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Dietary and Reproductive Responses of Arctic Foxes to Changes in Small Rodent Abundance

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ABSTRACT. Between 1988 and 1995, dens in three adjacent arctic fox (*Alopex lagopus*) territories were monitored in an alpine environment in south-central Norway (the Snøhetta plateau). A total of 675 scats were collected at dens in both winter and summer, and the numbers of resident adults and pups at emergence were counted each summer. Small rodents (mainly *Lemmus* sp. and *Microtus* sp.) were the most frequently consumed prey and made up the greatest volume within scats, in all seasons and at all stages of the rodent cycle. Small rodents were followed in frequency by reindeer (*Rangifer tarandus*), hares (*Lepus timidus*), birds, and vegetation. Birds and vegetation were more common in the summer diet than in the winter diet, reflecting their seasonal availability. The relative volume of reindeer and birds in the diet decreased with increasing rodent abundance. Increased pup production was associated with years of high rodent abundance and a high occurrence of rodents in the diet. Adult numbers were not associated with rodent abundance.

Key words: arctic fox, *Alopex lagopus*, diet, reproduction

RÉSUMÉ. Entre 1988 et 1995, on a observé les terriers du renard arctique (*Alopex lagopus*), dans trois territoires contigus situés dans un environnement alpin du centre-sud de la Norvège (le plateau Snøhetta). En hiver et en été, on a recueilli un total de 675 excréments sur le site des terriers, et chaque été, on a compté le nombre de résidents adultes et de petits qui faisaient leur première sortie du terrier. Les petits rongeurs (surtout *Lemmus* sp. et *Microtus* sp.) étaient la proie la plus fréquemment consommée et constituaient le plus gros volume des excréments, en toute saison et à toute étape de la vie du rongeur. Les petits rongeurs étaient suivis en fréquence par le renne (*Rangifer tarandus*), le lièvre (*Lepus timidus*), les oiseaux et la végétation. Les oiseaux et les plantes étaient plus courants dans le régime alimentaire estival que dans celui hivernal, ce qui reflétait la disponibilité saisonnière. Le volume relatif de renne et d'oiseaux dans l'alimentation diminuait avec l'augmentation de rongeurs. La production accrue de petits était associée aux années de grande abondance de rongeurs et à une occurrence élevée de rongeurs dans l'alimentation. Le nombre des adultes n'était pas relié à l'abondance de rongeurs.

Mots clés: renard arctique, *Alopex lagopus*, alimentation, reproduction

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INTRODUCTION

Throughout their Holarctic range, arctic foxes (*Alopex lagopus*) have an enormous variation in diet. Rodents, seabirds, waders, passerines, terrestrial and marine mammal carrion, fish, invertebrates, and berries have been recorded in arctic fox diets at various study sites (Macpherson, 1969; Nielsen, 1991; Prestrud, 1992; Frafjord, 1995; Hersteinsson and Macdonald, 1996). Despite the marked seasonality of the arctic environments that arctic foxes inhabit, relatively few studies have presented diet data from more than the summer season. Furthermore, although prey availability has been shown to affect arctic fox reproduction (number of dens occupied, litter size at conception, and pup survival), few studies have simultaneously studied both arctic fox diet and reproduction at a single site over several years (Macpherson, 1969; Angerbjörn et al., 1991; Fay and Rausch, 1992; Tannerfeldt et al., 1994; Kaikusalo and Angerbjörn, 1995).

Arctic foxes in south Scandinavia inhabit "islands" of alpine habitat that are separated from each other by forested valleys, in contrast to the continental tundra or coastal environments where most diet studies have been carried out. Previous diet studies have been limited to the summer season (Frafjord, 1995). In view of the endangered status of Scandinavian arctic foxes (Hersteinsson et al., 1989; Linnell et al., 1999), an understanding of both arctic fox diet and its effect on reproduction is important for the development of effective conservation plans (sensu Angerbjörn et al., 1991). This study presents data on summer and winter diet and reproduction collected over eight years from three neighbouring arctic fox territories

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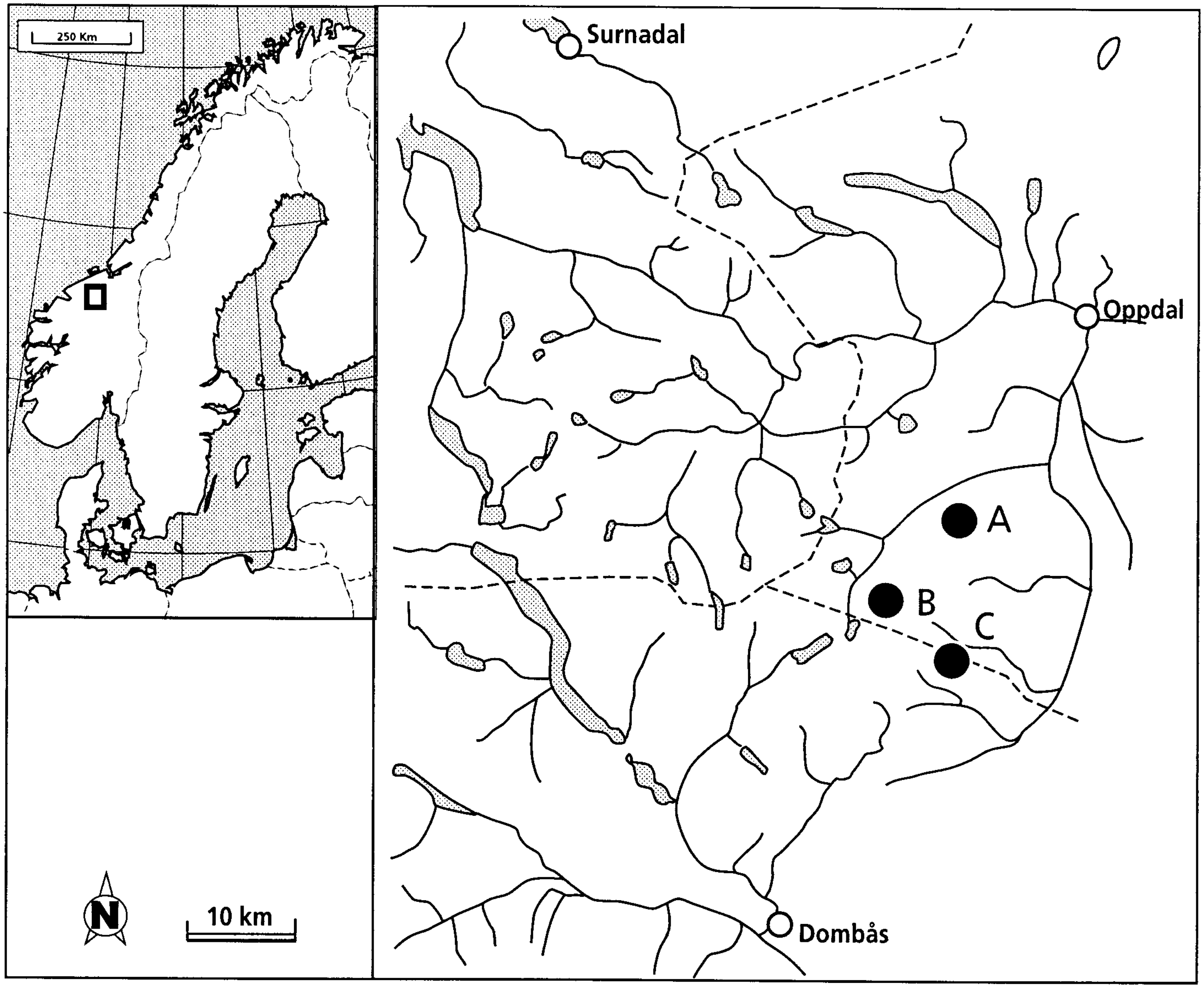

FIG. 1. The location of the Snøhetta area in south-central Norway, showing the three adjacent arctic fox territories (A, B, C) where reproduction was monitored and scats were collected between 1988 and 1995.

in the Snøhetta area of central Norway. Our aim is to compare seasonal and annual variation in food habits to prey availability and reproductive output.

STUDY AREA

Climate and Geography

The study area was located on the 4400 km^2 Snøhetta plateau in central Norway (62˚20′ N, 9˚30′E, Fig. 1). The plateau has an average altitude of 1300 m, with peaks reaching up to 2200 m. The tree line occurs between 900 m and 1000 m. Above the tree line there is a sequence of alpine meadow and lichen heath communities up to about 1500 m, above which there is little vegetation. Deep, narrow valleys of coniferous forest on almost all sides separate the plateau from neighbouring plateaux. The climate is relatively continental, with a mean annual temperature of -0.3˚C. January is the coldest month (-9.8˚C) and July is the warmest (+9.9˚C). An average of 440 mm of precipitation falls annually.

Potential Prey for Arctic Fox

The largest species available as food for the arctic fox is wild reindeer (*Rangifer tarandus*). Approximately 2000 live in Snøhetta. There are no large predators in the region apart from wolverines (*Gulo gulo*), which rarely kill wild reindeer. Therefore reindeer carrion is available only from animals dying from starvation or accidents and from slaughter remains left by hunters (Landa et al., 1997). Domestic sheep (*Ovis aries*) graze on the lower parts of the plateau during the summer. Many are killed by wolverines or die from accidents and are potentially available as carrion for foxes (Landa et al., 1997). Mountain hare (*Lepus timidus*) and ptarmigan (*Lagopus lagopus*) are abundant throughout the area all year round, although their populations are somewhat cyclic in nature. The commonest overwintering passerine is the snow bunting (*Plectrophenax nivalis*). In summer, many other species of migratory passerines and waders occur in the area (Kålås et al., 1995). Of the several small mammal species that inhabit Snøhetta, bank voles (*Clethrionomys glareolus*) and Norwegian lemmings (*Lemmus lemmus*) are the most abundant. These two species go through high-amplitude cycles, or quasi-cycles, with an irregular period of approximately four years (Myrberget, 1973; Framstad et al., 1993). Other sources of food include berries and garbage of human origin, obtainable from hikers and around holiday cabins. Wolverines, stoats (*Mustela erminea*) and red foxes (*Vulpes vulpes*) are the main terrestrial carnivores that might compete with arctic foxes.

METHODS

Den Monitoring and Faeces Collection

We studied arctic foxes in the region from 1988 until 1995. The study included the monitoring of all known arctic fox dens in the eastern part of Snøhetta. We intensively studied the dens within three neighbouring territories, known as territories A, B, and C. To assist in monitoring of reproduction, a total of 25 arctic foxes (8 adults and 17 pups) were captured and radio-collared in these three territories during the study (Landa et al., 1998; Strand et al., in press). The number of adult foxes present and the occurrence of reproduction were monitored at each den every summer. Visual observations, live trapping, and radio-telemetry were used to determine the numbers of adults and pups present in the weeks between first emergence and dispersal. Reproduction was not observed at any other dens, apart from those within territories A, B, and C. Scats were collected at dens during visits to those territories in both summer (June-August) and winter (January-April). For the purposes of this analysis, we pooled the data from the three territories.

Small Rodent Abundance

Detailed estimates of small rodent density based on trapping for the whole study period were not available. Following earlier arctic fox researchers (e.g., Østbye et al., 1978), we assigned to each year a subjective rodent abundance index based on the numbers of rodents seen during summer field work. “Low” implied that rodents were almost absent; “medium” implied some visible rodent activity; and “high” referred to a peak in rodent density (Landa et al., 1997). The population fluctuations were so pronounced that there were no differences of opinion between the two observers that conducted most of the field work.

Diet Analysis

Scats were frozen after collection. For analysis, individual scats were defrosted and soaked in water for 24 hours before being broken apart. The liquid was drained, and the solid remains (hairs, feathers, bones) were spread out in a petri dish. Results were first expressed as the widely used “percent frequency of occurrence” of each prey type, i.e., the percentage of scats that contained that prey type. A drawback to this method is that it gives equal weight to trace remains of a prey type and to the dominant prey. The “percentage volume” method overcomes this problem, although other sources of error, like differential prey digestibility, still make it difficult to extrapolate from volume in scat to contribution to energetic intake (Reynolds and Aebischer, 1991; Ciucci et al., 1996). However, as these biases are constant through time, the method should accurately reflect changes in the relative importance of the different prey categories. To determine the percentage volume of each prey type *within each scat*, 50 random samples were taken from a dish containing the remains of a *single* scat, and remains in each sample were assigned to one of six prey categories; small rodent, reindeer, hare, bird, vegetation, and other. Samples were identified under a dissecting microscope by comparison with a reference collection. No attempt was made to identify either small rodents or birds to genus or species level. We compared the mean percentage volume of a prey type in scats (each scat as a data point) for each of the different prey groups in different seasons (Mann-Whitney U) and in years with different indices (Kruskal-Wallis one-way ANOVA). A parametric one-way ANOVA was used to test the effect of rodent index on number of pups observed following emergence, while Pearson’s correlation coefficient was used to examine the relationship between the annual mean percentage volume of rodents in scats with the number of pups present at emergence. For analysis of the effects of diet on reproduction, the scats from winter and summer were pooled.

RESULTS

Dietary Responses to Changing Small Rodent Availability

A total of 675 scats (464 from summer, 211 from winter) collected from the three dens (A-C) between 1988 and 1995 were analyzed. The distribution of scats varied because of the irregular occupancy and use of the dens by foxes. Small rodents were clearly the most commonly occurring prey, followed by vegetation, reindeer, hares and birds (Table 1). The “other” category, which contained sheep wool and garbage of human origin, was of negligible importance. The large sum of frequency-of-occurrence percentages for the different prey categories (276%) shows that most scats contained more than one prey category. Individual scats contained a median of

TABLE 1. The frequency of occurrence and percentage volume of different prey items in 675 arctic fox scats from three territories in Snøhetta, Norway, and the percentage of scats in which a given prey item made up more than 50% of the volume and 100% of the volume.

Prey type	% occurrence	% volume	Percentage of scats with prey	
			> 50% of volume	100% of volume
Small rodents	85.2	54.7	51.1	7.7
Reindeer	43.4	13.3	8.7	1.8
Hare	26.2	12.0	9.3	2.4
Birds	39.7	9.8	4.6	0
Vegetation	76.0	9.5	1	0
Other	2.1	0.6	1	0

three prey categories. Only 12.1% of scats contained remains from a single prey category. Others contained remains from two (28.3% of scats), three (38.8%), four (16.3%), or five (4.4%) prey categories. When expressed as percentage volume, rodents still appeared as the major component, both in overall occurrence and as the prey category that most often made up the greatest volume of each scat (Table 1). Further analysis uses only the percentage volume estimate.

We did not have enough data to analyze each year or each territory separately, so we pooled the territories together into a study site sample, and for most analyses we pooled years with the same rodent index. We found significant differences between the average percentage volumes that prey groups constituted in arctic fox scats in different seasons and in years with different availability of small rodents (Fig. 2, Table 2). Small rodents were always the prey category with the highest average percentage volume in scats, even in years when rodents were scarce. The percentage volume of small rodents in the diet showed the most dramatic increase in years when rodents were most abundant, at the expense of reindeer and vegetation in the winter diet and of birds and hares in the summer diet. Small rodents were either more important in winter than in summer, or equally important in the two seasons, depending on the stage of the rodent cycle. The most pronounced seasonal change, regardless of the rodent cycle, was the increased use of birds in summer. In years with low and medium availability of rodents, reindeer was mainly a winter food, while in years of medium and high rodent availability, vegetation was mainly a summer food. Use of hares showed no seasonal variation.

Effect of Changing Rodent Availability on Reproduction

We found signs that pups had been born in at least one territory in seven of the eight years of the study period. In two cases the litters died when very young, and at least one adult female died just after giving birth in May (Table 3). Since those animals were not present during our routine den monitoring, they were not included in the following analysis.

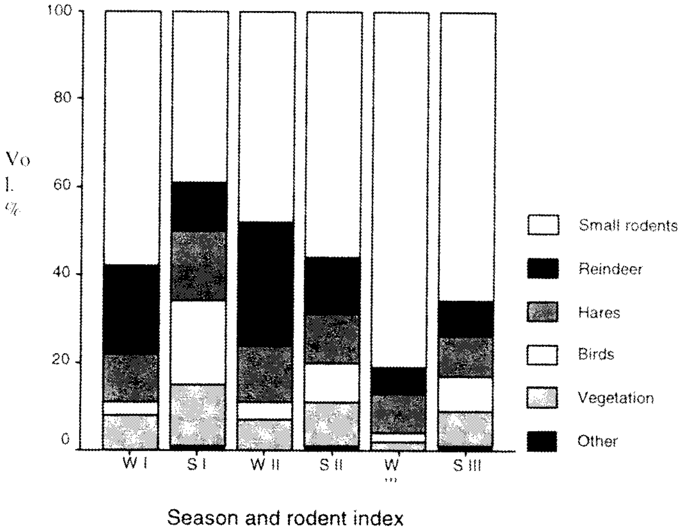

FIG. 2. Variation in the diet composition (mean percentage volume of scats) of arctic foxes in Snøhetta, Norway, from winter to summer seasons and during periods of low, medium, and high rodent abundance.

TABLE 2. Statistical tests for differences in the percentage volume of prey groups found in arctic fox scats from Snøhetta in different seasons (Mann-Whitney U-tests) and in years with different levels of small rodent abundance (Kruskal-Wallis one-way ANOVA). The numbers of scats analyzed in winter and summer for years with different rodent indices were 62, 178 (Low); 109, 166 (Medium); and 40, 120 (High).

Rodent Index	Winter (% volume)	Summer (% volume)	U	*p*
Small rodents				
Low	57.7	39.2	3738	< 0.001
Medium	48.1	56.4	6510	0.09
High	80.7	65.8	2443	0.001
χ^2	38.7	41.5		
p	< 0.001	< 0.001		
Hares				
Low	11.2	16.0	5285	0.6
Medium	12.5	10.7	7234	0.5
High	9.1	9.5	3361	0.5
χ^2	2.0	12.9		
p	0.370	0.002		
Vegetation				
Low	8.7	14.6	4768	0.1
Medium	6.8	10.2	5768	0.002
High	1.7	7.5	1346	< 0.001
χ^2	28.9	2.8		
p	< 0.001	0.3		
Reindeer				
Low	19.8	10.2	3858	< 0.001
Medium	28.2	12.6	4818	< 0.001
High	6.6	7.8	3500	0.9
χ^2	20.4	0.4		
p	< 0.001	0.8		
Birds				
Low	2.7	18.8	3760	< 0.001
Medium	4.5	9.7	5932	0.001
High	1.9	8.1	2071	< 0.001
χ^2	6.0	8.2		
p	0.049	0.017		

TABLE 3. The minimum number of pups alive at emergence and number of adults present within the study area in late summer during 1988–1995. The average percentage volume of small rodents in the diet and the small rodent abundance index (low, medium, or high) are shown for each year.

	1988	1989	1990	1991	1992	1993	1994	1995
Pups born	17	15	5	5[1]	4	0[1]	3	0
Adults present	6	4	6	8	8	4[2]	4	3
% rodent in diet	55	92	45	48	64	41	44	52
Rodent Index	High	High	Low	Med	Med	Low	Low	Med

[1] The remains of at least one extra pup were found in these years, but the pup did not survive until the monitoring period.

[2] One adult female died in spring, after giving birth but before the monitoring period.

There was a significant correlation between the annual average percentage volume of rodents in the diet and the number of pups born in that year (Pearson's correlation coefficient = 0.625, n = 8, $p = 0.049$). There was no other significant correlation between number of pups born and mean percentage volume of any other prey category ($p > 0.05$). The number of adults within the population did not correlate with the contribution of any prey types ($p > 0.05$). Similarly we found a significant relationship between the number of pups recorded in a given year and the rodent index for that year, with more pups present when rodents were most abundant (one-way ANOVA, F = 22.69, df = 2, 5, $p = 0.003$).

DISCUSSION

This study has demonstrated the existence of both a dietary response (arctic fox diet varied both seasonally and annually with changing resource availability) and a reproductive response (the availability of small rodents was an important determinant of pup production) in an alpine arctic fox population.

Dietary Response

Arctic foxes exploited all available food groups within the study area (large mammal, medium mammal, small mammal, birds, vegetation, and garbage). This concords with previous studies on arctic fox that have revealed their broad foraging niche (e.g., Kennedy, 1980; Nielsen, 1991; Prestrud, 1992; Hersteinsson and Macdonald, 1996). This generalist foraging strategy is confirmed by the finding of remains from more than one prey group in most individual scats. The implication is that arctic foxes are not constrained to a single search image during a foraging bout. Given the abundance of sheep carcasses (from accidents and killed by wolverines) within Snøhetta, it was surprising that there was little evidence of sheep in the foxes' diet. However, sheep generally use lower altitudes than arctic foxes, and the absence of wool in scats could merely indicate little spatial overlap between the two species (Landa et al., 1997, 1998).

Although there are no significant reindeer-killing predators in Snøhetta, reindeer was the second most common component found in scats. As few reindeer die during winter in this intensively managed population (few old or sick animals are present), most of the available carrion must have come from slaughter remains left over from the autumn hunt. It has been hypothesized that Scandinavian arctic foxes have reduced access to carrion left over from large predator kills now that most large predators are absent from the mountain ecosystems (Haglund and Nilsson, 1977; Hersteinsson et al., 1989). The fact that reindeer remains were common in the diet of the Snøhetta arctic fox population even in the absence of wolves does not support this hypothesis. Paradoxically, reindeer appear to be most common in the diet of foxes in study sites where large predators are absent or rare (e.g., Finland, Svalbard and West Greenland; Birks and Penford, 1990; Prestrud, 1992; Kaikusalo and Angerbjörn, 1995), rather than in sites where predators are more common (e.g., Macpherson, 1969; Kennedy, 1980).

Small rodents were the main prey of arctic foxes in all seasons and at all stages of the rodent cycle in Snøhetta. This is in keeping with results from other arctic fox populations at sites where small rodents exist (e.g., Chesemore, 1968; Macpherson, 1969; Smits et al., 1989; Frafjord, 1995; Tannerfeldt, 1997), especially those without access to the coastal environment (Fay and Stephenson, 1989). Despite this constant dominance of small rodents, we found clear seasonal and annual differences in their relative consumption. Generally, rodents (and reindeer) were more important in winter than summer. The summer diet always showed a higher proportion of birds and vegetation than the winter diet, corresponding to their greater availability during the summer season. In years with high rodent availability, rodents became even more common in the diet, and the use of other food groups decreased accordingly. This change reduced the seasonal difference between winter and summer prey consumption. Similarly, Macpherson (1969) showed that reindeer and bird consumption increased during summer to compensate for a decrease in rodent availability. However, the present study is the first of which we are aware that follows both winter and summer diet through multiple years of a rodent cycle.

The most surprising aspect of the results is the relatively small change in the occurrence of rodents in scats (less than a twofold difference) compared to the known changes in rodent availability (from a tenfold to a hundredfold difference) during a cycle (Framstad et al., 1993). Similar results were also found in Siberian and Canadian studies (Macpherson, 1969; Tannerfeldt, 1997). The implication is that diet composition does not vary in proportion to the changes in availability. This in turn implies that the major change in foraging dynamics must be in searching time, an aspect of arctic fox ecology on which there is little information. Only when these data become available will we be able to evaluate the foxes' true functional response.

Reproductive Response

A relationship between rodent availability and the number of pups produced in the study population has been demonstrated in previous arctic fox studies (Macpherson, 1969; Østbye et al., 1978; Kaikusalo and Angerbjörn, 1995) and is common for other canids such as red foxes (Englund, 1970; Goszczynski, 1989). Previous studies on arctic foxes indicated that food restriction acts mainly on pup survival, rather than on litter size or conception (Macpherson, 1969; Fay and Rausch, 1992). However, reanalysis by Angerbjörn et al. (1991) of Macpherson's data, which were based on placental scar counts in dead foxes, revealed effects on litter size at conception, indicating that food availability probably affects reproduction at all stages of development. Unfortunately, our method of estimating litter size (counts of pups in the weeks following emergence) did not allow us to determine whether a low density of rodents was reducing the number of litters conceived, the litter sizes at birth, or the number of pups surviving (Angerbjörn et al., 1991; Tannerfeldt et al., 1994).

Although pup production was closely tied to small rodent abundance, some pups were produced within the study area in all years except one. This indicates that even during a low phase of the rodent cycle, a pair of arctic foxes may be able to raise pups if they have access to enough alternative prey, such as birds or carrion, within their territory. Our rough index of rodent abundance, together with the general lack of data on the degree of spatial heterogeneity in alpine rodent cycles, does not allow us to determine whether the cycles may have been slightly out of synchrony between the territories.

In contrast to the large interannual variation in pup production, the number of adults within this three-territory system was relatively stable, and its variation was independent of the pattern of rodent abundance (Strand et al., in press). This contrast in stability between the adult and juvenile segments of the population is common among foxes facing varying food resources (Macpherson, 1969; Zabel and Taggart, 1989). No adult arctic foxes emigrated from the study area despite the changes in rodent availability (Strand et al., in press). Thus it appears that arctic foxes adopt a "sit and wait" strategy on their territories, rather than moving in search of better prey availability elsewhere (Switzer, 1993; Meia and Weber, 1995). The failure of reproduction in 1995 despite a moderate rodent density remains unexplained, as does the slow decline in the number of adults in the population.

Our results have three other implications relevant for arctic fox conservation. First, the diet analysis has identified the prey groups on which the arctic foxes are most dependent. This information can be used when mapping habitat suitability. Second, the pulsed pattern of reproduction implies that when monitoring an alpine (or tundra) population, the state of the rodent cycle must be taken into account. Lack of reproduction does not always imply a population decline: it may simply coincide with a year of low rodent abundance (Linnell et al., 1999). Therefore, monitoring must cover enough years to include at least one rodent cycle. Finally, this pulsed reproduction has implications for our understanding of arctic fox population dynamics and life history (Tannerfeldt and Angerbjörn, 1996; Tannerfeldt, 1997) and illustrates the importance of incorporating patterns of environmental variation into population models (Loison and Strand, 1998).

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