

Dynamics of the arctic fox population in Sweden

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Arctic fox populations fluctuate widely with the abundance of prey, i.e. lemmings and voles (*Arvicolinae*). We have investigated the patterns and mechanisms of these fluctuations in arctic fox numbers through den inventories during 20 years (1974–1993) in Sweden. Time series analyses confirmed a four-year cyclicality in both arctic fox numbers and litter size. However, the different geographical regions were not in synchrony. The fox population in the southern parts of the distribution range has shown regular peaks during the whole period, whereas those in the northern and middle parts of Sweden have declined since 1982. In the northernmost county, also litter sizes have decreased. These differences coincided with an absence of vole and lemming peaks in the north. Experimental feeding confirmed that food availability had a direct impact on breeding success and litter size, thereby limiting the population. We conclude that the total number of arctic foxes in Sweden in 1994 is as low as 40–80 animals.

1. Introduction

The size of a population of medium-sized mammals is often difficult to estimate. Direct counts are seldom possible as many of these animals are night-active and secretive in their behaviour. For the arctic fox (*Alopex lagopus*), the most commonly used census technique has been den inventories during the breeding season (Chesemore 1975, Østbye et al. 1978, Eberhardt et al. 1983,

Garrott et al. 1984). This is a useful method since arctic foxes are extremely dependent on large dens for successful breeding, and such dens are easily recognised from the ground or by aerial photography (Macpherson 1969, Ericson 1980, Smits et al. 1989). In Scandinavia, cub-rearing is confined to the snow-free period and all litters have emerged from their dens by late July and can be expected to stay at their natal den until mid August (Frafjord 1984, 1992b, Tannerfeldt

et al. 1994). Thus, a large proportion of the breeding population can be censused by den inventories during that time of the year.

The arctic fox is an opportunistic feeder whose inland populations fluctuate widely with prey abundance, i.e. microtine (Arvicolinae) cycles (Hersteinsson & Macdonald 1982, Hersteinsson 1984, Hersteinsson et al. 1989, Frafjord 1991). In some years, large litters are abundant and the population size increases rapidly, only to crash one or two years later. These population cycles are typically repeated every 4 years. The arctic fox population in Fennoscandia suffered a drastic decline at the turn of the century, apparently due to a very heavy hunting pressure. As a result of the alarming report by Lönnberg (1927) on the status of the population, the arctic fox was protected by law in 1928 in Sweden, in 1930 in Norway and in 1940 in Finland (Hersteinsson et al. 1989). The drastic decline stopped after the protection but the population has seemed unable to recover (Haglund & Nilsson 1977, Hersteinsson et al. 1989).

Studies in Sweden (Haglund & Nilsson 1977, Bjärvall & Lindström 1984, Ericson 1986, Angerbjörn et al. 1991, Tannerfeldt et al. 1994), Norway (Østbye et al. 1978) and Finland (Pulliainen 1965, Kaikusalo 1971, 1982, Pulliainen & Ala-Kotila 1982, Kaikusalo & Angerbjörn 1995) indicate that the arctic fox still is at very low numbers in all of Fennoscandia (Hersteinsson et al. 1989). The aim of the present study is to analyse data from arctic fox den inventories made in all of Sweden to give a picture of the population status and trends. The critical number for the survival of the population is the number of adult animals during population lows. Firstly, this number determines the potential number of breeding pairs and thus the possibility for the population to recover when circumstances improve. Secondly, there is a risk of detrimental inbreeding effects and also for extinction by catastrophic events when the population is very low (Frankel & Soulé 1981, Caughley 1994, but see also Lande 1993, for a criticism of the importance of environmental stochasticity and random catastrophes). At very low densities, individuals can also have difficulties in finding conspecifics of the opposite sex.

2. Methods

2.1. Inventories

The distribution of the arctic fox in Sweden is confined to the north-western mountain and tundra areas above the tree-line in the three counties Jämtland (Z), Västerbotten (AC) and Norrbotten (BD). Arctic fox dens have been investigated in most of the arctic fox range in Sweden by local authorities over a number of years. We have used data collected from a total of 206 different dens during 1974–1993. Of the dens inspected at least 4 years, 59 were never inhabited (Table 1). Many dens have not been used by foxes for decades (Macpherson 1969, our observations). Such dens were not interesting for our analysis purposes and we have excluded them in the following. Inventories were carried out in the following way. Field workers visited dens in late July or early August and observed each den for a period of 1 to 24 hours. Besides counting the number of foxes at the den, they checked it for signs of fox presence, i.e. scats, prey remains, fox fur, scent, and wear and tear around openings. The number of dens inventoried each year varied from 9 to 95 (mean = 54.8, md = 56.5) and the number of years each den was inventoried varied from 1 to 16.

Cubs emerge from the den at the age of 3 to 4 weeks, i.e. in June or July (Garrott et al. 1984, Frafjord 1992b). Even if no fox was observed, it was usually possible to recognise a whelping den from the presence of small scats and the strong wear of vegetation and soil on the den. If there were uncertainty of what fox species inhabited the den, or whether a den contained a litter or not, data were excluded from further analyses. The terms inhabited and occupied will be used to denote whelping arctic fox dens.

It can be difficult to estimate the exact number of cubs in an untagged litter. Estimates of litter size must therefore be considered as minimum numbers. There were dens where the number of cubs could not be counted at all. Many of these were reported as having a litter of one cub, so we have excluded litters of one from our calculations of litter size. The expected number of dens in this group was low and their exclusion is not likely to have had a significant impact on the results. Dens were confirmed to contain an arctic fox litter on 238 occasions, and in 195 litters, the cubs could be counted. No cases were reported of multiple litters in one den.

2.2. Quality index

Arctic foxes prefer some dens in favour of others within their home-range (e.g. Macpherson 1969, Eberhardt et al. 1983). In years of low reproduction, litters are almost exclusively born in these preferred dens (category 3, see below). There was a risk that such high quality dens were inventoried at a higher frequency, especially during years with low density of arctic foxes. To test this, we calculated

a quality index (QI) for each den by dividing the number of years it had been inhabited (with a litter) with the number of years it was inventoried. We classified the quality indices into five categories: 0) $QI = 0$, 1) $QI < 0.25$, 2) $0.25 \leq QI \leq 0.5$, 3) $QI > 0.5$, and 4) dens inventoried less than 4 years (Table 1). We chose these categories because of the basic pattern of 4 year cycles exhibited by arctic fox populations. Thus, dens in category 0 were never inhabited and were excluded from all calculations; dens in category 1 were not (on average) inhabited every population cycle; dens in category 2 were sometimes inhabited also between peak years; and dens in category 3 were inhabited most years. Dens in category 4 were treated as a sub-sample with the same proportions of the other categories as in the whole sample. In total, 1096 inspections were made of dens in categories 1 to 4. On average, 15.0% of the inventoried dens were inhabited (md = 9.1%, range 0–58.3%), when all data were pooled and experimentally fed dens (see below) were excluded.

2.3. Number of arctic foxes

The arctic foxes were generally monogamous. Adult foxes were observed on 320 occasions. Only 4 were occasions of 3 or 4 adults at the same den, and the remaining 316 were observations of 1 or 2 adults. We thus assumed that every occupied den was inhabited by 2 adult foxes. Some parts of each county have not been investigated for arctic fox dens and there are unknown dens also in areas where inventories have been performed. We therefore needed to estimate the number of unknown dens in each county by relating our data on the observed proportion of inhabited dens to an independent population estimate. Bjärvall &

Lindström (1984) summarised winter tracking data from BD 1974–1983. Tracking was made in a grid system from February to May, covering all arctic fox habitat in the county. The first increase year after a population low and during the peak year, food availability is good and a high proportion of the arctic foxes can be assumed to breed and stay at their dens. Thus, a relatively accurate population estimate can be made from den inventories in such years. Assuming low spring mortality, tracking data from the years 1974, 1977, 1981 and 1982 could be correlated with our den inventories in BD ($r = 0.975$, $P < 0.025$, $n = 4$). Estimates from den inventories had to be multiplied by a factor of 1.312 to give the same population mean as the winter tracking data.

Another way to estimate the number of unknown dens was to compare the intensity of the performed inventories, topography and vegetation with information from our intensively studied areas. In doing so, we estimated the total number of dens in BD to be an additional 30% to the number of known dens. This was so close to the other estimate of 31.2% that we were confident in using the same method for Z and AC. We thereby arrived at a difference of 20% for both Z and AC. Hence, the estimated total number of dens in each county was calculated by multiplying the number of known dens by 1.2 in Z and AC, and by 1.312 in BD. To summarise, the estimates of the number of adult foxes were calculated by multiplying the proportion inhabited dens each year by the estimated total number of dens in each county, multiplied by 2. We also performed time series analyses of occupancy and litter size. For each county and for all data pooled, we made autocorrelation analyses to investigate the cyclicity of these variables and possible differences between the counties.

Table 1. Arctic fox dens in each county. Dens were assigned a quality index (QI) by dividing the number of years it had been inhabited (with a litter) with the number of years it was inventoried. They were then classified into five categories based on this index: 0) $QI = 0$, 1) $QI < 0.25$, 2) $0.25 \leq QI \leq 0.5$, 3) $QI > 0.5$ and 4) dens inventoried less than 4 years. Percentages are given in parentheses.

County (symbol)	Jämtland (Z)	Västerbotten (AC)	Norrbotnen (BD)	Total
Approx. area above tree-line	6 000 km ²	5 000 km ²	22 000 km ²	33 000 km ²
Known dens	40	102	64	206
Dens in Category 0	8 (20.0)	31 (30.4)	20 (31.2)	59 (28.6)
Dens in Category 1	22 (55.0)	12 (11.8)	25 (39.1)	59 (28.6)
Dens in Category 2	10 (25.0)	11 (10.8)	11 (17.2)	32 (15.5)
Dens in Category 3	0 (0)	3 (2.9)	1 (1.6)	4 (1.9)
Dens in Category 4	0 (0)	45(44.1)	7 (10.9)	52 (25.2)
Known dens inhabited at least once 1974–93	32	48	41	121
Estimated % unknown dens	20%	20%	31.2%	
Calculated no. of potential breeding dens	38	58	54	150

2.4. Food

Arctic fox populations are strongly dependent on microtines where they are present (Macpherson 1969, Kaikusalo 1971, Chesemore 1975, Hersteinsson et al. 1989). We have not been able to obtain quantitative data on microtine numbers, but large population peaks were easily identified in the field and were noted for each county. We conducted field experiments with supplementary feeding in AC 1985–1993. Food was provided at 17–50 dens each year (of which 11–14 were used by foxes) during winters 1985–1993 and at 6 (2–3 inhabited) dens each year in the summers 1990–1993. Winter food was provided 50–200 m from each den in the form of remains from reindeer (*Rangifer tarandus*) or moose (*Alces alces*). The meat was cut into small pieces and dug 1–2 m into the snow to avoid other scavengers, such as ravens (*Corvus corax*) or wolverines (*Gulo gulo*), from taking it. From January to May every year, 50–100 kg of food was put out at each den. In the summer, dog food pellets were provided in automatic feeders at the dens. The feeders were refilled whenever necessary from June to late August, totalling 30–40 kg at each den (Tannerfeldt et al. 1994). Both winter and summer feeding was substantial, but the arctic foxes could not totally rely on our feeding (Konnerup-Madsen & Hansen 1980). Adults continued hunting and when there was very little natural food, many cubs starved. Some results from the first years of these experiments have been published elsewhere (Angerbjörn et al. 1991, Tannerfeldt et al. 1994). In total, 33 litters were born in dens that were fed either during the preceding winter, during the summer or both. We have included all these in the group ‘fed dens’, and it will always be indicated when fed dens were included in

calculations. Since winter feeding started in 1985 and summer feeding in 1990, we have analysed occupancy and litter size from the periods 1985–1989 and 1990–1993 separately.

3. Results

3.1. Inventories

To find out if any category of dens was visited more or less often in some years, which might have biased the results, we tested associations between year of inventory, den category, and if the den was inhabited or not, in a log-linear likelihood test (Sokal & Rohlf 1981). Inventories were unbiased with regard to den quality (no significant association between den category and year; Table 2). As expected, the two-way association between inhabited and year was significant ($P < 0.0001$), which simply means that the proportion of inhabited dens varies between years. The significant association between inhabited and den category was caused by the definition of den category (see above). The 3-way association year–inhabited–category was not significant and thus excluded from the model. The results were the same for all three counties (Table 2).

Table 2. Log-linear likelihood analysis of inventories in the counties Z) Jämtland, AC) Västerbotten, and BD) Norrbotten. All 3-way associations were non-significant and excluded from the model. The partial association χ^2 shown was the value obtained when all other associations were controlled for.

County	Effects	χ^2	df	P	Comments
Z	category - year	14.59	15	0.48	No bias in inventories with respect to categories
	inhabited - year	91.74	15	0.000	Proportion inhabited dens differed between years
	inhabited - category	33.36	1	0.000	Trivial, caused by definition
AC	category - year	56.38	57	0.49	See above
	inhabited - year	75.77	19	0.000	See above
	inhabited - category	21.73	3	0.000	See above
BD	category - year	72.95	57	0.076	See above
	inhabited - year	79.12	19	0.000	See above
	inhabited - category	63.06	3	0.000	See above

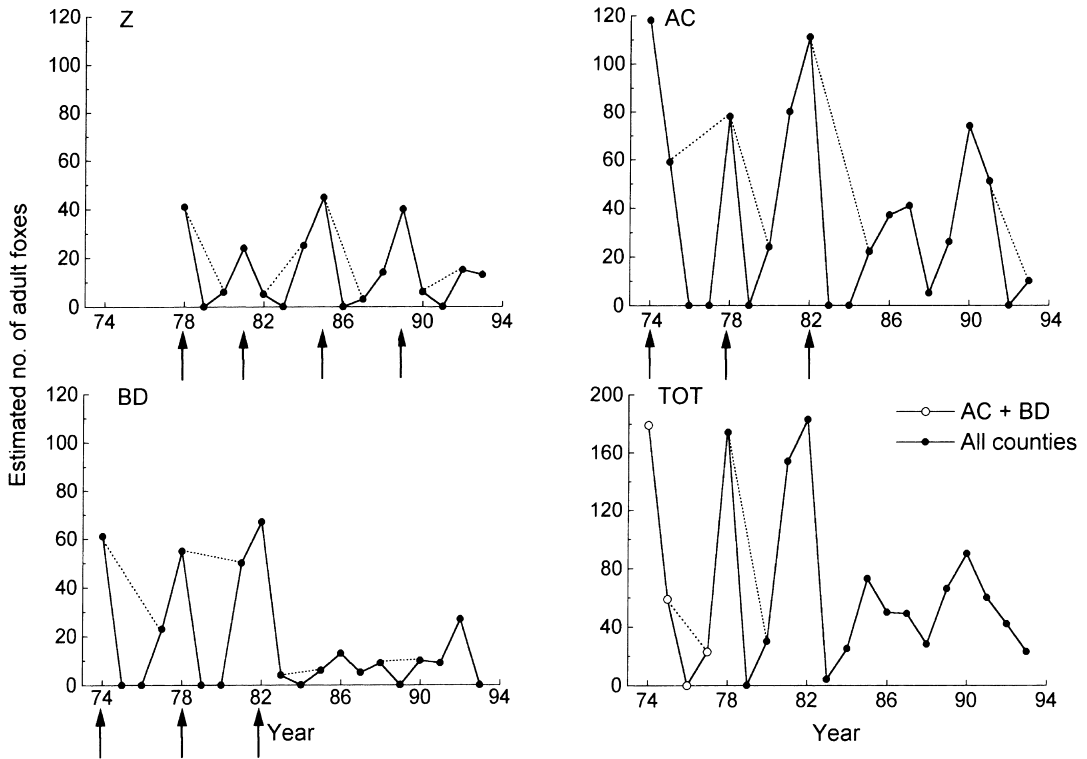


Fig. 1. Estimated number of adult arctic foxes in Z) Jämtland, AC) Västerbotten, BD) Norrbotten and TOT) all of Sweden. Dashed lines emphasise that den inventories tended to underestimate numbers during population lows. Arrows indicate peak years in microtine populations.

3.2. Number of arctic foxes

There were large population fluctuations in all counties but the patterns differed (Fig. 1). The population in Z was small but seems to have remained relatively stable over the last two decades. The situation in AC was intermediate, whereas there was a drastic decline in BD after 1982. We used a Student's *t*-test to examine differences between the first and the last 10-year period (i.e. 1974–83 and 1984–93 respectively) in proportion inhabited dens. As we were interested in the general population trend, also fed dens in AC were included. There were significant decreases in AC (despite feeding at 33 whelping dens) and in BD (AC: $t_{12} = 2.61$, $P = 0.02$; BD: $t_{11} = 3.22$, $P = 0.008$) even when years of no reproduction were excluded. In Z and for all data pooled, there were no differences (Z: $t_{10} = -0.09$, $P = 0.93$; All: $t_{16} = 1.56$,

$P = 0.14$). Adults that did not reproduce could escape detection through den inventories. It should therefore be noted that zero values in Fig. 1 indicate that no foxes reproduced, not that the actual population number was zero. Our estimates of population and litter sizes are summarised in Appendix I.

Another feature of the population fluctuations is their apparent cyclicity. We investigated the proportion inhabited dens for cyclicity with an auto-correlation analysis (Fig. 2). We performed separate analyses on all dens and on non-fed dens only. There was a strong 4 year cyclicity in the counties Z and BD, as well as for all data pooled. In AC, the cyclicity was not as strong for non-fed dens (i.e. the auto-correlation was slightly smaller than the 95% confidence limits). When fed dens were included, a 4 year cycle was marked also in AC, and an 8 year cycle was detectable.

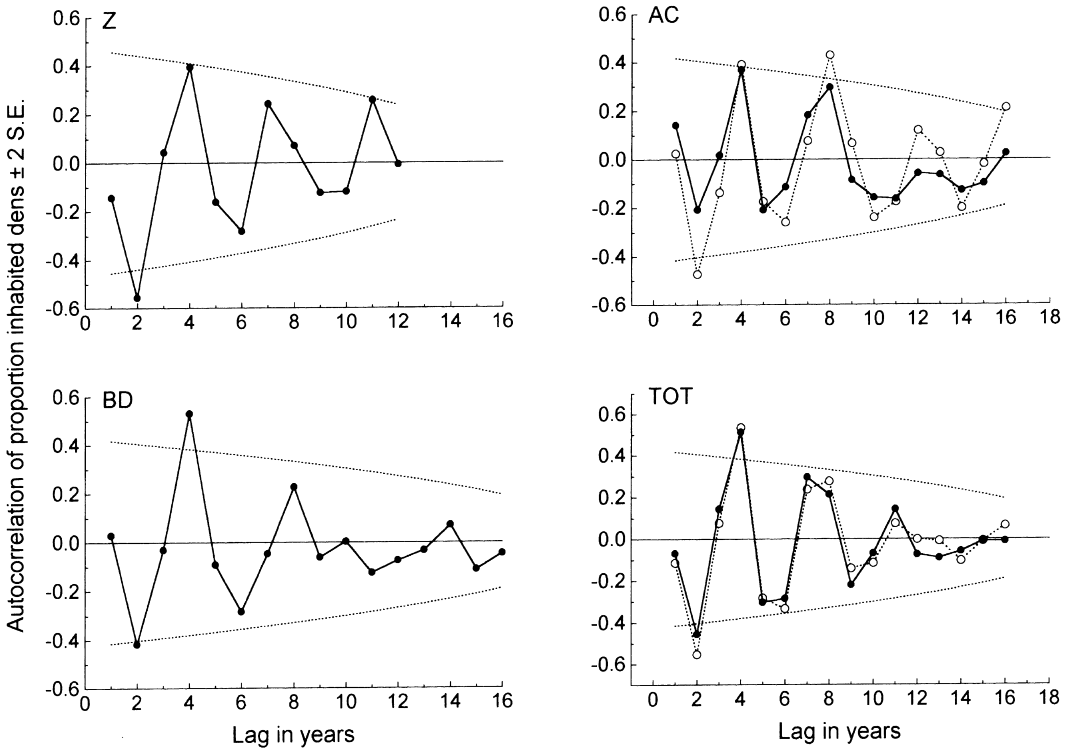


Fig. 2. Autocorrelograms for the proportion inhabited dens in Z) Jämtland, AC) Västerbotten, BD) Norrbotten and TOT) all of Sweden. Open symbols: experimentally fed dens. Converging dotted lines: $\pm 2 SE$

3.3. Litter size

Litter size varied greatly between years (Fig. 3). Minimum litter size ranged from 2 to 16 (6.3 ± 3.3 , $\bar{x} \pm SD$, $n = 164$) when the uncertain litter sizes of 1 and experimentally fed litters were excluded. In years of den occupancy below 25%, mean litter size was 5.1 ± 2.5 ($n = 57$), whereas in the more productive years it was 7.0 ± 3.5 ($n = 107$). We also compared litter sizes 1974–1983 to those 1984–1993. There was a significant decrease in litter size in BD (Student's t -test, $t_{58} = 3.64$, $P = 0.0006$). In all other cases, there were no differences (Z: $t_{65} = -0.36$, $P = 0.72$; AC: $t_{66} = 0.29$, $P = 0.77$; All: $t_{193} = 1.23$, $P = 0.22$). Litter size showed a 4 year periodicity in all counties as well as for all data pooled. In AC, there were both 4 and 8 year cycles (Fig. 4). A linear regression showed that litter size and the number of breeding attempts, measured as proportion inhabited dens, covaried ($R^2 = 0.55$, $P = 0.001$, $n = 16$; Fig. 5). Years when no litters

could be counted were excluded from calculations. This test showed that there was no negative effect of population density on litter size, but instead a positive correlation. All evidence indicated that this was affected by food abundance, viz. microtine numbers.

3.4. Natural food and extra feeding

Arctic fox and microtine rodent population peaks coincided as indicated in Fig. 1. Rodent peaks were either in lemming (*Lemmus lemmus*) or vole (*Microtus agrestis*, *Clethrionomys rufocanus* and *C. glareolus*) populations, or both. In the northern counties BD and AC, there have been no large rodent peaks since 1982, whereas the cyclicity continued in Z. There was no time lag between rodent and arctic fox peaks, but the southernmost population (Z) peaked one or two years earlier than the northern populations (AC and BD) on all occasions except in 1978.

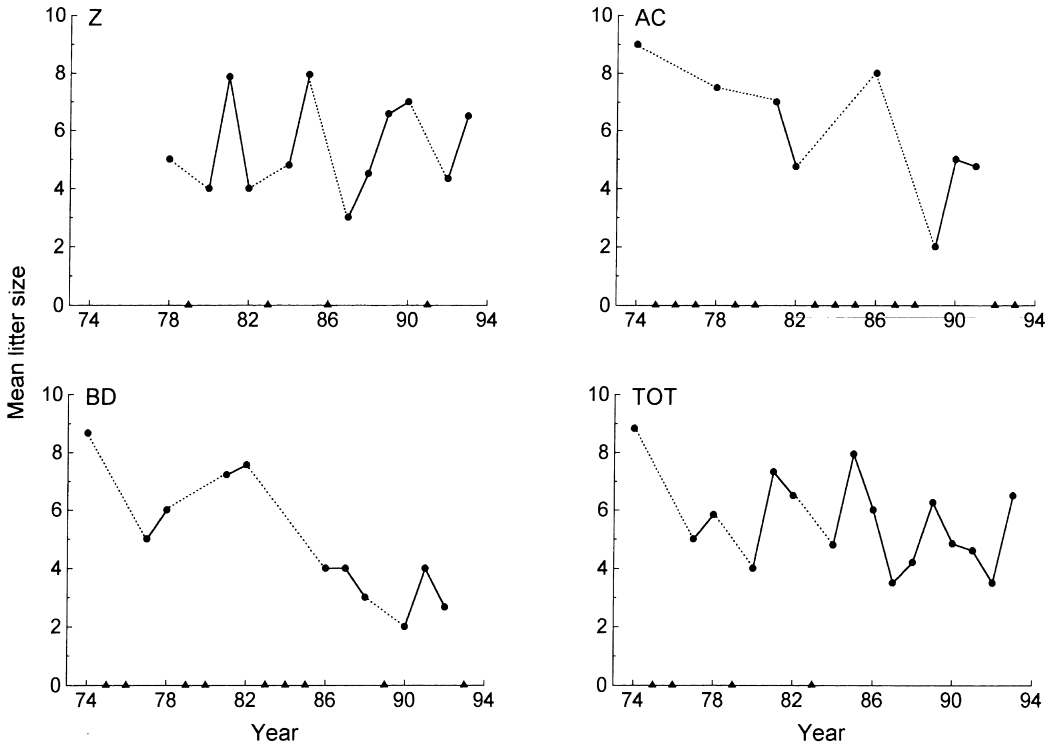


Fig. 3. Mean litter sizes in Z) Jämtland, AC) Västerbotten, BD) Norrbotten and TOT) all of Sweden. Triangles: years when no litters were found or could be counted.

The field feeding experiments were continued and we now present data on dens in AC experimentally provided with supplementary food from 1985 to 1993. We have compared winter fed and non-fed dens with respect to occupancy, using a log-linear likelihood test with year as an extra factor (Fig. 6). Fed dens were inhabited more often than non-fed dens independent of differences between years (partial association between occupancy and winter feeding, $G = 10.13$, $df = 1$, $P = 0.001$). Occupancy also varied between years ($G = 35.40$, $df = 8$, $P < 0.001$), whereas the association between year and winter feeding was not significant ($G = 8.60$, $df = 8$, $P = 0.38$). These results were the same both before and after summer feeding started in the area (1985–1989, proportion inhabited dens among feddens $P = 0.25$, for non-fed $P = 0.05$; 1990–1993, fed $P = 0.27$, non-fed $P = 0.08$). As can also be seen in Fig. 2, feeding did not interrupt the cyclicity but rather enhanced it.

When only winter feeding was performed, i.e. before 1990, there was no effect on litter size (two-way ANOVA with year as the second factor, fed $\bar{x} = 5.00$, non-fed $\bar{x} = 5.35$, $P = 0.86$, $F(1,12) = 0.03$). But with both summer and winter feeding, mean litter sizes were larger in supplementary fed dens (fed $\bar{x} = 7.06$, non-fed $\bar{x} = 4.88$, $P = 0.04$, $F(1,16) = 5.01$; Fig. 7).

4. Discussion

Comparing to North America and Russia, the proportion of occupied dens have been very low in Sweden during the last 10 years. This means that at the present density of arctic foxes, available dens and territories are not limited. For Sweden after 1982, levels of over 50% occupied dens were only reached in Z (Appendix I). The figures reported for North America were 58% in NWT (Macpherson 1969), 54% in the Yukon (Smits et

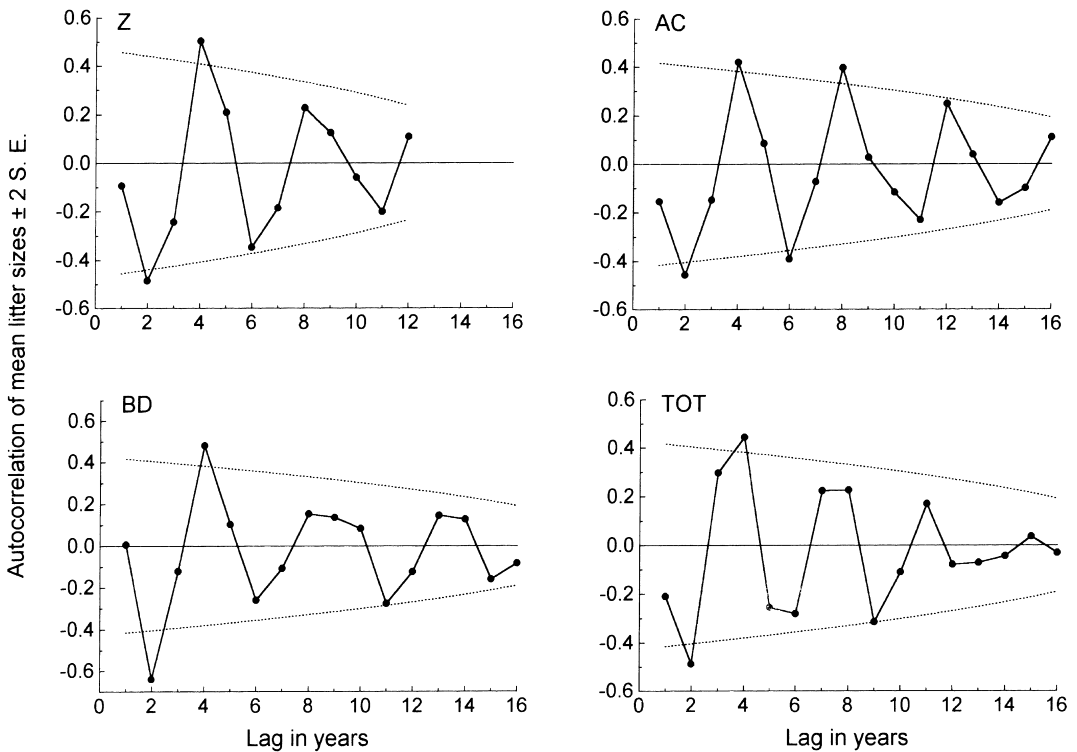


Fig. 4. Autocorrelograms for mean litter sizes in Z) Jämtland, AC) Västerbotten, BD) Norrbotten and TOT) all of Sweden. Data on non-fed litters only. Converging dotted lines: $\pm 2 SE$

al. 1989), and in Alaska up to 74% (Eberhardt et al. 1983). In Russia, Bannikov (1970) reported up to 80% of the dens being occupied.

When we estimated the total number of arctic foxes in Sweden, we used the proportion inhabited dens as the base for our estimates. This approach has to our knowledge not been used before. A large proportion of adult foxes breed successfully when prey populations are increasing or peaking. In years with low food availability, a large fraction of the population was unsuccessful in breeding and these animals escaped detection through inventories at den sites. Calibrating population estimates from den inventories with winter tracking results (Björvall & Lindström 1984), we confirmed that den inventories tended to underestimate population size during population lows, but that estimates for increase and peak years were unbiased.

There are two basic features of the population fluctuations in arctic foxes in Sweden. The first is the striking cyclicality with a period of four

years. Already Collett (1912) noted that several species on the Fennoscandian tundra, in addition to the Norwegian lemming, fluctuated widely in numbers. When Finerty (1980) re-analysed a combined data set on red (*Vulpes vulpes*) and arctic foxes from Norway (Johnsen 1929), he found a 4 year cycle. He also found a cyclicality with the same period, 4 to 4.2 years, for arctic foxes in Labrador. Kaikusalo & Angerbjörn (1995) found arctic foxes to be cyclic with a five year period in northern Finland. Hanski et al. (1991) found a close relationship between latitude and the amplitude and length of the microtine cycle periods, with longer cycles and higher amplitudes in the north. This agreed with their hypothesis that cycles are driven by specialist predators and dampened by generalists, which are more abundant in the south. The second feature of the population dynamics of Swedish arctic foxes is the decline in numbers after the peak year 1982. This decline was most pronounced in BD, and detectable in AC, but not in Z.

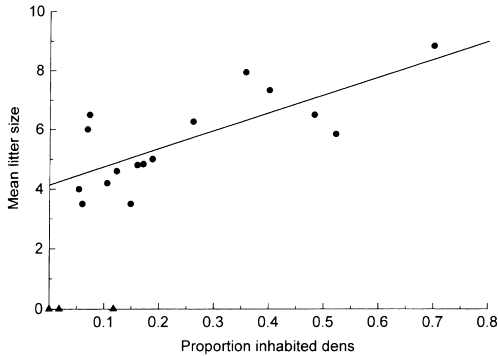


Fig. 5. Regression of mean litter size on proportion inhabited dens. Data for all of Sweden, one data point per year ($P = 0.001$, $R^2 = 0.55$, $N = 16$). Triangles: years when no litters were found or could be counted ($N = 4$). These years were excluded from the regression.

4.1. Litter size

Arctic foxes have among the largest litters in the order Carnivora (e.g. Gittleman 1989). An arctic fox female can produce 20 or even 22 cubs in a single litter (Braestrup 1941, Bannikov 1970 citing other Russian authors). Arctic foxes are thus very well adapted to respond numerically to ameliorating conditions. In our study, the largest litter size was 16 and mean litter size for all non-fed litters was 6.3. This mean was slightly lower than figures from other studies, which indicate a mean litter size of around 7 for inland arctic fox populations (Gittleman 1989, Kleist 1992, Tannerfeldt 1993). Coastal foxes have litter sizes around 5.5 and a much lower variation (Hersteinsson 1984).

There was a strong correlation between the proportion of inhabited dens and the litter size in late July and early August. This could be expected, since low food availability would lead to a low number of successful breeding attempts and also low cub survival rates (Angerbjörn et al. 1991, Tannerfeldt et al. 1994). When Hersteinsson (1984) compared litter size with the proportion inhabited dens, the correlation was positive. The test was performed in a gradient from coast to inland, which he concluded to also be a gradient from high to low food availability. Hersteinsson's findings are thus in agreement with our conclusion that low-

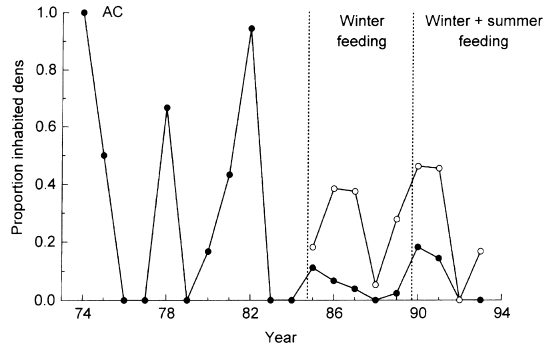


Fig. 6. The effect of feeding on the proportion inhabited dens in AC (Västerbotten) each year. Open symbols: experimentally fed dens. Filled symbols: non-fed (control) dens.

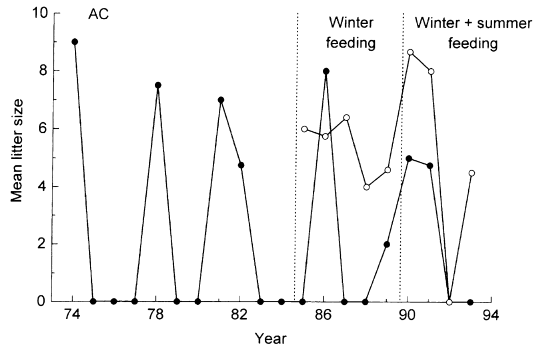


Fig. 7. The effect of feeding on litter size in AC (Västerbotten) each year. Open symbols: experimentally fed dens. Filled symbols: non-fed (control) dens.

ered food availability affects both the number of breeding attempts and litter sizes negatively.

It is noteworthy that there was no general time lag between peaks in litter size and the number of occupied dens. Considering the counties separately, we have studied 15 population peaks. On two occasions litter size peaked the year before den occupancy did, and on two occasions the opposite was true. A time lag between litter size and den occupancy would be expected if a large proportion of the cubs born in a peak year survived to breed during the next year. Yearling arctic foxes do breed, but they are not as successful as older foxes (Macpherson 1969, Hersteinsson 1984). There are two possible explanations for the absence of a time lag.

One is that during years of low microtine abundance, yearlings failed early in their breeding attempts. Another, perhaps more plausible, explanation is that only a very small fraction of the cubs survived their first winter even after a 'good' year (Tannerfeldt *et al.* 1994). This would explain why the population has not increased even after years of high summer food availability.

4.2. Food

Peak years in fox numbers coincided with those in rodents. In the arctic fox and many other canid species, population fluctuations are caused by changes in prey availability and the response in breeding attempts is immediate (Macpherson 1969, Bjärvall & Lindström 1984, Hersteinsson 1984, Ericson 1986, Hall 1989). The mechanism behind this has been suggested to be female condition limiting breeding attempts in some years (e.g. Angerbjörn *et al.* 1991, Frafjord 1992a). We have in this and earlier studies (Angerbjörn *et al.* 1991, Tannerfeldt *et al.* 1994) confirmed the importance and immediate effect of food availability on litter size and the number of breeding attempts for arctic foxes.

A likely reproductive pattern could be as follows. Most females mate every year (Macpherson 1969), but the number of eggs at ovulation or the number of embryos that implant vary with stored fat (Hall 1989), i.e. winter food availability. Pre-implantation losses, resorption and abortion, functions known to be common in foxes (Macpherson 1969, Englund 1970, Lindström 1981), take place at a frequency that is dependent on food availability (Englund 1970). At delivery, litter size has been reduced in relation to female condition. Birth weight might also be related to female condition, and would affect offspring survival. Food availability during early summer is contributing to offspring survival during the denning season (Tannerfeldt *et al.* 1994). So, dependent on winter and spring food availability, females carry a litter as far as possible, but may lose parts of it at any step in the process. This would explain why supplementary feeding does not interfere with the population cyclicity. When there is very little natural food, the supplement does not give a female enough

energy to breed successfully, and so, through physiological constraint, she resorbs or aborts her litter. Only when natural food abundance reaches a certain level can the supplementary food have an effect on breeding success. This means that the lower the level of natural food, the less likely is supplementary feeding to be an effective management tool for an endangered population.

It has been demonstrated that in the boreal zone of Sweden, red foxes exhibit a numeric response with a time lag of one year, with respect to rodent populations (Lindström 1982, 1989). Bjärvall & Lindström (1984), from winter tracking, found that arctic and red fox populations in northern Sweden (BD county) fluctuated synchronously. However, they made no inventories of red fox dens and did not discuss the reproductive pattern. In this study, we have seen that arctic fox population peaks have occurred one or two years earlier in southern Sweden than in the northern part. Such shifts have previously been noted in Scandinavian rodent population peaks from Norway to the Kola peninsula (Kalela 1949, Curry-Lindahl 1975, Stenseth & Ims 1993). Apparently, the multi-annual rodent population fluctuations in Z are synchronised with those of Hardangervidda in Norway (Stenseth & Ims 1993). Henttonen & Kaikusalo (1993) suggested that lemmings in central Fennoscandia have more regular cycles than lemmings in northern Finland due to climatic differences. It was also noted by Finerty (1980) that cyclicity of foxes was stronger in central than in northern Norway. This raises the question whether the absence of vole and lemming peak years in the bare mountain areas of BD is an effect of natural, long-term fluctuations. Alternatively, this could be connected to changes in predation pressure or an increased reindeer grazing. Thus, the reasons for continued microtine cycles in the south (Z) and a ceased cyclicity in the north (BD) still remain unclear and certainly warrant further studies.

4.3. Conservation

Haglund & Nilsson (1977) estimated the total Swedish arctic fox population in the early 1970's to be 45–145 animals between rodent peaks. Our

estimation for 1990, the last year before a 3 year decline, was 90 animals. Even assuming low mortality rates, the present (spring of 1994) Swedish population number is then between 40 and 80 animals. This can be compared with the situation in the winter 1911–12, a peak year in fox numbers, when one hunter in AC county was reported to have killed 60 arctic foxes (Zetterberg 1927).

When conservation of the Scandinavian arctic fox is considered, the number of breeding foxes in the first years of increase is the most important. These years are the 'bottle-necks' for the population and the total population size has often been reduced with 80–90% from peak years (Bannikov 1970, Hersteinsson et al. 1989, this study). As long as the population quickly recovers, the loss of genetic variation will not be detrimental (Frankel & Soulé 1981). But if the recovery is slow, genetic drift, directional selection or inbreeding can have a strong impact on the resulting population. When population numbers are small, there is also a risk for catastrophes to drive the population extinct. Examples of catastrophes that could affect the arctic fox population are epizootics of sarcoptic mange or arctic rabies. The Scandinavian arctic fox population has not experienced epizootics of rabies in modern times, but the disease could easily be transferred from Russia. Bannikov (1970) cites figures of rabies infection rates of 10–75% in Russian arctic foxes, and cub mortalities of 87–88% during an epizootic (compared to 30–40% in other years). Arctic foxes are known to make long-range migrations (up to 945 km, Eberhardt & Hanson 1978, over 1000 km, Frafjord pers. comm.) and they are thus likely to be both transmitters and the first victims, should arctic rabies spread to Scandinavia.

Although catastrophic events are a potential risk at these low numbers, the main problem for the Scandinavian arctic fox population is the low abundance of available food. We have here discussed their summer food, i.e. rodents. Winter food availability is also important in arctic fox population regulation (Angerbjörn et al. 1991). During winter, reindeer carcasses and ptarmigan (*Lagopus mutus*) are the most important food sources for arctic foxes (Angerbjörn et al. 1994, Kaikusalo & Angerbjörn 1995). The number of available reindeer carcasses is not necessarily in

proportion to the live population. In Swedish arctic fox habitat, the potentially important predators on reindeer are wolf (*Canis lupus*), golden eagle (*Aquila chrysaetos*) and wolverine. Both wolf and wolverine populations in Sweden have been small for more than 60 years, and eagles only kill young of the year (Björvall et al. 1990). Furthermore, arctic foxes experience competition for carcasses from other scavengers (e.g. wolverines, eagles, ravens and red foxes). Winter food availability has thus been low for more than six decades, whereas summer food has decreased during the last 20 years. The combined effect is that, as long as there are no microtine peaks, the population is unable to recover and will probably continue to decline. Should the cyclicity in rodents in Z also cease, the survival of the Scandinavian arctic fox population is at stake.

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Appendices

Appendix I. Summary of den inventory results. Given are the number of inventoried dens excluding those that were never inhabited, average litter sizes, the proportion of inhabited dens and the estimated number of adult arctic foxes.

Year	Jämtland (Z)				Västerbotten (AC)						Norrbotten (BD)			
	Inv. dens	Litter size	Prop. inh.	Adults	Inv. dens	Non-fed litter size	Fed litter size	Non-fed prop. inh.	Fed prop. inh.	Adults	Inv. dens	Litter size	Prop. inh.	Adults
1974					3	9.0		1.00		118	7	8.7	0.57	61
1975					4	0		0.50		59	13	0	0	0
1976					1	0		0		0	8	0	0	0
1977					3	0		0		0	29	5.0	0.21	23
1978	13	5.0	0.54	41	3	7.5		0.67		78	30	6.0	0.50	56
1979	21	0	0	0	3	0		0		0	32	0	0	0
1980	24	4.0	0.08	6	6	0		0.17		24	26	0	0	0
1981	29	7.9	0.31	24	29	7.0		0.45		80	37	7.2	0.43	51
1982	30	4.0	0.07	5	18	4.8		0.94		111	37	7.6	0.62	67
1983	24	0	0	0	3	0		0		0	27	0	0.04	4
1984	25	4.8	0.32	25	3	0		0		0	22	0	0	0
1985	31	7.9	0.58	45	16	0	6.0	0.11	0.18	22	18	0	0.06	6
1986	26	0	0	0	19	8.0	5.8	0.07	0.38	37	24	4.0	0.12	13
1987	22	3.0	0.04	3	22	0	6.4	0.04	0.38	41	20	4.0	0.05	5
1988	28	4.5	0.18	14	33	0	4.0	0	0.05	5	12	3.0	0.08	9
1989	31	6.6	0.52	40	34	2.0	4.6	0.02	0.28	26	16	0	0	0
1990	24	7.0	0.08	6	16	5.0	8.7	0.18	0.46	74	11	2.0	0.09	10
1991	20	0	0	0	25	4.8	8.0	0.14	0.45	51	12	4.0	0.08	9
1992	25	4.3	0.20	15	25	0	0	0	0	0	12	2.7	0.25	27
1993	24	6.5	0.17	13	24	0	4.5	0	0.17	10	16	0	0	0