[1]	Fox ID	Sex	Age	Weight (kg)	Reproductive status	Associations
1985	1	203	F	5	3.65	≥ 11 pups	Paired with 226
	2	226	M	4	3.54		Paired with 203
	3	222[2]	F	1	2.72	Barren	Paired with unmarked fox
	4	223	F	-	3.79	≥ 10 pups	Paired with 224
	5	224	M	5	3.47		Paired with 223
	6	227	F	-	3.77	≥ 8 pups	Paired with unmarked fox
	7	221	F	-	3.22	Barren	Unknown
1986	8	512	F	1	2.50	Barren	Paired with 938
	9	938	M	1	-		Paired with 512
	10	525[2]	F	2	3.07	Barren	Paired with 496
	11	496	M	-	4.40		Paired with 525
	12	613	M	1	3.42		Unknown
	13	637	F	1	2.90	Barren	Paired with unmarked fox
	14	675[3]	M	1	3.25		Cohabitant with 699
	15	699	M	1	3.18		Cohabitant with 675
1987	17	587	F	2	3.68	≥ 6 pups	Paired with 538
	18	538	M	4	4.10		Paired with 587
	19	575	F	3	3.03	Pups at den	Paired with 649
	20	649	M	2	4.00		Paired with 575
	21	599	M	1	3.19		Paired with unmarked fox
	22	775[3]	M	2	3.25		None
	23	474[4]	F	1	2.95	Barren	

[1] Numbers correspond with identification numbers in Figures 5 and 6.

[2, 3] Foxes with duplicate superscript are the same fox in different years.

[4] Fox was found shot with collar removed on 20 May, about two weeks after being marked.
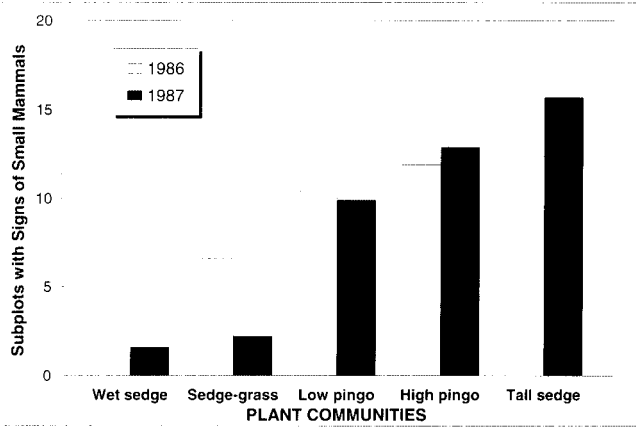
FIG. 3. Number of subplots with signs of small mammals in five plant communities at Kokechik Bay, Alaska in 1986 and 1987.
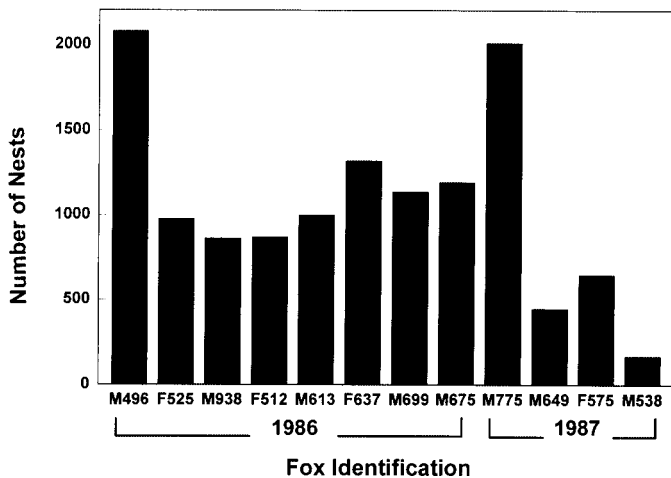

FIG. 4. Estimated number of bird nests in home ranges of foxes at Kokechik Bay, Alaska in 1986 and 1987.

6.83 ± 1.89 km^2. Home ranges covered 60.5% of the study area. As in 1985, one female red fox left the study area shortly after being marked. Four of the foxes radio-collared in 1986 were harvested in the Kokechik Bay area by trappers during winter; two were unaccounted for after February 1987; one male was found dead from unknown causes within his summer home range in February 1987; and one male reoccupied the study area in 1987. Although average area of home ranges $(9.73 \pm 7.76 \text{ km}^2)$ was not larger in 1987 than in 1985 $(p = 0.11)$ or in 1986 $(p = 0.32)$, distribution of foxes was different (Fig. 5). Two breeding pairs and one male were located on the border or periphery of the study area. The only fox to survive from 1986, when it had occupied a 7.81 km^2 area, now had a home range of 12.87 km^2 that enveloped its 1986 home range in the center of the study area. Only 50.5% of the study area was occupied by home ranges. Two radio-collared red foxes maintained home ranges on the borders of the study area, in drier upland communities. Mean home range of males combined for all years was 10.22 ± 6.18 km^2, which was larger $(F = 7.59, p = 0.01)$ than that of females $(4.57 \pm 1.94 \text{ km}^2)$. Home ranges of five non-breeding females $(5.25 \pm 1.39 \text{ km}^2)$

were larger $(F = 5.17, p = 0.05)$ than those of five breeding foxes $(3.43 \pm 1.15 \text{ km}^2)$.

Mean overlap of home ranges among neighbouring foxes in 1986–87 was $6.95 \pm 9.30\%$ (n = 43, range 0.0–41.9%). Paired foxes shared $68.9 \pm 8.90\%$ of their home ranges (n = 10, range 57.8–82.8%); this behaviour was different $(F = 236.60, p < 0.001)$ from that of neighbouring foxes. Sharing of home range areas occurred for breeding and nonbreeding pairs in both years and for two one-year-old males that had 57.8% and 71.0% overlap of home ranges in 1986. One of these males maintained a similar home range in 1987, and the other was trapped about 24 km from its home range in March 1987. The 4.1 km^2 overlap area between the combined home ranges of the only two pairs that had significant overlap during the entire study comprised 26% high pingos, 29% low pingos, and 45% sedge-grass meadows. The occurrence of these communities was disproportionate to their availability in the entire study area (8%, 17%, and 35%, respectively). The area of overlap contained 20 of the 83 total dens found in the study area (Anthony, 1996). Overlap between these pairs increased slightly during the nesting period of geese (from 43.7% to 48.0% and from 59.7% to 67.5%). Conversely, the home range of a radio-collared male fox that bordered these pairs did not overlap during the goose nesting period, but had a mean overlap of 10.1% of neighbouring home ranges for the entire summer. Temporal analysis of locations of neighbouring foxes (distance between individuals at similar times) did not indicate interaction or avoidance along home range boundaries and areas of overlap.

Generally the proportion of major plant communities in the home range of each fox was similar to those for the entire study area in 1986 and 1987. However, in all fox home ranges at least one plant community occurred at a different proportion $(\chi^2 \geq 25.48, p \leq 0.001)$ than in the study area (Fig. 6). Most of these differences between composition of fox home ranges and the entire study area occurred in high pingo and tall sedge communities. These communities were unevenly distributed and small, which reduced the probability that they would occur in a given home range. Use of plant communities in individual home ranges was not explained by distributions of nests or small mammals. When availability data from 1986 were weighted by small mammal abundance indices, use by foxes was different $(\chi^2 \geq 55.79, p \leq 0.01)$ than expected 53% of the time. This compared to 17% unexpected results with unweighted data and 25% unexpected results when data was weighted by nest density. In 1987, use was unexpected 38%, 69%, and 75% of the time when data was unweighted, weighted by nest density, and weighted by small mammal abundance, respectively. Similarly, there was no apparent relationship between use and prey abundance when these data were analyzed for all foxes combined for each year (Table 3).

Observations

Unmarked arctic foxes observed in this study and other concurrent studies in the area were often identified by unique molt patterns and by associations with marked foxes. In 1985,
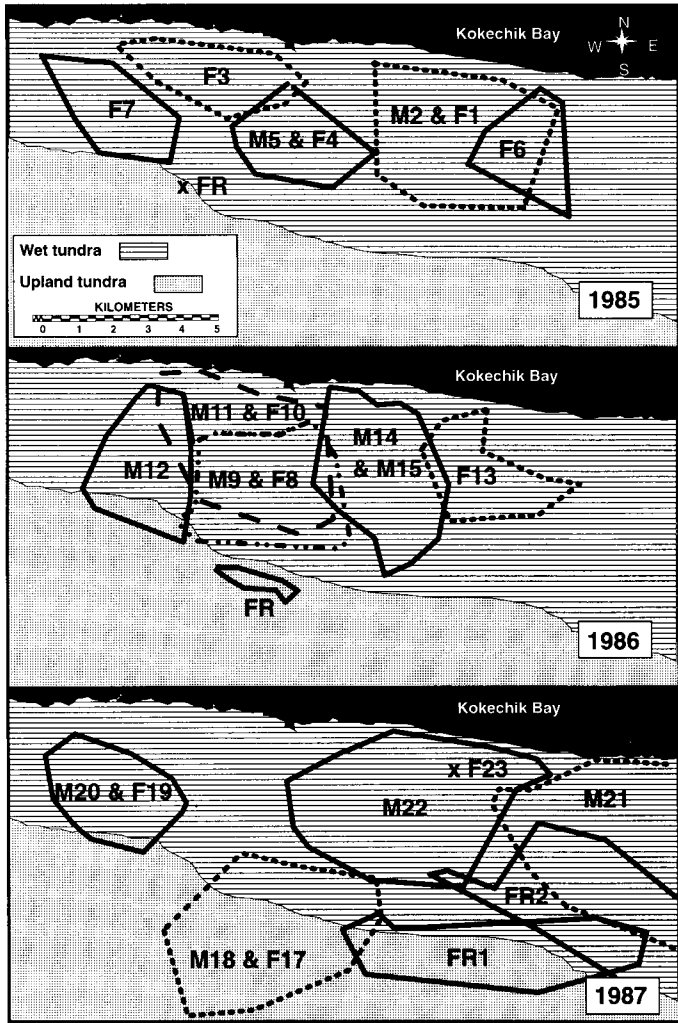
FIG. 5. Minimum convex polygon home ranges of radio-collared foxes at Kokechik Bay, Alaska in 1985, 1986, and 1987. Refer to Table 2 for descriptions of foxes. Home range boundaries of paired, radio-collared foxes are combined. "FR" refers to radio-collared, female red foxes.
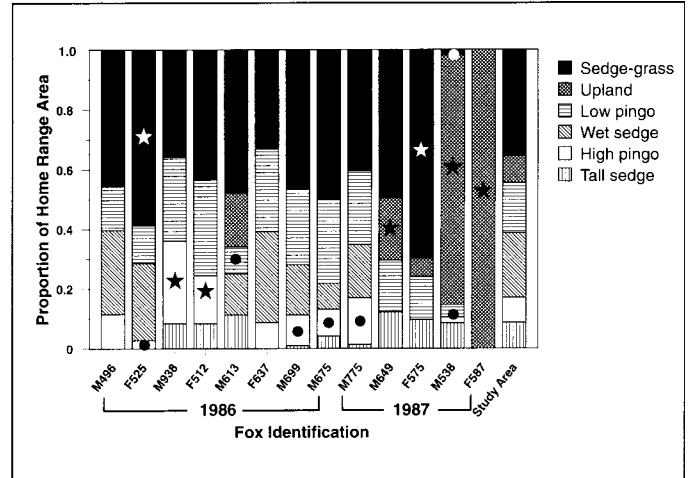

FIG. 6. Proportional occurrence of six plant communities in the entire study area and in individual home ranges of foxes at Kokechik Bay, Alaska in 1986–87. Smaller occurrences than expected are marked with a circle; those that are greater than expected are marked with a star. Plant communities are based on classification by Jackson (1981).

TABLE 3. Use of five plant communities by all radio-collared foxes at Kokechik Bay, Alaska in 1986 and 1987. Analyses were conducted with availability data unweighted (None), data weighted by nest density (Nests), and data weighted by small mammal abundance indices (Mice). Use of plant communities compared to their availability was expected (=), less than expected (<), or greater than expected (>).

Weighting factor:	1986			1987		
	None	Nests	Mice	None	Nests	Mice
Wet sedge	>	<	>	<	<	<
Sedge-grass	=	=	=	<	<	>
Low pingo	=	>	<	<	>	>
High pingo	=	<	<	=	>	>
Tall sedge	=	>	=	=	>	<

two unmarked males were paired with radio-collared females. A third unmarked fox was observed several times in the home range of a marked female, but no interactions were observed. A single observation of an unmarked arctic fox was made in uplands on the southern border of the study area outside the home ranges of marked foxes in low, wet tundra. In 1986, an unmarked male was paired with a radio-collared female on the western border of the study area. In July a one-year-old, female arctic fox was trapped in the home ranges of male foxes that shared the central portion of the study area. In 1987, no unmarked foxes were observed. During all years there were no observations of adult foxes in addition to parents at active dens (Anthony, 1996).

Seasonal Movements

Radio-collared foxes were relocated 149 times during aerial surveys (Fig. 7). Mean elapsed time between relocations was 57.1 ± 37.9 days (range 6–207). Males travelled farther from capture locations in winter ($F = 4.00$, $p = 0.05$) than

females (Table 4), but there were no other differences in distances between relocations in winter ($F = 2.40$, $p = 0.12$) or summer ($F = 1.33$, $p = 0.25$) between or within sexes. The difference between males and females in winter was not significant ($F = 0.63$, $p = 0.43$) when I had eliminated four relocations of two foxes that moved 48.4 and 20.2 km from their capture sites to establish a home range. Movements along the east-west axis were greater ($\bar{x} = 2.42 \pm 3.22$ km, $F = 4.20$, $p = 0.04$) than those along the north-south axis ($\bar{x} = 1.65 \pm 2.28$ km). However, despite relatively long periods between relocations, there was no difference between westward ($\bar{x} = 2.68 \pm 3.12$ m, N = 57) and eastward ($\bar{x} = 2.15 \pm 3.34$ km, N = 53, $F = 0.74$, $p = 0.39$) movements (Fig. 8).

Seven of fourteen arctic foxes that were tracked intensively at Kokechik Bay during the summer were also relocated by aerial radio-tracking the following October–April. Eight of 29 relocations of these foxes occurred in their summer home ranges. All other relocations were 3.4 ± 2.4 km from the geometric center of summer home ranges.
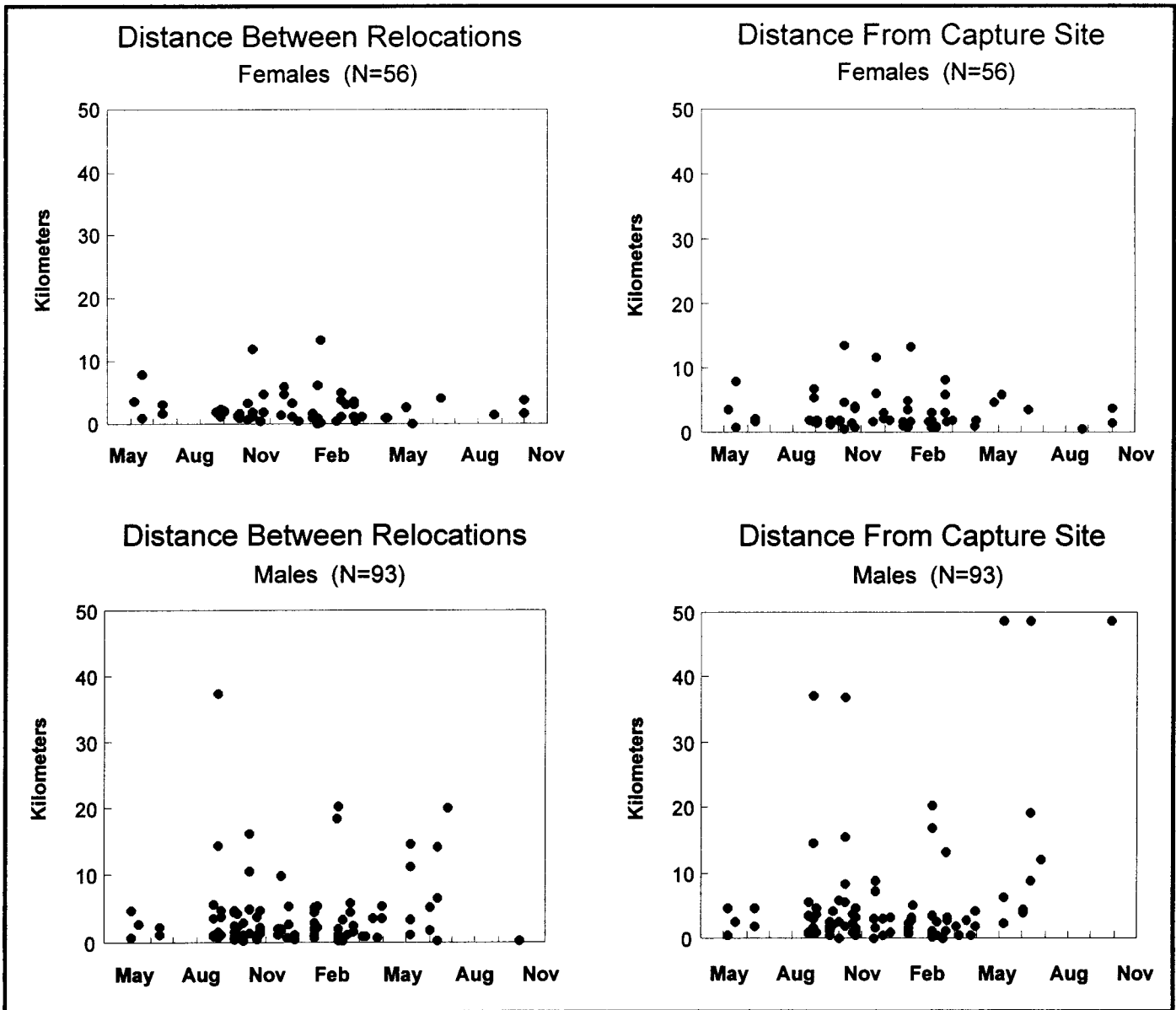
FIG. 7. Temporal distribution of 149 aerial relocations and distance travelled between relocations by radio-collared male and female foxes on the Yukon-Kuskokwim Delta, Alaska during 1985–90.

DISCUSSION

Summer home ranges of arctic foxes at Kokechik Bay were smaller than those estimated for radio-collared arctic foxes in northern Alaska (Eberhardt et al., 1983a; Burgess, 1984), Iceland (Hersteinsson and Macdonald, 1982), Greenland (Birks and Penford, 1990), and Svalbard (Frafjord and Prestrud, 1992; Prestrud, 1992). Frafjord (1995b) observed home ranges of radio-collared foxes in Svalbard that were about the size of those in this study and also many that were much larger. Speller (1972) estimated a 3.2 km² hunting range of a pair of arctic foxes in Northwest Territories, Canada during a year when lemmings were abundant. Small home ranges and limited overlap are consistent with a highly productive habitat and evenly distributed prey (Sandell, 1989). Estimates of prey density in this study indicated that hundreds of birds' nests were available in all home ranges and that decreasing density of nests was correlated with increasing availability of small mammals among major plant communities. The abundance of prey throughout the study area may explain the lower-than-expected use of the wet sedge community with its large brant nesting colony. Stickney (1991) observed in 1986 that this population of foxes fed primarily on mammalian prey in spring, nesting birds and their eggs in summer, and eggs that were cached when other prey were less abundant. The foxes that she observed cached eggs throughout the nesting period, but the rate of caching declined when fewer eggs were available. Access to cached eggs may justify the continued use of summer home ranges throughout the year.

Despite the abundant prey in home ranges, which could support more foxes, there was only one possible case of a

TABLE 4. Mean distance (km) from capture sites to aerial relocations and between consecutive aerial relocations of radio-collared arctic foxes on the Yukon-Kuskokwin Delta, Alaska during 1985–90. Comparisons by sex and season with no common letters are significantly different at α = 0.05.

	Distance from capture to relocation		Distance between relocations	
	Summer	Winter	Summer	Winter
Males	4.85 ± 7.73 [a,c]	7.79 ± 13.24 [a,d]	3.97 ± 6.13 [a,c]	4.12 ± 5.16 [a,d]
Females	3.39 ± 6.62 [b,c]	3.03 ± 2.75 [b]	2.52 ± 2.43 [b,c]	2.57 ± 2.70 [b,d]
All foxes	4.34 ± 6.54 [e]	5.88 ± 6.54 [e]	3.47 ± 5.17 [e]	3.50 ± 5.18 [e]

FIG. 8. Direction and distance between aerial relocations of radio-collared arctic foxes on the Yukon-Kuskokwim Delta during 1985–90.

home range supporting more than two foxes as observed by Hersteinsson and Macdonald (1982) and Ovsyannikov (1988). That was a one-year-old female trapped in the home ranges of two males of the same age in 1986. The sharing of home ranges by these two males and the matching ages of all three foxes suggest that they were from a litter of the previous year that had occupied a den near their capture locations. Eberhardt et al. (1983b) observed two males and one or more females at two dens in northern Alaska. Frafjord (1991) also reported more than two adult foxes at dens in Scandinavia. Neither radio-telemetry nor observations indicated that more than two foxes used dens at one time. Indications from den surveys (Anthony, 1996) that red foxes made minimal use of wet tundra areas were supported by radio-telemetry and observations.

Most foxes that were successfully radio-tracked remained near summer home ranges during other times of the year. There was no mass movement by foxes from summer home ranges to the coast in winter. Because marked foxes had ear tags with telephone numbers, and notices of rewards for marked foxes were distributed in the region, observations of greater movements by foxes was expected. However, given the high proportion of marked foxes dying from anthropogenic causes near their home ranges within a year of marking (including one that was found shot with its collar removed about two weeks after marking), it is likely that results of this study were representative of a significant portion of the population. Hersteinsson (1984) also observed use of summer home ranges throughout the year by arctic foxes in Iceland. In Svalbard, Prestrud (1992) observed that breeding arctic foxes used their home ranges throughout the year.

Home ranges of males were larger than those of females. Although my estimates included nonbreeding females, home ranges of barren vixens were larger than those of breeding females, which spent more time at dens tending to young. Use of natal dens coincided with the nesting period of geese. The coincidence of denning and nesting probably affected nest predation rates by generally limiting the time available for foraging by vixens and thus requiring males to hunt more for birds and small mammals, which were the most common prey remains found at dens (pers. obs). The difference in home ranges between nonbreeding females and males was probably influenced
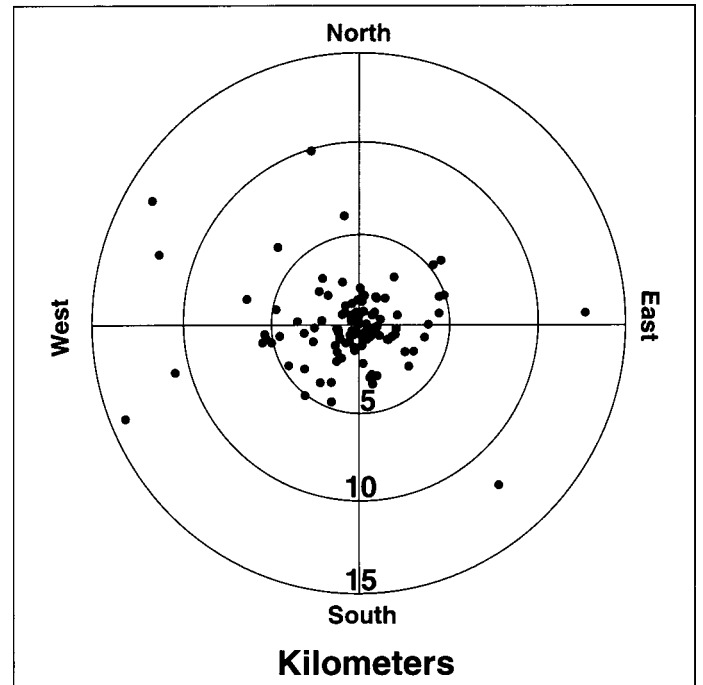
by differences in body mass (McNab, 1963; Harestad and Bunnell, 1979; Lindstedt et al., 1986) and also behavioural differences between sexes. Furthermore, some of the data used to estimate home ranges by the minimum convex polygon method were from 1985, when fewer relocations compared to subsequent years underestimated home range size (White and Garrott, 1990). Small sample size precluded detecting differences in home range areas among years. However, the apparent difference in size and distribution of home ranges in 1987 was probably a result of high harvest rates in the area by local trappers and hunters. This high mortality rate also undoubtedly contributed to the apparent simple social structure. In an unexploited population, a highly productive habitat would likely have more than two foxes in some territories (Hersteinsson and MacDonald, 1982).

Limited overlap among neighbouring foxes and sharing of large portions of home ranges by pairs in 1986 and 1987 indicated that foxes were territorial at Kokechik Bay. Arctic foxes in northern Alaska (Eberhardt et al., 1982; Burgess, 1984), Iceland (Hersteinsson, 1984), and Svalbard (Prestrud, 1992) also exhibited territorial behaviour. The small territories at Kokechik Bay could be relatively easily defended by a pair of foxes and an abundance of prey could be protected with acceptable energy cost. The slight increase in overlap of home ranges during goose nesting between the only pairs of foxes not exhibiting strong territoriality was unexpected. One explanation of this relationship is that abundant resting sites and dens rather than nest densities attracted foxes to these areas of overlap in low pingo and high pingo communities. On the other hand, overlap of neighbouring home ranges by a radio-collared

male decreased during the goose nesting period, which was consistent with a hypothesis that territoriality among foxes in this area was manifested by defense of prey resources.

Use of plant communities by foxes was not explained by distribution of prey. All communities had abundant prey, even though not all available prey species were included in my estimates. The abundance and even distribution of prey probably allowed foxes to forage successfully throughout their home ranges, interspersing their foraging with other daily maintenance activities. The lack of concentrated spatial or temporal foraging activity could explain why relocations of foxes and prey abundance were unrelated. Furthermore, small sample size and variable behaviour among foxes made it difficult to detect a relationship between these factors. Direct observation or continuous radio-tracking would be a better approach to investigating this relationship.

In summary, arctic foxes in the coastal areas of the Yukon-Kuskokwim Delta had smaller home ranges than reported elsewhere, which suggested an abundant, evenly distributed prey in this region. Like foxes in some other coastal habitats (Eberhardt et al., 1982; Burgess, 1984; Hersteinsson, 1984; Prestrud, 1992), these foxes were territorial, and most inhabited areas near their summer home ranges throughout the year. There were no records of extreme movements (>50 km) by radio-collared foxes that were successfully tracked; however, the fate of a significant proportion was unknown. Analyses of fox movements and prey abundance, which indicated no selection of any one plant community by individual foxes, further supported my hypothesis of an evenly distributed prey base in the region. Despite the high productivity of the region, there were no complex social groups of foxes among the population that was studied, probably as a result of high annual mortality from trapping and hunting.

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