SOCIAL ORGANIZATION AND PARENTAL BEHAVIOR IN THE ARCTIC FOX

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We studied social organization and behavior of arctic foxes (*Alopex lagopus*) in 3 adjacent territories from 1988 to 1995 in central Norway, where the major rodent prey were cyclic. Twenty-five foxes were equipped with radiotransmitters and several other individuals could be recognized visually. Paired adult foxes and their cubs had home ranges that overlapped more with each other than with neighboring foxes (37% versus 2.9%) and therefore seemed to be territorial. Family composition varied from monogamous pairs, to pairs with additional adults, to an example with 2 reproducing females and 1 male in the same den. Presence of additional family members was independent of the state of the rodent cycle and the reproductive state of the breeding pair. Additional family members contributed only 2% of the food provided to young pups and were therefore not regarded as true helpers. Breeding adults remained resident within the same territory even in years with low abundance of rodents, when they did not breed. All pups left their natal territory by 6 months of age, although some subsequently returned to their natal range or one of the adjacent dens.

Key words: *Alopex lagopus,* arctic fox, dispersal, reproduction, social behavior, social organization

Larger species of canids tend to have larger litters and a relatively greater maternal investment in each reproductive event (Geffen et al. 1996). As a consequence, it has been proposed that larger species should be more social because assistance from nonreproductive group members (helpers) would be important to provide for the large number of offspring (Moehlman 1989; Moehlman and Hofer 1997). We refer to this idea as the parental investment hypothesis. The arctic fox (*Alopex lagopus*) deviates from this general trend by giving birth to larger litters (maximum litter size = 12–15 cubs) than expected for its small body size (3–4 kg) (Frafjord 1993). Although limited data are available on social organization of the arctic fox and the role of helpers is unclear, it appears that arctic foxes have helpers less frequently than expected for their litter size (Frafjord 1991; Goltsman et al. 1996; Hersteinsson and

Macdonald 1982). Moehlman and Hofer (1997) therefore suggested a hypothesis linking litter size and cost of parental investment to the superabundant food provided to arctic foxes during peaks in lemming or small-rodent populations. Abundant food might allow arctic foxes to reduce their searching time for food and thereby maintain a high investment in each pup with relatively low cost in years when food is abundant. We refer to this idea as the abundant-food hypothesis.

To better understand the role of the individual in the social system and population dynamics of arctic foxes, we designed our study to follow transmitter-equipped individuals through consecutive years (Macdonald and Courtenay 1996). We focused on composition and continuity of families, parental behavior, and the dispersal of pups and their settlement either as independent breeders or as additional group members. Our objectives were to describe social or-

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ganization of the arctic fox and to test predictions from the parental investment and abundant-food hypotheses. We focused our research on 4 different predictions: 1) arctic foxes are expected to be confined to home ranges and (similar to canids in general) to show high fidelity to their breeding areas, 2) arctic foxes are expected to be mainly monogamous but to occasionally have helpers at their breeding dens, 3) arctic fox helpers are expected to contribute significantly to parental care (parental investment hypothesis), and 4) arctic foxes are expected to be able to sustain high food-provision rates without helpers because of superabundant food in years when lemmings are numerous (abundant-food hypothesis).

MATERIALS AND METHODS

Study area.—In Scandinavia, arctic foxes inhabit alpine habitats (Landa et al. 1998) and are presently found in remnant populations in southern Norway and in the mountain ranges along the border between Norway and Sweden (Hersteinsson et al. 1989; Linnell et al. 1999). The arctic fox was a common species in Norway and subject to intensive harvest up until the early decades of the 20th century. Changes in management regulations protected declining populations in 1930 in Norway, 1928 in Sweden, and 1940 in Finland. Despite this long period of protection, populations have failed to recover, and the arctic fox is regarded as vulnerable or threatened with extinction in Fennoscandia (Frafjord and Rofstad 1998; Hersteinsson et al. 1989; Linnell et al. 1999). Recent population estimates indicated that the total population of arctic foxes in Fennoscandia probably is as few as 100 adult foxes (Angerbjörn et al. 1995; Linnell et al. 1999).

Our main study area (about 800 km²) was located in the eastern part of the 4,400-km² Snøhetta plateau in central Norway (62°20′N, 9°30′E). Average altitude of the plateau is 1,300 m, with peaks reaching up to 2,200 m. At this latitude, tree line occurs between 900 and 1,000 m. Above the tree line, there is a sequence of alpine meadow and lichen-heath communities up to about 1,500 m, above which there is little vegetation. The plateau is separated from neighboring plateaus by narrow but deep forested (co-

niferous) valleys on almost all sides (Landa et al. 1998). The climate is continental with a mean annual temperature of −0.3°C; January is the coldest month ($\bar{X} = -9.8$°C) and July is the warmest ($\bar{X} = 9.9$°C). An average of 440 mm of precipitation falls annually. The diet of arctic foxes in the Norwegian alpine areas consists mainly of rodents (primarily *Lemmus lemmus*) that undergo temporal fluctuations with a somewhat irregular period of about 4 years (Angerbjörn et al. 1995; Ims and Steen 1990). Secondary prey includes birds, hares (*Lepus timidus*), and scavenged remains of wild reindeer (*Rangifer tarandus*—Strand et al. 1999).

Capture and marking.—Foxes were trapped at breeding dens and other locations associated with high activity in single-door, collapsible box traps (50 by 50 by 130 cm). Traps were prebaited for a minimum of 1 week before trapping and checked at least once daily when in use. Foxes older than 10 months (captured in winter) were equipped with transmitters on a fixed collar (80 g), and pups were equipped with an expanding collar (60 g) with a drop-off weakness zone that caused collars to drop after ca. 8 months (Televilt International AB, Lindesberg, Sweden). All foxes were restrained manually and released at the capture site after handling. Foxes were recaptured for collar replacement each year. In addition, about 20 other dens were checked for evidence of use by foxes, both in winter (February–April) and in summer (June–September). Although some tracks and other signs of fox activity indicated that foxes visited other dens, no reproduction occurred at those sites. Foxes included in our study, therefore, represented a large proportion of foxes living in the Snøhetta area. Because of the relatively intense trapping effort (150–200 trap nights each winter) and the amount of time spent in the field each year, we were confident that no individuals were overlooked in the vicinity of the study dens.

Range use and fidelity to breeding areas.—We studied reproductive behavior and family composition of transmitter-equipped adult foxes and pups on 3 adjacent territories (A, B, and C) in 1988–1995. Territories A and B were studied from 1988, but territory C was included from 1991 to 1995. Initial behavioral studies in 1988 and early 1989 were based on short-term individual recognition of pelt color or other individual characteristics. From 1989, foxes were equipped with transmitters. Locations of trans-

mitter-equipped foxes were obtained from air-craft, from snowmobiles, and on foot. We calculated the sizes of home ranges using a standard computer program (RANGESV—Kenward and Hodder 1996) and estimated home ranges using outer convex polygons (Harris et al. 1990). A complete analysis of home-range sizes and habitat selection was completed by Landa et al. (1998). Here, we used the home-range data of Landa et al. (1998) to test for overlap in spatial distribution between and within families of arctic foxes. We calculated overlap between individual and family ranges as the percentage of overlap between successive combinations of individual foxes within and between different family groups. The linear distance from individual locations to the natal den was used to express dispersal. A fox pup was considered to be outside its family range when the distance to the natal den exceeded 2 times the approximate radius of a family range.

Behavioral observations.—Parental behavior and time budgets were recorded at breeding dens in July and August when pups were 6–12 weeks old. Observations of behavior were made from a tent located 100–400 m from dens. Data were recorded during 3-h observation bouts unless prevented by poor visibility. We analyzed data of behavioral observations only when we were able to categorize each of the adult animals as at the den, away from den, or inside the den. Thus, we did not record data if we did not know if an animal was inside or away from the den. We imposed those restrictions to make sure that all individuals had an equal probability of being assigned to each of the categories. Adult foxes were classified as breeding foxes (males and females) or additional family members. We based social status on behavioral observations and relocations of foxes. Because additional family members were young from previous litters that used their natal (or parental) range and also occupied the den site, we are confident of our classification of those animals as family members.

Parental investment.—To test predictions 3 and 4, we recorded the number of times that adults returned to the denning area with food and the number of times that adult individuals provided pups with food (either by arriving at the den with food or by collecting cached food from the den or the near vicinity of the den). Time spent by adults away from the den and rate at which they provided pups with food were lat-

er calculated as frequencies in relation to total observed time at each den, total observed time, and litter size. Because home range size, parental behavior, reproduction, and rates of food collection were expected to vary with prey availability (prediction 4), it was important to control for abundance of rodents. An annual index of abundance of rodents (I = low, II = medium, III = high) was prepared from limited trapping data and direct observations (Landa et al. 1997). By assuming that parents divided their time and parental effort between food collection (when away from the den) and other activities at the den (e.g., guarding behavior), it was possible to determine if food availability (rodent index) affected parental effort in food gathering (prediction 4). Effects of varying abundance of rodents on diet and reproduction were described by Strand et al. (1999).

Statistical treatment.—Because data used to test the percentage of overlap in range use between individuals and families were calculated from pairwise combinations, we applied a randomization test to create a probability distribution for these data (Manly 1991). Differences in time budgets were tested using Kruskall-Wallis tests and chi-square tests when comparing time budgets of adult foxes. Means are presented with 1 standard deviation. Linear associations between variables were tested by calculations of nonparametric correlation coefficients. Computations were performed in the SPSS program (Nurosis 1996), and the bootstrap calculations were performed using the RT program (version 1.02—Manly 1991).

RESULTS

Home-range use and family continuity.—During the study, we equipped 8 adult foxes (>1 year) and 17 pups with radiotransmitters. Eight pups were followed beyond 1 year of age. We estimated annual home ranges for 11 different arctic foxes. Paired foxes and pups staying as additional family members had annual home ranges that overlapped by 37% ± 29% ($n = 32$). That overlap was greater ($F = 139$, *d.f.* = 1, 123, $P < 0.01$) than the overlap among foxes from different families, which overlapped by 2.9% ± 10% ($n = 92$). On average, an adult survived and remained at its breeding territory for 4 ± 1 seasons. That was likely
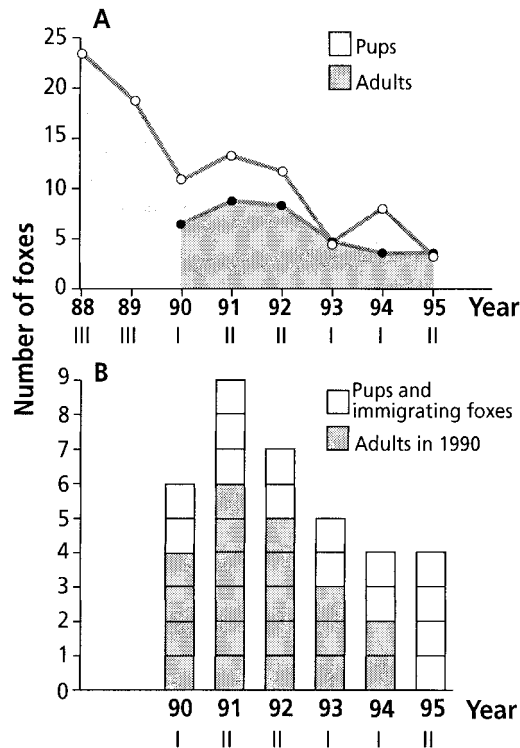
FIG. 1.—A) Number of pups and adult arctic foxes at Snøhetta, Norway, 1988—1995. B) Number of adult foxes resident at the breeding dens in 1990 and those that replaced the residents during the study.

an underestimate because the individual histories of residents prior to 1989 were unknown. We found 6 resident adult foxes at dens A and B in 1988 and 1989 (Fig. 1A). In 1991, 9 foxes >1 year of age (territory C was not studied prior to 1991) occupied the 3 territories. By 1995, all adult foxes collared during the 1st years of the study had died or vanished from the study area (Fig. 1B). The abundance of adult foxes at the 3 territories thus declined by 55%, and the total population declined by 83% (Figs. 1A and 1B). Adults were replaced by 3 pups that remained in their natal territory, by 1 pup reared at 1 of the other dens, and by 3 animals that apparently were born outside the study area (Fig. 1B).

Family composition and reproduction.— Single adult foxes occupied dens in 3 sum-

mer seasons, monogamous pairs in 9 seasons, and monogamous pairs with 1 additional adult in 7 seasons (Fig. 2). Four adult foxes also used den A in 1991 (Fig. 2). One of the dens was left unoccupied in 1 year (den A in 1995). Dens A and B also contained additional family members in 1988 (Fig. 2). Both females at den A in 1988 were lactating, and the pups suckled from both of them. Because both females were lactating, we judged this to be 2 different litters raised in a common den. We do not know to which extent females shared the litters (i.e., whether they had a cooperative reproduction or simply shared the den).

Eight litters, totaling 45 pups, were observed. Litter size was higher in years with high rodent indices (Kruskall-Wallis $\chi^2 = 9.0$, $d.f. = 2$, $P < 0.01$). Three of the reproducing families consisted of a monogamous pair with an additional family member, and 5 of the reproducing families consisted of monogamous pairs. Families with additional members failed to reproduce in 5 seasons; the monogamous pairs failed to reproduce in 4 seasons (Fig. 2). We observed no relationship between family size and probability of breeding.

Den use and parental behavior.—We recorded 459 h of parental behavior during the 8 reproductive events included in our study. Breeding males and helpers spent a larger proportion of their time away from the breeding den ($\bar{X} = 94\%$ and $\bar{X} = 100\%$, respectively) than did breeding females ($\bar{X} = 75\%$; $\chi^2 = 3.84$, $d.f. = 1$, $P < 0.05$ as compared with males, and $\chi^2 = 6.25$, $d.f. = 1$, $P < 0.01$ as compared with helpers). Males and females used less time away from the den in years with a high rodent index (Kruskall-Wallis $\chi^2 = 8.9$, $d.f. = 2$, $P < 0.01$). Parents were away from the den nearly 100% of the time in years with few rodents (Fig. 3A), and the pups tended to be unattended for a larger proportion of time in these years (Fig. 3B). The parents also tended to bring food to the den at a higher rate in years with high rodent indices (Kruskall-Wallis $\chi^2 = 3.6$, $d.f. = 2$, $P =$

FIG. 2.—Composition and changes in 3 arctic fox family groups at Snøhetta in south-central Norway. Arctic foxes equipped with transmitters were studied from 1990 to 1995. Large circles illustrate the 3 adjacent territories; small shaded circles illustrate the pool of floating or dispersing foxes. Open squares indicate dead foxes or foxes with which we lost contact. Arrows between symbols represent movements or changes in social status of the different foxes. α = reproducing and resident foxes; β = additional family members. Litter size is given by the number of individual pups seen and marked at each den. Unmarked animals are given without numbers, and pups are noted together with their parents.

0.16). Because litter size also varied with food availability, we corrected the rate that parents provided their pups with food for litter size and found that relative food provisioning rates tended to be higher in years with high rodent indices (Spearman's rank correlation $r_s = 0.66$, $n = 7$, $P = 0.07$; Fig. 3C).

Adult foxes were seen bringing food to the den on 42 occasions. Of those, 56% of returns with food were by breeding females ($n = 25$) and 40% were by breeding males ($n = 15$). Additional family members only brought food to the den on 2 occasions (4%). We did not observe any attempts by parents to partition food distribution between pups. Pups that failed to receive food when parents appeared at the den usually started to beg additional food. About 30% of observed begging sequences (26 of 77) elicited a positive response from breeding

females as they regurgitated food. On a few occasions ($n = 5$), the pups also begged from breeding males, who never regurgitated food. Pups did not beg from additional family members, who did not regurgitate food.

Dispersal and settlement.—Of 45 pups seen at the dens, 31 were eartagged, and 18 of those eartagged pups were equipped with transmitters. All 10 pups that we maintained contact with for >6 months increased their distance from the natal area during their 1st winter (Fig. 4). On average pups were 1st found outside their natal range at 6 ± 2 months of age ($n = 10$). The longest maximum distance to the natal den recorded for a single cub was 40 km, whereas the cub that moved the shortest distance was recorded at a maximum of 20 km from the natal den (Fig. 4). Three pups returned to their natal area after trying to
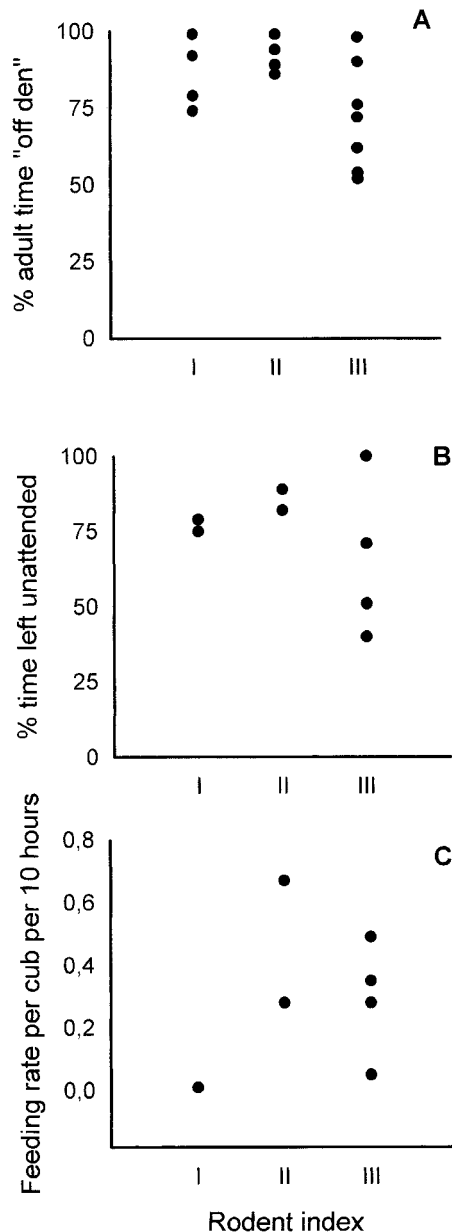
FIG. 3.—A) Percentage of the time adult foxes at Snøhetta were away from their den site. B) Percentage of time the pups were left unattended. C) Rates at which parents fed their pups in relation to rodent abundance. Rodent abundance index: I = low density; II = intermediate density; III = high density.

disperse. We only found 1 litter during the last years of the study (den A in 1994, Fig. 2), and none of the pups that returned to their natal area reproduced.

DISCUSSION

Range use.—Arctic foxes belonging to the same families had an extensive overlap in range use, but foxes belonging to different family units overlapped less. Although no aggressive encounters were seen in Snøhetta, the spatial pattern observed is usually taken as evidence for territoriality in other canid studies (Macdonald and Courtenay 1996; Zoellick and Smith 1992). Analysis of home-range sizes and habitat preference showed that males in our study had ranges of about 45 km^2 in the breeding season and 49 km^2 during the whole year; females on average used 16 km^2 in the breeding season and 28 km^2 during the entire year (Landa et al. 1998). Although reported home ranges of arctic foxes vary greatly through the species range, the ranges used by the foxes in our study area are similar to those reported from other comparable environments (Angerbjörn et al. 1997; Anthony 1997; Eberhart et al. 1982). These results, combined with the fact that no adults dispersed, support prediction 1.

Fewer data are available for comparisons of dispersal distances. Returned ear tags in Alaska and Canada have shown that some foxes can travel large distances (Eberhardt and Hanson 1978; Garrott and Eberhardt 1987). Our data and those of a study of earmarked foxes in Sweden concur in placing normal dispersal distances at <40–60 km (Tannerfeldt and Angerbjörn 1996). These results are in general agreement with DNA fingerprinting data and frequencies of mitochondrial DNA haplotypes, which suggest a general differentiation and isolation between foxes at our study site at Snøhetta and a population in Børgefjell, which is 425 km further north (Strand et al. 1998).

Family composition and parental behavior.—In accordance with others studies (Eberhart et al. 1982; Frafjord 1991; Her-
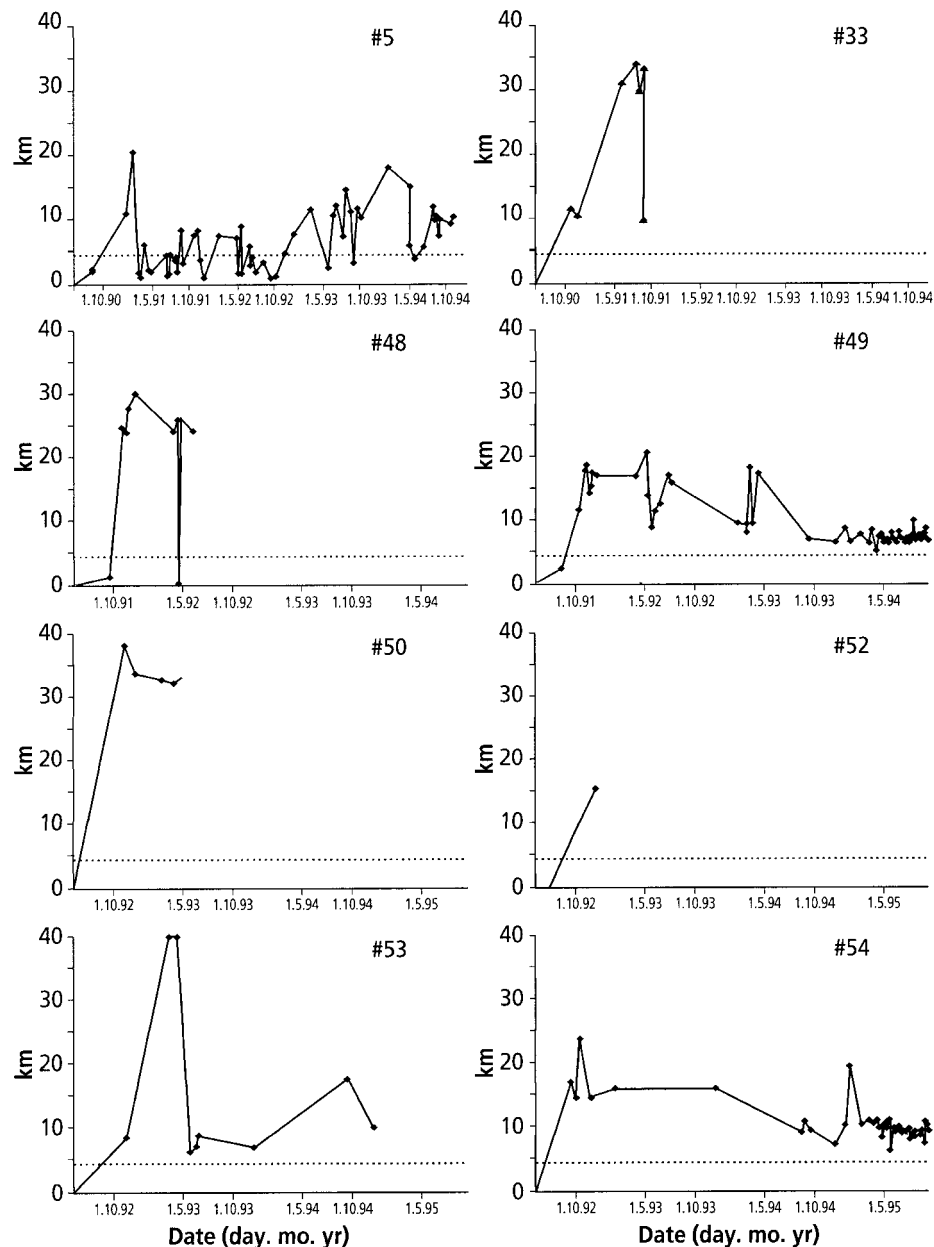
FIG. 4.—Individual dispersal distances of transmitter-equipped arctic fox pups in the Snøhetta area in south-central Norway. Distances of individual relocations are plotted against time, and the horizontal and dotted lines indicate the approximate borders of the parental home range (size of the horizontal axes may differ for some individuals).

steinsson and Macdonald 1982) and prediction 2, we found foxes in monogamous pairs, in polygynous groups, and as breeding pairs with additional nonbreeding

adults. Because we found additional group members in years when residents failed to reproduce and because these additional group members only provided limited food

for pups, we conclude that factors other than the need for assistance in food provisioning to pups must determine group formation in arctic foxes. Therefore, our data do not support prediction 3. As such, these additional group members cannot be regarded as true helpers (see Moehlman 1989). However, our methods could not detect benefits associated with activity away from the den, such as caching food or assisting with defense of the territory, and benefits such as vigilance at the den.

Because the return of juveniles of independent age to the natal den has been documented in other canid species (Macdonald and Courtenay 1996), the presence of additional group members must be considered relative to the costs and benefits of their own dispersal or philopatry in addition to the possible benefits they might provide to the reproductive pair. Our data on parental time budgets showed that adult foxes used virtually 100% of their time away from the dens in years with few rodents. This adjustment in foraging time helps explain how rodents can still dominate the diet in years of low rodent availability (Strand et al. 1999). Studies of uteri of Canadian arctic foxes have shown that they also give birth to large litters in years with few rodents (Macpherson 1969). The smaller litter size recorded at the dens in years with few rodents might therefore be largely a result of reduced survival following food limitation, as suggested by Macpherson (1969).

In our study, pups born in years with low food availability were left unattended for a large proportion of time and could have been exposed to a higher predation risk, as suggested by Frafjord et al. (1989). Our analysis indicated that parents used less time to gather food in years when rodents were numerous. Parents also tended to provide their pups with food most frequently in years with high lemming indices. Even when these data were corrected for litter size, parents had a higher food-provisioning rate per pup in years with high food availability. If parents optimize their time between food gathering and time with the pups at the den (e.g., guarding behavior), our data support prediction 4 and Moehlman's (1989) explanation, linking large litter size body mass ratio in arctic foxes to their variable environment. This line of argument also follows general life-history theory, because fluctuating environments are expected to select for an increased litter size if generation length corresponds to fluctuations in the environment (Tuljapurkar 1985). Generation length of arctic foxes is in fact identical to the period of their population cycles in Scandinavia (Angerbjörn et al. 1995; Loison and Strand 1998).

Alternative hypothesis.—In addition to Moehlman (1989) and Moehlman and Hofer (1997), several authors have suggested other hypotheses to explain evolution of social behavior in small canids (Lindström 1986; Macdonald 1983; von Schantz 1981). These hypotheses consider the distribution and variability of resources used in reproduction as possible evolutionary mechanisms. For example, von Schantz (1981) proposed a model for red foxes (*Vulpes vulpes*) that included both territoriality and environmental variability. He assumed a constant territory size but allowed availability of food to vary annually. He concluded that a cyclic environment might provide a territory with surplus resources in peak years because territory size was expected to be adjusted to secure survival in bad years. He predicted that adults would accept additional family members in good years. In contrast, Lindström (1986) suggested that a selection for delayed reproduction might by favored by the potential to inherit the parents' breeding territory. Tannerfeldt and Angerbjörn (1996) also suggested a hypothesis explaining delayed reproduction in terms of smaller and stage-dependent dispersal. In our study, no philopatric individuals reproduced within their natal range, which supports Tannerfeldt and Angerbjörn's (1996) hypothesis involving a high risk of reproductive failure connected to a philopatric strategy. However, we only de-

tected 1 incidence of reproduction in the last years of our study, providing no possibility to separate the hypothesis of Lindström (1986) from that of Tannerfeldt and Angerbjörn (1996).

Individual behavior and fluctuating resources.—The total number of foxes declined by 83% during our study. Although this decline might seem dramatic, declines of 80–90% in years following a peak in rodent abundance are documented elsewhere and are one of the basic characteristics of population dynamics of arctic fox (Angerbjörn et al. 1995; Bannikov 1970; Hersteinsson 1993; Kaikusalo and Angerbjörn 1995; Loison and Strand 1998). This variability, with successive and autocorrelated shifts in food availability, might provide a link between environmental variability, life histories, and social behavior of arctic foxes. Recent studies on small rodents and arctic foxes have shown that spatial synchrony of populations of lemmings and arctic foxes decreases over larger geographic distances (Angerbjörn et al. 1999; Ims and Steen 1990; Mackin-Roglska and Nabalgo 1990; Steen et al. 1996; Tannerfeldt 1997). Populations of arctic foxes might thus be expected to have both strong temporal and spatial variation in reproduction. Arctic foxes are reproductively mature during their 1st winter. The fact that all pups initially left their natal home ranges might therefore be explained as attempts to find a breeding area or an area where the phase of the rodent cycle was favorable for reproduction. If no breeding area is found, the next best strategy might be to return to the natal range and stay there, waiting to inherit the territory, or alternatively to try to disperse again in a later year. Failure to find a mate, a distinct possibility when populations are at such low levels as in Snøhetta, also may encourage young foxes to return to their natal area.

An important result, although our data set is limited, is the faithfulness that resident animals showed to their territories despite resource fluctuations. Tannerfeldt and An-gerbjörn (1996) and others (Anthony 1997; Frafjord and Prestrud 1992) also have confirmed that residents might stay at their dens in 2 successive years. Other species, such as Canadian lynx (*Lynx canadensis*), which also exhibit cyclic population fluctuations, show postreproductive dispersal during the decline phase of cycles of the snowshoe hare (*Lepus americanus*—O'Donoghue et al. 1997; Poole 1997). Population cycles of the lynx have a longer period (ca. 10 years—Royama 1992) compared with those of arctic foxes. These contrasting strategies, involving postreproductive dispersal in the lynx and adult philopatry in arctic fox and red fox (Meia and Weber 1995), might be 2 alternative solutions to cyclic environments with differing periodicity.

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