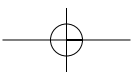
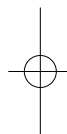
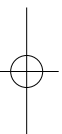
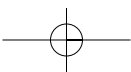
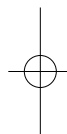
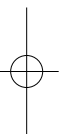
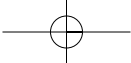


PART II

Case studies





CHAPTER 8

Arctic foxes

Consequences of resource predictability in the Arctic fox—two life history strategies

Anders Angerbjörn, Pall Hersteinsson, and Magnus Tannerfeldt



An adult Arctic fox *Alopex lagopus* female of the 'white' polar morph in summer fur. The Arctic fox has very thick and soft winter fur with two distinct colour morphs, 'blue' and 'white'. In winter, the 'white' morph is almost pure white, while in summer it is brown dorsally and light grey to white on its underside. The 'blue' moults from chocolate brown in summer to lighter brown tinged with blue sheer in winter (see Fig. 8.1) © M. Tannerfeldt.

Introduction

Considerable interspecific variations in life history characteristics are found among mammals. These include age at maturity, maximum life span, fecundity, gestation length, rates of mortality, and natal dispersal (Roff 1992). These variations are, in many cases, species-specific which makes it hard to separate adaptation to different habitats (Southwood 1977) from long-term evolutionary changes or phylogenetic constraints (Stearns 1992).

Considering the consequences of environmental variability, characteristics of individual organisms, for example, natal dispersal, territoriality, and reproductive success, can influence population and community dynamics as well as geographical range, genetics and risk of population extinction (Lomnicki 1988). By intraspecific comparisons between populations living in contrasting habitats, the selective forces specifically connected to the ecological factors that differ between contrasted habitats can be separated from the general selection

164 **Biology and conservation of wild canids**

on a species. The Arctic fox (*Alopex lagopus*) exhibits considerable intraspecific variation in litter size, where rodent and non-rodent eating Arctic fox populations, respectively, are reported to have different reproductive strategies (Braestrup 1941; Tannerfeldt and Angerbjörn 1998) (Fig. 8.2). The relationship between food availability and life history strategy is crucial to many questions on predator population dynamics. In some cases there are even distinct intrapopulation differences in Arctic fox territorial behaviour, apparently linked to differences in food predictability and dispersion (Eide 2002).

We have examined life history characteristics of two Arctic fox populations, a relatively stable one in Iceland and a fluctuating one in Sweden, and we compare them in relation to abundance and fluctuations of their main food resources.

Resource distribution in time and space

Fluctuating food resources

In the Arctic fox's Holarctic range, productivity in inland areas is low but food resources can be extremely abundant in small patches and during short time periods. The dominant pattern in these resource fluctuations is determined by lemming (*Lemmus* and *Dicrostonyx* spp.) and vole (*Clethrionomys* and *Microtus* spp.) population peaks. These prey are superabundant every 3–5 years but are otherwise scarce (e.g. Hansson and Henttonen 1985; Stenseth and Ims 1993). However, there is considerable variation around this mean periodicity (Hanski *et al.* 1993), making these rodents an unpredictable resource for Arctic foxes. Population sizes of Arctic foxes in lemming areas are regulated by lemming numbers through variation in the recruitment of fox cubs each year (e.g. Macpherson 1969; Hersteinsson *et al.* 1989; Strand *et al.* 1999). Lemming population fluctuations are generally synchronized over large areas (Angerbjörn *et al.* 2001). Some avian predators, such as the snowy owl (*Nyctea scandiaca*), may respond to scarcity of lemmings by moving hundreds or even thousands of kilometres. Although Arctic foxes have been recorded as dispersing over similarly great distances (Eberhardt and Hanson 1978; Garrott and Eberhardt 1987), movements of that magnitude are probably very risky for them. Arctic foxes are

short-lived in the wild and cannot expect to experience more than one rodent peak event (Hiruki and Stirling 1989; Tannerfeldt and Angerbjörn 1996). In Sweden, lemmings go through classic fluctuations and the Swedish Arctic fox population is a typical example of the strong relationship between Arctic foxes and lemmings (e.g. Angerbjörn *et al.* 1995).

Stable food resources

In other areas, Arctic foxes are sustained by more stable food resources. This occurs, for example, at bird cliffs and along ice-free coastlines, where food is available in all seasons although there may be substantial seasonal variability in both food abundance and type of prey available (Hersteinsson and Macdonald 1982; Prestrud 1992b). Under these circumstances, food resource levels are more predictable from year to year than in rodent areas. This is exemplified by Iceland where there are no lemmings or voles and the non-cyclic wood mouse (*Apodemus sylvaticus*) is the only rodent available to Arctic foxes. Iceland can roughly be divided into two main habitat types, coastal and inland, with prey availability generally higher in coastal habitats where the foxes feed on anything from tidal invertebrates to seal carcasses, although seabirds make up the most important constituent of the diet (Hersteinsson and Macdonald 1996). Inter-annual variation in food abundance is insignificant and irregular rather than cyclic, with a 10-year population cycle of the rock ptarmigan (*Lagopus mutus*) the only known exception (Gudmundsson 1960; Nielsen 1999). However, the ptarmigan is of minor importance as food to Arctic foxes in coastal habitats and only in northern and northeastern inland habitats do Arctic foxes show a numerical response, albeit slight, to ptarmigan fluctuations (Hersteinsson 1984).

Life history strategies

Litter size

Fluctuations in essential resources cause a strong selection pressure on the ability to adjust parental investment accordingly. Amongst canids, variance in female pre-birth investment is adjusted by litter

size (Geffen *et al.* 1996). However, recruitment to the winter population can be divided in three phases: the number of litters produced, litter sizes, and cub survival rates. These are related to food supply for several canid species, but the mechanisms are largely unknown (e.g. Englund 1970; Bronson 1989). Lindström (1989) supplied large amounts of additional food to wild red foxes (*Vulpes vulpes*) in southern Sweden, causing an increase in the number of litters born. Also, Angerbjörn *et al.* (1991) conducted a field experiment with winter feeding of Arctic foxes and observed an increase in number of litters and litter size at food manipulated dens. Thus, in the Arctic fox, the number of litters and litter sizes seem to be regulated by food supply during winter and spring, through female condition (Hall 1989; Angerbjörn *et al.* 1991).

The Arctic fox has the largest known litter size in the order Carnivora, up to 19 young, and litter size is highly variable. Comparing data on placental scars and weaned litter sizes from a large number of populations (Tannerfeldt and Angerbjörn 1998), the range of litter sizes was shown to be larger in unpredictable than in predictable environments. Further, animals from unpredictable environments had more placental scars and larger weaned litters than those from predictable environments. Reviewing published Arctic fox studies, Tannerfeldt and Angerbjörn (1998) found that none of the several hundred observed

'non-rodent' litters comprised more than 12 cubs. This is well illustrated by a comparison between the fluctuating Arctic fox population in Sweden and the stable population in Iceland (Fig. 8.2). Some areas in Iceland, such as bird-cliffs, are consistently highly productive but the maximum number of placental scars found was only 10 ($N = 1048$; Hersteinsson 1990 and unpublished data). This is only half of the maximum scar counts in rodent areas (Macpherson 1969). We suggest, therefore, that energetic limitations explain intra-population differences in mean litter sizes, but that there is a genetic component behind the observed differences between populations related to food predictability. According to the 'jackpot hypothesis', populations with unpredictable food resources generally have larger litter sizes (Fig. 8.3).

Cub survival

Boutin (1990) reviewed field experiments involving food additions, and found a positive effect on juvenile survival for 9 out of the 12 mammal species, none of them carnivores. The relationship between food availability and cub survival was examined in a field experiment on Arctic foxes in northern Sweden (Tannerfeldt *et al.* 1994). Supplementary feeding at



Figure 8.1 An adult Arctic fox (*Alopex lagopus*) of the 'blue' colour morph in winter fur. Originally Braestrup (1941) connected non-rodent eating foxes in Greenland to the 'Blue' colour morph, more common along coasts, and rodent eating foxes to the 'White' colour morph, more common in inland areas
© M. Tannerfeldt.

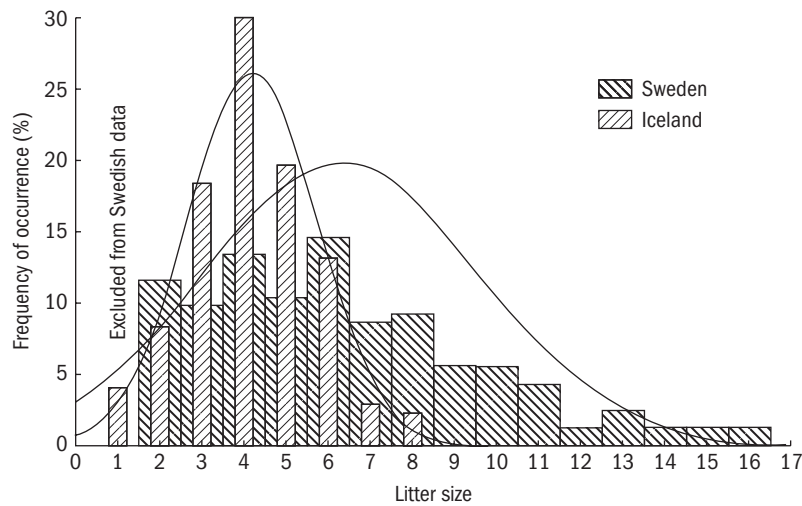
166 **Biology and conservation of wild canids**

Figure 8.2 The frequencies of litter size at weaning in a habitat with unpredictable food resources (Sweden: Mean 6.3, S.D. \pm 3.3, $N=164$) and in a habitat with stable food resources (Iceland: Mean 4.2, S.D. \pm 1.5, $N=309$).

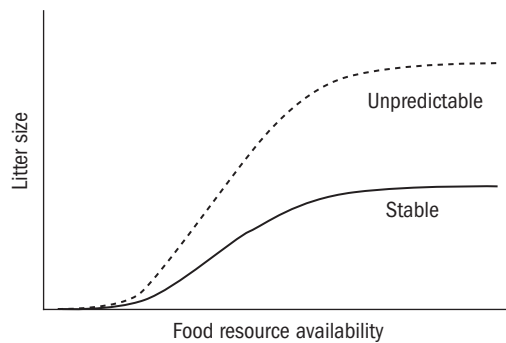


Figure 8.3 A conceptual model on the reaction norm for litter size in stable versus unpredictable environment against food resource availability (Tannerfeldt and Angerbjörn 1998).

dens during a year with medium food availability increased cub survival rates. Juvenile survival from weaning and over the next 6 weeks that year was 42% for non-fed and 92% for supplementary fed animals. During years with low food availability and no artificial feeding, no cubs survived at all (Angerbjörn and Tannerfeldt unpublished data). Only 8% of all juveniles (both fed and non-fed) survived from weaning until the first breeding season. Without artificial feeding, survival during the first year varied from 0% at low food availability to 12% at medium food availability (Tannerfeldt *et al.* 1994). The study was performed during a 20-year period without lemming peaks (Angerbjörn *et al.* 2001). Juvenile survival may be much higher during a lemming peak year.

In Iceland, on the other hand, Hersteinsson (1984 and unpublished data) found by analysing size of litters captured at breeding dens by foxhunters, and placental scars counts in their mothers, that survival from birth to 6 weeks of life was 85%, and 70% from early pregnancy to about 10 weeks of age (Fig. 8.4). This indicates that juvenile survival in Iceland is routinely similar to that during peak lemming years in Sweden. Excluding humans, the only predator on Arctic foxes in Iceland is the white-tailed sea-eagle (*Haliaeetus albicilla*), and mortality due to humans was excluded from the analysis. The hunting by people of Arctic foxes at breeding dens in Iceland peaks when cubs are 5–7 weeks old, and mostly occurs after they have reached 4 weeks of age (Hersteinsson 1988; see also sample sizes in Fig. 8.4).

Some authors have found high rates of predation on Arctic fox cubs. Garrott and Eberhardt (1982), for example, found dead cubs at 19% of the occupied breeding dens in their study area in northern Alaska, and attributed 65% of the registered deaths to predators. Macpherson (1969) suggested siblicide as a major cause of juvenile mortality, but we agree with Arvidson and Angerbjörn (1987) and Sklepkovych (1989) that there is no direct evidence of infanticide or siblicide even if young foxes feed on dead siblings.

Adult survival

In Iceland, hunters were the main cause of death, both in winter and at breeding dens in summer

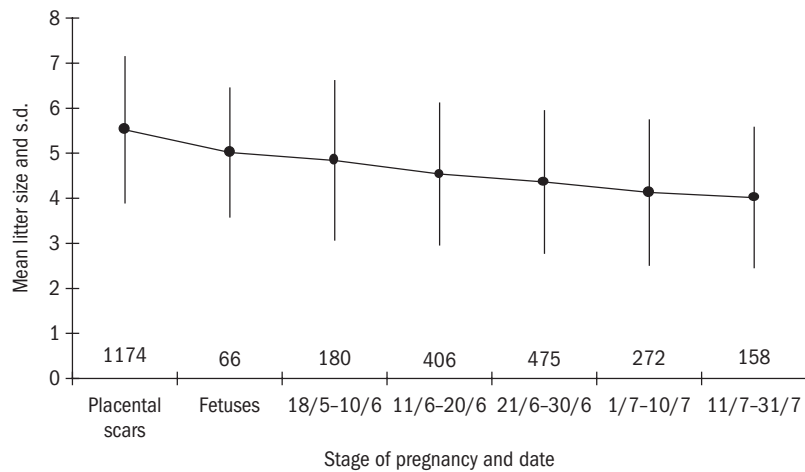


Figure 8.4 Arctic foxes are hunted in all seasons in Iceland, also at dens in summer. Dissections of vixens and data obtained from foxhunters can thus be used to track changes in mean litter size with time from early pregnancy (placental scars) through late pregnancy (fetuses) and at different periods from birth to late July (size of litters captured by foxhunters when hunting Arctic foxes at breeding dens in summer). The observed fall in mean litter size suggests that mortality from early pregnancy to weaning in early July is only about 30% (Hersteinsson 1984, 1988, unpublished). Mean date of birth is believed to be around 15 May. Numbers show sample sizes (no. of litters) and vertical lines show standard deviation.

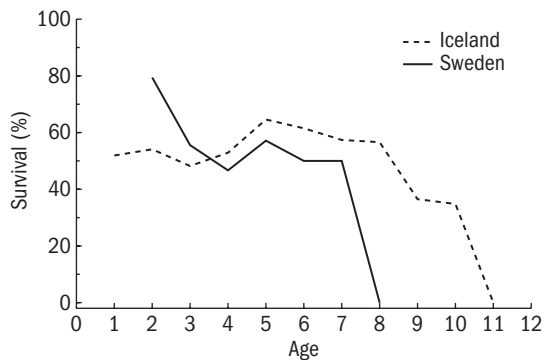


Figure 8.5 Pooled age-specific survival for Icelandic Arctic foxes born in 1985–90 (based on 1699 foxes born in these years and killed after the age of 4 months; Hersteinsson, unpublished data) and Swedish Arctic foxes born 1986–2001 (followed from birth to death, or from the time they immigrated to the study area assumed to have been 1.5 years old, $n = 34$, Tannerfeldt and Angerbjörn 1996, unpublished data).

(Hersteinsson 1992). An age-specific life table for foxes born in 1985–90 and killed after the age of 4 months, suggests that survival is sharply reduced at around 8 years of age with a maximum life expectancy of 11–12 years (Fig. 8.5).

In Sweden, some animals were followed from birth to death, others from the time they first settled in the

area (assumed to have been at 1.5 yrs old, Tannerfeldt and Angerbjörn 1996). There, all adult mortality occurred during winter, from October to May, but the causes of death could not be established. There is a striking difference between Sweden and Iceland in maximum life expectancy with no fox exceeding 7 years of age in Sweden. There was no significant difference in longevity between the sexes in either population.

Natal dispersal

Natal dispersal appears to be a discrete event taking place mostly during the first or second year of a fox's life. Most Arctic foxes settle close to their natal areas. In Iceland dispersal distances were almost normally distributed with more than half of the foxes dispersing 10–30 km (Fig. 8.6). In Sweden, on the other hand, 50% of the foxes settled within 10 km of their natal den, mostly in an adjacent territory. However, 3 of 16 foxes tagged in Sweden as cubs dispersed 80–220 km from their natal den to successful reproduction. Thus in Sweden two strategies could be detected—going far or staying close. So, although the mean dispersal distance did not vary between

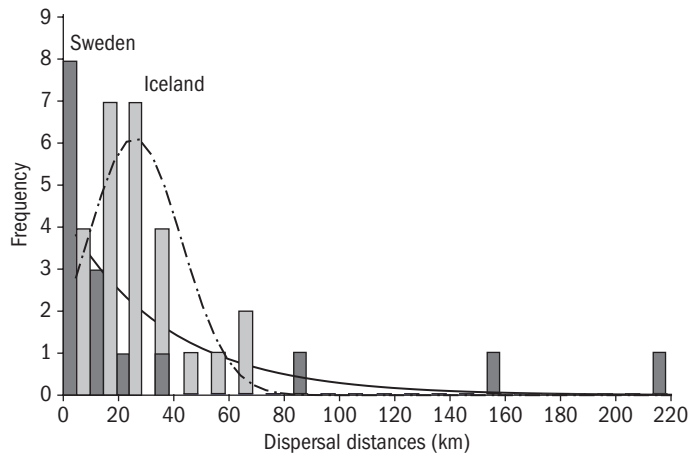
168 **Biology and conservation of wild canids**

Figure 8.6 Dispersal distances of juvenile foxes in Iceland and Sweden. Two of the Icelandic foxes were females tagged as yearling non-breeders and recaptured as breeders the following year. All others were ear-tagged as cubs. Foxes were either observed to have settled down as adults or for some individuals in Iceland killed at ≥ 12 months of age. A normal distribution was fitted to the Icelandic data (Kolmogorov-Smirnov $d = 0.07$, $p > 0.05$) but not to the Swedish data ($d = 0.34$, $p < 0.05$) where instead a log-normal distribution was fitted ($d = 0.07$, $p > 0.05$).

Sweden and Iceland, the variance in dispersal was much larger in Sweden (Levene $F_{(1, 40)} = 12.3$, $p < 0.01$). The prevalences of the alternative dispersal strategies in Sweden were associated with the population phase of small rodents. We compared immigrating settlers (dispersing from at least 50 km away) with those born in the area (dispersing < 10 km), that is, local settlers (Tannerfeldt and Angerbjörn 1996). Of 22 Arctic foxes, more immigrants (8) than locals (1) settled in the study area in pre-saturation years (increasing rodent populations). In saturation years (peak or decreasing rodent populations), the opposite was true (three immigrants compared with five locals: Fisher's exact test, 2-tailed $p < 0.05$). Further, immigrant females had a higher lifetime reproductive success (LRS) than did local females, whereas there appeared to be no difference in LRS between immigrant and local males (assuming monogamy—Tannerfeldt and Angerbjörn 1996).

There was no difference between sexes in dispersal distances (Sweden: $t = 1.50$, d.f. = 13, $p = 0.16$; Iceland: $t = 1.21$, d.f. = 24, $p = 0.24$). The dispersal strategy observed in areas where rodents are the mainstay of the diet is probably related to the large fluctuations in food resources that occur there. A disperser during decreasing rodent abundance in its natal area would be successful if it settled in an area where prey density was increasing or high, thus vastly improving the odds of it reproduced successfully. Further, a high quality individual has, by definition, a higher probability than average to survive long-distance dispersal

and thus to gain large reproductive success—the 'jackpot'. It is likely that dispersal is a state-dependent life history characteristic of individuals. Thus weaker individuals might be predicted to avoid the risks of long-range dispersal and stay in the vicinity of their natal site although that entails a low probability of breeding until the next rodent peak. Strong individuals, on the other hand, might be predicted to capitalize on their superior fitness to disperse long distances in search of a resource-rich habitat (Tannerfeldt and Angerbjörn 1996).

Social organization

The basic social unit of the Arctic fox is the breeding pair. Both parents take an active part in rearing the cubs. For the first 3 weeks after birth, while the cubs are mostly dependent on milk, the female rarely leaves the den for any length of time and the male brings most of the food on which the female feeds during what is, for her, an energetically demanding period. As meat becomes a larger constituent of the cubs' diet the roles of the parents converge and the female takes an active part in hunting and provisioning the cubs.

In Sweden, detailed observations during the breeding season revealed that in 46 of the 55 reproductive events (84%) foxes reproduced in pairs (Table 8.1; Angerbjörn and Tannerfeldt, unpublished data). There were only two cases with a confirmed extra

Table 8.1 Arctic fox group composition during the breeding season in Iceland and Sweden. Percentage of groups against all reproductive events

Country	Habitat or pop. phase	Pre-weaning %					Post-weaning %					
		<i>N</i>	Pairs only	Single female	Extra adult	Cooperative breeding	<i>N</i>	Pairs only	Singles female	Extra adult	Split litter	Cooperative breeding
Iceland												
(stable food resources)	Coastal	11	36		64		10	100				
Sweden												
(fluctuating food resources)	Crash		4									
	Low		24	2				23				4
	Increase		55	4	4	4		45	4	4	8	8
	High		2			4						6
	Total	55	84	5	4	7	53	72	4	4	8	17

adult (one female and one of unknown sex) and another three instances of females without a helping male. In nine cases fox families reproduced cooperatively in the same den. In five of these cases two families merged post-weaning. For example, in one case a lone female with cubs joined her mother in a neighbouring den and territory after an attack by a red fox when one cub was killed. In another case three females, one male and three litters with a total of 27 cubs were together in a single den. The adults came from neighbouring territories and were related: mother and her two yearling daughters and yearling son (B. Elmhagen, unpublished data). In four cases a pair split the litter in two dens and reared the cubs separately.

In protected areas in Iceland, non-breeding females are frequently found within a breeding pair's territory and these appear to be mostly yearling offspring of the pair (Table 8.1; Hersteinsson 1984, 1999, unpublished data; Hersteinsson and Macdonald 1982). This appears to be less common where and when intensive foxhunting takes place, insofar as foxhunters rarely observe more than the pair at breeding dens.

In coastal habitats in Iceland the breeding pair maintains a territory throughout the year. Overlap between territories is generally small and borders between neighbouring territories are frequently maintained from year to year (Hersteinsson and Macdonald 1982; Hersteinsson 1984) although in

some cases their exact location may shift by over 1 km (Hersteinsson, unpublished data). Scent marking by urination is much more frequent in areas of territory overlap than elsewhere and in addition the foxes use vocalizations and tail displays to advertise their presence on or near territory borders, which they patrol at least daily (Hersteinsson 1984, Frommolt *et al.* 2003). Thus they appear to expend much more time and energy in territorial defence and maintenance in Iceland than in Sweden. As food availability is stable from year to year, all territories are occupied each year where foxhunting is prohibited and there appears to be minimal scope for territory reduction. In the Hornstrandir Nature Reserve in northwest Iceland, mean territory size was estimated in 1999 at 12.1–13.5 km² or 4.0–4.5 km of coastline per territory and the number of occupied territories appears to be stable at 43–48 territories (Hersteinsson 1999; Hersteinsson *et al.* 2000). This is comparable to the 12.5 ± 5.3 km² (s.d.) mean size of territories and 7.2 ± 2.9 km (s.d.) length of coastline per territory in an earlier study elsewhere in northwestern Iceland, (Hersteinsson and Macdonald 1982).

In Sweden, on the other hand, where the population size and number of territories fluctuate widely from year to year, summer territories of the foxes varied between 17 and 31 km² with a mean of 24.6 km² (Angerbjörn *et al.* 1997). For Sweden we have no information regarding winter home ranges, but

170 Biology and conservation of wild canids

adults tend to stay in their summer ranges (Fig. 8.7). Territorial boundaries remain basically the same from year to year, although the location of the breeding den may change.

Discussion

By comparing Arctic foxes in the unpredictable habitat of northern Sweden and those in Iceland, where food availability is stable and predictable from year to year, we have pinpointed some important differences in selective forces on their reproductive and social strategies.

First, litter size at gestation and birth varies significantly between the two environments. The Swedish study area was characterized by the unpredictable availability of lemmings and other rodents, which were the mainstay of the foxes' diet. Fluctuations in the rodent population were translated into a numerical response by the Arctic fox, with a delay of about 1 year (Angerbjörn *et al.* 1999). Consequently, by the time rodent numbers are recovering from a population trough, the Arctic fox population is still small and intraspecific competition for resources is low. Thus, a superabundance of food becomes available and the foxes channel surplus energy into reproduction.

Reproductive output appears to be limited only by the vixen's physiological constraints with regard to maximum litter size during late pregnancy and lactation. In Iceland, on the other hand, the Arctic fox population is adapted to a high population density that varies little from year to year, with severe competition for territories. Furthermore, while food availability is stable, it is generally lower than in peak rodent years in Sweden. Consequently litter sizes at gestation and birth are much smaller than in Sweden (Fig. 8.2). Even in Svalbard, with stable food availability, where individuals had a body fat content up to 40% in winter, maximum litter sizes were still low (Prestrud 1992a; Prestrud and Nilssen 1995). Litter size is then adjusted to the degree of predictability in resource variation. Within each reaction norm litter sizes are adjusted through a number of plastic traits, influenced by nutritional constraints and including reduced ovulation rates, prenatal losses, and litter size reduction during the lactation period. Because of these mechanisms of pre-natal litter size regulation, large litters are only produced when resources are abundant, and reproductive costs can be kept small. If reproductive costs are small, maximum litter sizes should be larger in strongly fluctuating and unpredictable environments than in stable environments (Fig. 8.3).



Figure 8.7 An adult Arctic fox *Alopex lagopus* at a den. Arctic Foxes in Sweden often stay at their dens during the winter
© L. Liljemark.

Second, cub survival varies considerably in Sweden, depending on the abundance of rodents (Tannerfeldt *et al.* 1994). In years of low food availability very few cubs survive while survival is high in rodent peak years. In contrast, cub survival is high and inter-annually stable in Iceland, that is, about 70% from early pregnancy to the age of about 10 weeks (excluding mortality due to hunters).

Third, there is a difference in maximum life span between the two populations that could be related to breeding strategy, where a jackpot strategy has a cost in life span (Promislow and Harvey 1990).

Fourth, dispersal patterns vary between habitats. In Sweden, where fluctuations in rodent abundance are synchronized over large areas, young foxes seem either to stay close to their natal area or disperse over long distances. Dispersal over intermediate distances appears to be the least preferred strategy, perhaps because it is likely to lead to places where food availability differs little from those in the natal area, and thus the benefits of dispersal are unlikely to outweigh the risks. The heavy risk-taking associated with long-distance dispersal might make this option advantageous for only the highest quality individuals; indeed, immigrants to our Swedish study area had higher lifetime reproductive success than did non-dispersers (Tannerfeldt and Angerbjörn 1996). In contrast, Icelandic Arctic foxes showed a normal distribution of dispersal distances, most of them settling at intermediate distances of 10–30 km from the natal area. In conditions where there is a stable and predictable food supply with little prospect of significantly improved conditions with increased distance from the natal area, we deduce there would be selection against risky long-distance dispersal through areas densely populated by territorial foxes.

Fifth, social organization differed between the two populations. While a breeding pair was the core social unit in both areas, non-breeding yearling vixens were commonly found on their parents' territories in early summer in areas where foxes are protected in Iceland. We suggest that young vixens in Iceland use their natal territory as a base for exploration of their surroundings as they search for a vacant territory or a mate. As food availability of foxes is generally patchy in Iceland, particularly in coastal habitats, the minimum territory that can sustain a breeding pair and their cubs of the year, will frequently also support an

extra adult, in agreement with the Resource Dispersion Hypothesis (Hersteinsson and Macdonald 1982; Kruuk and Macdonald 1985; Eide 2002). In contrast, non-breeding yearling females were rarely found on their natal territories in Sweden but were frequently found on adjacent territories. This is probably due to the presence of non-occupied territories during an increase phase of the population cycle. Thus the foxes on neighbouring territories may be closely related, facilitating the complex social structure occasionally observed.

Conclusions

Intraspecific variation in reproductive and social strategies of Arctic foxes in Sweden and Iceland suggests that adaptations to different resource distributions in time and space have resulted in divergence in strategies between the two populations. In Sweden, where food availability fluctuates widely in time but less in space (except on a large geographical scale), the foxes have adopted the 'jackpot' strategy of enormous variation in reproductive output from year to year with much inter-annual variation in cub and juvenile survival, depending on food availability. They have also adopted two dispersal strategies. One involves only minimal dispersal and correspondingly limited risks, with the possibility of forming a larger social unit with close relatives during the breeding season—probably for predator defence. The other involves very long-distance dispersal, with attendant high risks and no possibility of forming a large social group during the first year of breeding but with the possibility of discovering an area with superabundant food.

In Iceland, on the other hand, where food availability is predictable in time and space, reproductive output is stable with small litter sizes, high cub survival, intermediate dispersal distances, and female yearlings frequently using their natal territories as a base while searching for a vacant territory or mate in the neighbourhood. While helping behaviour occurs (Hersteinsson 1984), food contributed by yearlings to their younger siblings is generally of minor importance (Strand *et al.* 2000).

We suggest that these different strategies—and particularly variation in litter size—have a genetic

172 **Biology and conservation of wild canids**

basis. Furthermore, we hypothesize that individuals in the two populations should have different competitive abilities. It seems likely that the Icelandic population has experienced strong selection for competitive ability whereas the Swedish population has not, in that it generally only breeds when food is abundant and population density is low. Our conclusions accord with an early suggestion by Braestrup (1941) that Arctic foxes in inland (lemming) and coastal (non-lemming) habitats had different life history strategies. The differences we report between the Icelandic and Swedish circumstances resonate with the notions of r and K selection (MacArthur and Wilson 1967), a concept which, despite its shortcomings in interspecific comparisons, is applicable to our intraspecific contrast (Charlesworth 1980). It remains to be seen whether the consequences of this contrast between predictable and unpredictable resources extend to the different regulatory mechanisms, but we

hypothesize that regulation of the Icelandic population is density dependent, and that of the Swedish population is density independent.

Acknowledgement

We extend our warmest thanks to all devoted, hard-working field workers in Sweden and Iceland and to the many foxhunters in Iceland who provided information and carcasses for research. LIFE-Nature and WWF Sweden provided economic support to The Arctic Fox Project SEFALO (AA and MT). This Science Research Fund of Iceland and the Ministry of the Environment in Iceland provided funds for the Icelandic part of the study (PH). We are grateful for funding from Oscar and Lili Lamms Stiftelse, Carl Tryggers Stiftelse, Magnus Bergvalls Stiftelse and the Royal Swedish Academy of Science.