

Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*

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The geographical distribution of red and arctic foxes differ. The hypothesis that this difference results directly from their relative adaptations to extreme cold is evaluated and dismissed. An alternative hypothesis is developed from considerations of body size and biogeographic effects on productivity. This suggests that the northern limit of the red fox's geographic range is determined directly by resource availability (and thus ultimately by climate), whereas the southern limit of the arctic fox's range is determined, through interspecific competition, by the distribution and abundance of the red fox. Predictions from this hypothesis are fulfilled, particularly by data on fur harvests. The argument is extended to other pairs of similar canid species, with the conclusion that equivalent interactions between body size, secondary productivity and direct competition have general relevance to their geographical distributions.

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The geographical distributions of red and arctic foxes (*Vulpes vulpes* L. and *Alopex lagopus* L.) are largely separate, but overlap in the tundras of North America and Eurasia (Fig. 1). These areas of overlap are partly the result of changes in the distribution of red foxes during the early 20th century. During this period, red foxes expanded the northern limits of their distribution into higher latitudes and altitudes. Since the behaviour and biology of arctic and red foxes are quite similar (Hersteinsson and Macdonald 1982), interspecific competition probably occurs where they are sympatric. Indeed, decreases in arctic fox distribution and abundance occurred concomitantly with red fox range expansions (Lönnberg 1927, Skrobov 1960, Macpherson 1964, Chirkova 1968, Haglund and Nilsson 1977, Østbye et al. 1978, Ericson 1984). Proposed explanations of these changes include adaptation by red foxes to harsher climate (Macpherson 1964), ameliorating climate, favouring the red fox (Skrobov 1960), and decline in the number of wolves (*Canis lupus* L.) and consequential reduction in carcasses available for arctic foxes (Ha-

glund and Nilsson 1977, reviewed by Hersteinsson et al. 1989).

In this paper we present evidence that changes in climate, affecting food availability and competition for food and den sites, have been responsible for these shifts in distribution and abundance of red and arctic foxes. This hypothesis is developed following the presentation of salient background information concerning interference competition, cold tolerance, and body size for red and arctic foxes.

Competition

Competition between North American canid species has been summarized based on the spatial segregation of sympatric populations (Sargeant et al. 1987). Resident coyote (*Canis latrans* Say) groups apparently exclude red foxes from core areas of their home ranges (Voigt and Earle 1983, Harrison 1986, Major and Sherburne 1987) and inverse relations between coyote and

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Fig. 1. A map showing the geographical distribution of red and arctic foxes.

fox populations have been reported for red, gray (*Urocyon cinereoargenteus* Schreber), and swift foxes (*Vulpes velox* Say) (Robinson 1961, Soulé et al. 1988). Coyote-induced mortality of red, kit (*Vulpes macrotis* Merriam), and swift foxes is known to occur (Scott-Brown et al. 1986, 1987, Sargeant and Allen 1989). Furthermore, coyotes are known to avoid wolf territories, and inverse relations in the numbers of wolves and coyotes have been reported (Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982).

Little information is available concerning interactions between fox species. Rudzinski et al. (1982) observed interactions between red and arctic foxes in an enclosure. Red foxes dominated these encounters and usurped preferred den, resting, and feeding areas. However, only threats and chases, not fights, were witnessed. In the wild, Schamel and Tracy (1986) twice witnessed avoidance by arctic fox upon the approach of a red fox, and one chase of an arctic fox by a red fox, but no fighting.

Early in this century, to boost fur harvests, arctic foxes were introduced on numerous Alaskan islands. Such introductions were usually successful (West and Rudd 1983) except where red foxes were also introduced or already established; these arctic foxes were soon eradicated (Evermann 1914, Bower and Aller 1917). Few observations of interspecific encounters exist to bolster this circumstantial evidence of competition. Eberhardt (1976) saw none during the denning season in an area on the North Slope in Alaska where both species bred. However, red foxes are reported to attack and kill arctic foxes which are helpless in traps

(Marsh 1938), and Alaskan trappers apparently consider red foxes to be the primary predators of the arctic fox (Chesemore 1975). Frafjord et al. (1989) report the killing of an adult arctic fox by several red foxes at a reindeer (*Rangifer tarandus* L.) slaughter site in winter as well as the killing of an arctic fox cub by a red fox vixen in summer.

Fur characteristics and cold tolerance

Most of the morphological differences between the two species are related to the superior adaptations of arctic foxes to extreme cold. The arctic fox has relatively smaller, more rounded ears than the red fox, the tail and neck of arctic foxes are relatively shorter than those of red foxes, the braincase is more rounded and the muzzle is slightly shorter and broader (Clutton-Brock et al. 1976). There are obvious pelage differences between red and arctic foxes. Over 99% of arctic foxes in the Siberian and Canadian tundra are of the "white" colour morph (Boitzov 1937, Fetherston 1947), i.e. they are almost totally white in winter but brownish-grey in summer. The remaining arctic foxes are of the "blue" variety, i.e. dark brownish-blue throughout the year. On the other hand, most red foxes are, as the name implies, red in colour with some black and white marking, while others are black or silver-black (silver foxes) or between these extremes (Ashbrook 1937, Adalsteinsson et al. 1987).

The capability of an endothermic animal to withstand cold depends upon insulation, body mass and the capacity for production of metabolic heat (Hart 1971). About 70% of the arctic fox's fur consists of fine under-fur compared to 20% of the red fox's (Cole and Shackelford 1946). Due to the arctic fox's 50% better insulation (Scholander et al. 1950a), and in spite of its smaller body mass, its lower critical temperature (T_{lc} : the ambient temperature below which metabolic heat production needs to be increased to maintain normal core temperature) has been estimated by Scholander et al. (1950b) and Underwood (1981) at -40 to -50°C and -35°C , respectively. For an Alaskan red fox T_{lc} was -13°C in winter (Irving et al. 1955). In contrast, Finnish farmed arctic foxes of the blue colour morph (blue foxes) had a T_{lc} similar to that reported for the Alaskan red fox (Korhonen and Harri 1986). The discrepancy in these results is unexplained, but might arise because of (1) different methodologies, (2) a genuine difference between white and blue foxes, or because (3) selection of farm-bred blue foxes, over 30 generations or more, on criteria determined by fashion has diminished the insulating qualities of their fur. It remains clear that both species can tolerate extreme cold.

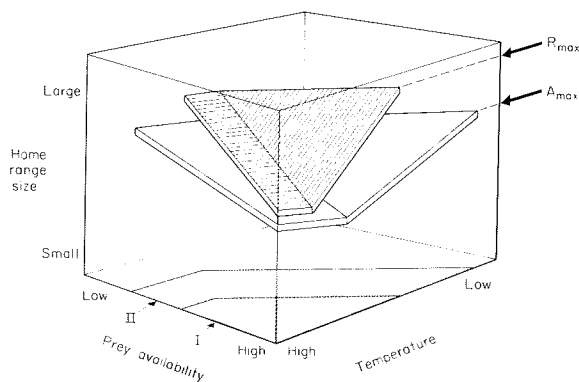


Fig. 2. A three-dimensional schematization of a model depicting geographical limits to the tolerance of low prey abundance and temperature by arctic and red foxes, respectively. While red foxes can maintain larger home ranges than arctic foxes, their tolerance of low food availability and low temperatures are less than those of arctic foxes. Area of overlap (I), shown on the two-dimensional map or shadow at the bottom of the diagram, is an area of potential competition and exclusion of arctic foxes. Area marked II represents the area of too low productivity or too low temperature for a sustainable red fox population.

Body size, movements and home range

Body size appears to be a function of environmental productivity (Geist 1987). Whereas the body size of most mammals increases with latitude up to 60–65°N, species which are found north of 60°N (e.g. arctic fox) may tend toward smaller size with increasing latitude. In areas of limited productivity, body size apparently is limited by the scarcity of food (Rosenzweig 1968).

The biomass of food available per unit area to mammals appears to decrease with increasing body weight (Harestad and Bunnell 1979, Swihart et al. 1988) and amongst cogenic predators, larger species generally require more food than smaller ones. These factors are likely to be reflected directly in minimum distance travelled while foraging, and thus in home range size. This would be particularly true in the relatively homogeneous tundra with low diversity of prey (Hagmeier and Stults 1964, Haukioja and Koponen 1975), and where territory size and prey availability may be more directly related than in habitats with patchily distributed food resources (viz. Macdonald 1981, Voigt and Macdonald 1985, Carr and Macdonald 1986).

Red foxes are approximately 60% heavier and 25% larger in linear dimension than arctic foxes (Hersteinsson and Macdonald 1982). Harestad and Bunnell (1979) found that mean home ranges varied interspecifically in proportion to mass^{1.36}. If this relation holds true for red and arctic foxes then the former would require a home range 90% larger than arctic foxes. This figure ignores the probable superiority of the arctic foxes' insulation.

Pedersen (1985) found that red foxes take 46% larger strides at a slow trot than arctic foxes under similar

conditions. However, Peters (1983) calculates that velocity of movement is related to (mass)^{0.21}, i.e. the 60% heavier red fox should only move 10% faster, covering its 90% larger home range in 1.9/1.10=1.7 times longer than an arctic fox covers its smaller range. That this is true for the two fox species is supported by Pedersen's (1985) observations that arctic foxes travel at a slow gallop 60–70% of distance moved in winter while red foxes in the same area travel at a trot almost 90% of the distance moved.

Thus for the red fox to maintain a 90% larger home range its daily minimum travels would take around 70% longer than those of the arctic fox. Moreover, the red fox is likely to be further disadvantaged by the practicalities of defending a larger home range, and increased demand for energy during winter due to poorer insulation. Therefore a red fox must reach the point at which prey are so scarce, that it cannot maintain an adequately large home range, well before an arctic fox reaches that point. Food availability in the breeding range of the arctic fox is generally so low during lemming population minima that arctic foxes are unable to breed successfully (Macpherson 1969, Ericson 1984, Hersteinsson et al. 1989). Red foxes also will be unable to breed under these conditions and presumably have a lower survival too. Mortality or emigration due to starvation may thus be too high to sustain a red fox population in the region.

The hypothesis

On the basis of the foregoing arguments, our hypothesis is as follows:

The northern limit of the red fox's geographical range is determined by the consequences of climate for prey availability, whereas the southern limit of the arctic fox's range is determined, through inter-specific competition, by the distribution and abundance of the red fox.

This situation is schematized in Fig. 2. Several predictions follow from the hypothesis:

1. The relative distributions of red and arctic foxes correlate with summer temperature.

We would expect the northern limit of the red fox to follow a summer isotherm, not a line of latitude, as primary productivity is far more dependent on summer temperatures and the length of the growing season than on winter temperatures (Larsen 1971, Lieth 1975, Cropper and Fritts 1981, Hustich 1983). Therefore, we use January and July temperatures, respectively, to distinguish between the direct effects of cold temperature, and indirect effects operating via productivity, upon the distribution of the foxes. Furthermore, as moisture probably does not limit productivity in the arctic (Jacoby 1983), we would not expect precipitation, either in the form of snow or rain, to have a significant effect on

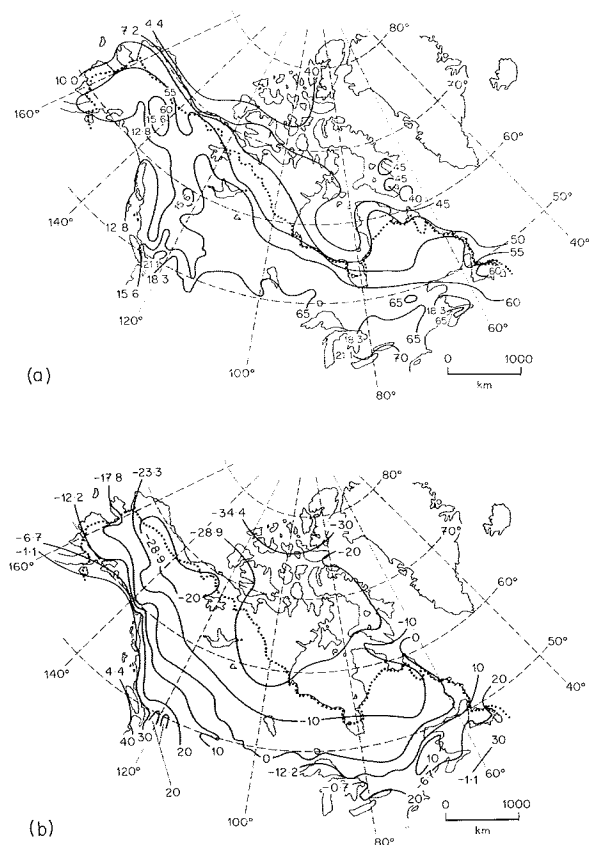


Fig. 3. July (a) and January (b) isotherms in Canada and Alaska. Redrawn from Thomas (1953). Dotted line shows the tree-line (redrawn from Hustich 1953). Degrees in Fahrenheit on the right and in Celsius on the left.

productivity of the environment or distribution of the foxes.

2. Any change in the position of isotherms will be mirrored in a changed distribution of the foxes.

As climatic north (i.e. direction perpendicular to an isotherm towards colder temperatures) retreats or advances, many plant species are predicted to extend their ranges to higher or lower latitudes and altitudes, respectively (e.g. Erkamo 1952), albeit after a time lag (determined by dispersal distances and factors such as that many trees can survive at mean summer temperatures 1–2°C colder than those at which they can reproduce). In practice, forests may take decades to adopt their theoretical limits. We predict that at the same time as plant distributions change with climate, so also will plant communities change, with altered productivity leading to concomitant changes in the density of both invertebrate and vertebrate populations, including the foxes' prey.

3. Changes in the distribution of red and arctic foxes will be most conspicuous where summer isotherms are widely spaced.

The distance between successive isotherms varies enormously across continents (Fig. 3). Therefore, a given change in temperature will be translated into correspondingly different shifts in distribution across a continent. A change in the distribution of foxes would thus be more conspicuous where isotherms are widely spaced.

Materials and methods

Climatic variables

Climatic information was obtained from the Canadian Climate Centre, Ontario, for all meteorological stations in the NWT, Canada. Analysis of these climatic variables was based on two data sets:

(1) *Meteorological Data A (MD-A)*. Data for the period 1931–1981 from 13 meteorological stations in the NWT which were also fur trading stations. Climate variables were: 1. Mean July temperature, 2. Mean January temperature, 3. Mean annual temperature, 4. Mean total annual snowfall, 3. Mean total annual rainfall.

(2) *Meteorological Data B (MD-B)*. Data interpolated from meteorological maps of Canada (in Thomas 1953) for fur trading stations from which there are no meteorological data. Climatic variables used were: 1. Mean July temperature, 2. Mean January temperature, 3. Mean annual minimum temperature, 4. Mean annual number of days with snow cover, 5. Mean annual snowfall, 6. Maximum recorded depth of snow, and 7. Mean annual total rainfall.

Fox variables

Fox harvest data for individual hunting seasons between 1931/32 and 1980/81 were obtained from fur export tax returns for individual fur trading stations in the NWT (Ministry of Natural Resources, Ontario). Arcsine transformations of the proportion of *Alopex* in the total fox harvest were used in the analyses. Mean prices of fox furs were obtained from the same source; Log_{10} of the ratio of arctic fox/red fox fur prices were used in the analyses.

Analysis

Stepwise multiple regression was used to assess the spatial relationship between mean proportion of *Alopex* in the fox harvest and the climatic variables, and to determine the rank order of the effects of fur prices and individual climatic variables on temporal variation in the proportion of arctic foxes in the fox catch during 1931–1982.

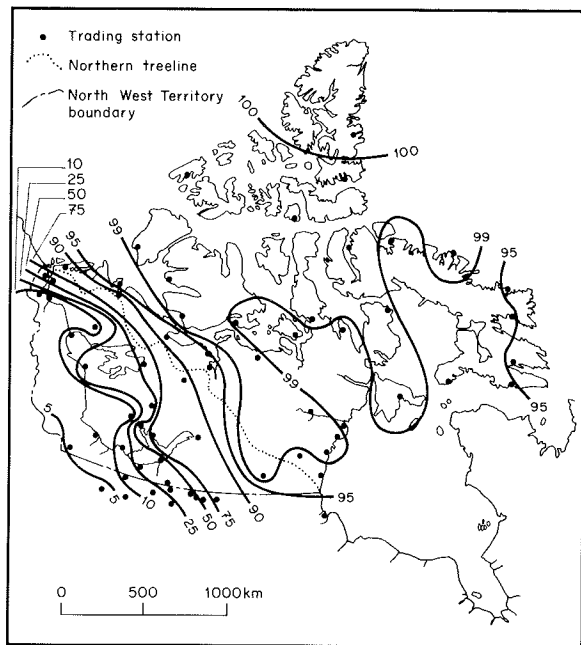


Fig. 4. Isoclines of the proportion of arctic foxes in the total fox harvest in the NWT, Canada. Note how close the isoclines lie in the west. Based upon fur export tax returns for individual trading stations in the NWT (courtesy of Min. of Natural Resources, Ontario), for individual hunting seasons between 1931/32 and 1980/81; the isoclines are drawn by hand.

Testing the hypothesis

Changes in climate

Our evidence rests fundamentally on the fact that since the end of the Ice Age 10000 yr BP, there have been considerable fluctuations in climate (Bergthórsson 1969, Dansgaard et al. 1971, 1975). In the northern hemisphere the mean annual temperature increased by ca. 0.73°C during 1880–1940 with a brief period of cooling between 1900 and 1910 (Jones and Wigley 1980). A 0.27°C drop occurred between 1940 and 1965, with no significant change thereafter. Long-term variation in annual temperature was significant throughout the Arctic during the period 1881–1980 (Kelly et al. 1982). However, such climatic changes are exaggerated at higher latitudes (Ångström 1939). Thus the increase in the mean annual temperatures between the ten-yr averages 1899–1908 and 1929–1938 in Oslo was 0.88°C, in Sørvaranger in northern Norway 1.98°C, and in Spitsbergen 2.47°C (Hesselberg 1940). Furthermore, warming neither began simultaneously nor continued consistently throughout the northern hemisphere: winter temperatures began to rise in Stockholm around 1800 (Liljequist 1943), summer temperatures only did so in 1930, with a sharp increase of 1.5°C, whereas in northern Swedish Lapland (Karesuando) summer temper-

atures began to rise in 1910 and increased by 2.3°C in 25 yr (Liljequist 1950).

In Sweden, during the summer, there is a linear decrease in the average temperature (reduced to sea level) of 1°C for every 5°20'N latitude (i.e. 590 km) (Ångström 1938). Thus a rise in temperature of 1.0 to 2.5°C there, would result in a movement of isotherms by 600–1500 km northward at the same altitude. Similarly, as summer temperature falls by about 0.6°C per 100 m in altitude, altitudinal isotherms would rise by 160–400 m for a 1.0–2.5°C increase in temperature. A 2°C rise in temperature would thus have pushed the isotherms up by about 330 m, potentially expanding the altitudinal range of the red fox, and diminishing that of the arctic fox. If, for the sake of argument, the isotherm that determined the lowest altitude of the arctic fox's range in Swedish Lapland had been at 600 m in 1900, then it would now be at 930 m and this would actually translate into a two-thirds reduction in land area available to the arctic fox.

Primary productivity

Evidence from Fennoscandia supports the prediction that climate has ameliorated and primary productivity has increased in subarctic and arctic regions in this century. There are signs of both sexual and vegetative regeneration amongst forests, which have become denser and colonised higher altitudes (Jensen 1940, Jones 1947, Ve 1951, Sonesson 1980). Payette et al. (1985) found that a 660-yr tree-ring chronology in northern Quebec showed a period of slow growth in northern Quebec between 1398 and 1890 and a period of faster growth since then. Ball (1986), comparing present day tree limits to those mapped by Samuel Hearne (1772) in the Northwest Territories of Canada, shows that the tree limit has advanced 50–200 km north in the last 200 yr.

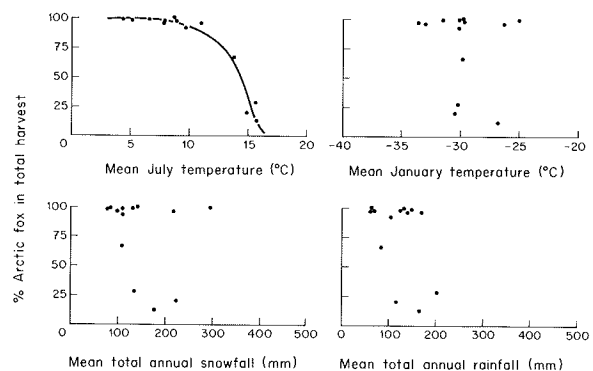


Fig. 5. Scatter diagrams of the proportion of arctic foxes in total fox harvest at 13 trading stations that were also meteorological stations during 1931–1982.

Table 1a. Linear correlation coefficients between proportion arctic foxes (with arcsine transformation) and 7 climatic variables from MD-B. PA = Proportion arctic foxes, JUL = Mean July temperature, JAN = Mean January temperature, MT = Mean minimum temperature, DS = Mean number of days with snow-cover, SD = Mean maximum snow-depth, SF = Mean number of days with measurable snow-fall. RA = Mean annual total rainfall.

	PA						
JUL	-0.797 **	JUL					
JAN	-0.395 *	0.426 **	JAN				
MT	0.451 **	-0.382 *	0.141	MT			
DS	0.583 **	-0.644 **	-0.125	0.337 *	DS		
SD	-0.169	0.035	0.295	0.240	0.384 *	SD	
SF	-0.075	-0.025	0.292	0.299	0.488 **	0.799 **	SF
RA	-0.567 **	-0.707 **	0.469 **	-0.028	-0.132	0.470 **	0.510 **

Distribution of foxes

Spatial distribution in Canada

The proportion of arctic foxes in the overall Northwest Territories fox harvest varied spatially (Fig. 4), with a change from 10% to 90% arctic fox over a distance of only 200–700 km (note that the isoclines lie approximately parallel to the northern tree limit). Changes in the proportions of breeding foxes may take place over an even narrower zone in so far as arctic foxes are known to move considerable distances during winter (Chesmore 1968, Wrigley and Hatch 1976, Eberhardt and Hanson 1978) as may red foxes in the far north (Novikov 1956, Macdonald 1980).

Data on food availability are limited. Primary productivity, however, on which the foxes' prey depend, is in turn largely dependent upon summer temperature, and temperatures have been better documented. Fig. 5 plots arctic fox pelts traded as a percentage of the total number of fox pelts traded, versus 4 different climatic variables (MD-A) at 13 trading stations during 1931–1981. Mean July temperature was the only climatic variable to be correlated with the percent arctic foxes in the catch ($r = -0.89$; $p = 0.0001$; arcsine transformation).

The result of Pearson's correlation analysis between percent arctic fox skins traded and MD-B, as well as the substantial intercorrelation between the seven climatic variables of MD-B are shown in Table 1a. Again, July temperature correlates best with percent arctic foxes traded ($r = -0.797$). Furthermore, snow stays longer on the ground where arctic foxes are more common, mean January temperatures are lower in these areas and there is less rain, while minimum winter temperatures are lower where arctic foxes are rare and red foxes com-

Table 1b. Multiple regression analysis shows that three independent variables (Mean January temperature, mean number of days with measurable snowfall, and mean annual rainfall) were not good predictors and did not add significantly to the model. They were left out of the final model.

Source	d.f.	MS	F	p	R ²
Model:	4	1.891	26.59	0.0001	0.73
JUL	1	1.121	15.77	0.0003	
MT	1	0.451	6.34	0.0161	
SD	1	0.738	10.38	0.0026	
DS	1	0.413	5.81	0.0209	
Residual:	38	0.071			

d.f. = degrees of freedom

MS = Mean square

JUL = Mean July temperature

MT = Mean minimum temperature

SD = Mean maximum snow-depth

DS = Mean number of days with snow-cover.

The F values show how well the model fits the data and how good each independent variable is at predicting the proportion of *Alopex* in the catch. Significance of F values is given by p values. The R² for the model shows the proportion of the variance in the data that is explained by the model.

mon. However, stepwise multiple correlation totally removes the effects of January temperature and rainfall. Only three weather variables improve the overall correlation after taking July temperature into account. These are mean minimum temperature, mean maximum snow-depth and number of days with snow cover (Table 1b).

The "invasion" of Baffin Island by red foxes

Baffin Island (Canada) was invaded by red foxes in 1918 and Macpherson (1964) monitored their subsequent

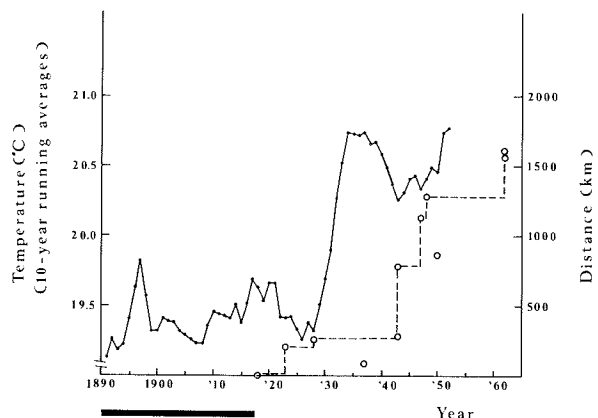


Fig. 6. Changes in mean summer temperature at Toronto during 1886–1955 and change in the northern-most confirmed distribution point of red foxes on Baffin Island, measured as distance from the southern-most point of Baffin Island. The black bar indicates a period of unsuccessful "invasions" by red foxes into Baffin Island (Macpherson 1964).

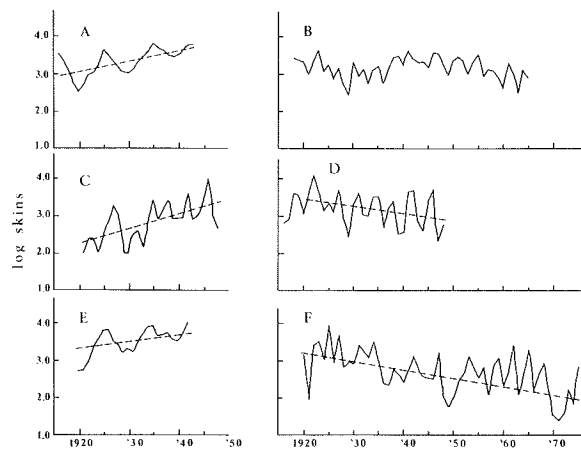


Fig. 7. Diagrams of the number (\log_{10}) of foxes traded in three different areas of Canada: A) red fox and B) arctic fox in NWT; C) red fox and D) arctic fox in Ungava; E) red fox and F) arctic fox in Manitoba.

northward spread by examination of fur-trappers' bags. He interpreted the successful spread of these foxes, in comparison to the documented failures of earlier invasions, as an indication that these foxes were better adapted than their predecessors to the northern climate. Conversely, we suggest that the northern climate had become more favourable to red foxes. The successful spread of red foxes occurred about 10–20 yr after a sharp rise in summer temperature in eastern Canada (Fig. 6). However, climatic fluctuations are exaggerated to the north (Jones and Wigley 1980). Therefore, this amelioration in climate will have been amplified in Baffin Island. In addition, the effect on primary productivity of a unit increase in summer temperature is likely to be greater in the cool summers of Baffin Island than in areas with warmer summer temperatures. The observed time-lag between the change in climate and the expansion of red fox range is probably explained by the time taken for ecological processes leading to increased prey availability to respond to the warming climate.

Temporal changes on mainland Canada

A northward range extension by the red fox can be detected at the south of the arctic fox's range by a review of annual trading figures:

(1) Manitoba: arctic foxes: 5.5% decrease p.a. from 1919/20 to 1974/75 (data from Wigley and Hatch 1976); red foxes: 4.6% increase p.a. from 1919/1920 to 1941/42 (data from Calhoun 1950) (Fig. 7a). (2) Ungava district, Quebec: arctic foxes 4.4% decrease p.a.; red foxes: 9.6% increase p.a. from 1921 to 1948 (data from Butler 1951). (3) Ontario: arctic foxes: harvest decreased from ca. 50 p.a. in 1923–1935 to ca. 15 p.a. in 1936–1955 (Peterson 1957). (4) Northwest territories: arctic foxes: no significant trend in the pelts traded at Baker Lake

during 1917/18–1964/65 (Macpherson 1969); red foxes: 6.5% increase p.a. in the Northwest Territories as a whole from 1915/16 to 1942/43 (data from Calhoun 1950). Thus the proportion of red foxes in the catch increased although arctic fox numbers remained stable.

Despite similar temperature increases, range extensions of the red fox have apparently not been recorded in Alaska or the western Canadian Arctic. However, the summer isotherms lie much closer together in the west than in the east (Fig. 3). The distance between the summer isotherms at the critical latitudes in the western, central and eastern Canadian Arctic are approximately 40, 150 and 550 km respectively, for every 1°C . Thus for a temperature increase of $1.0\text{--}2.5^{\circ}\text{C}$, the isotherms would move north by 40–100 km, 150–350 km, and 550–1350 km respectively in these regions. Thus range extensions of the red fox are in accordance with movements of the isotherms in western and eastern Canada, as predicted.

In contrast, between 1930–1982 we find no temporal correlation between the red/arctic ratio or the species harvests and climatic variables. However, there was substantial annual variation in the fox parameters, and two of the probable causes of this are fur prices and rabies. The values of red and arctic fox furs vary with fashion and the ratio of these prices is correlated with the ratio of the two species traded in seven of 12 provinces of Canada for which data were available (Table 2).

Rabies was recognized in Alaska and Canada in the 1800's and subsequently became enzootic in fox populations in these regions (Plummer 1947a, b, Rausch 1958). A particularly bad epizootic seems to have erupted in the Mackenzie Delta in 1944–45 and spread widely from there. The fur trading data indicate a peak in the catch of red foxes immediately preceding the outbreak, and a persistent trough thereafter. This rabies epizootic, combined with perturbations in the arctic/red

Table 2. The relationship between the price ratio of arctic fox and red fox pelts and the proportion of arctic foxes in the traded total for each province in Canada during 1930–1982 (statistical analyses performed on the arcsine transformed square root of the proportion of arctic fox pelts traded).

State/Province	No. of obs.	Corr. coeff.	p	Sign.
Alberta	59	0.476	0.0001	**
British Columbia	59	-0.187	0.1560	N.s.
Manitoba	59	0.471	0.0002	**
New Brunswick	58	-0.070	0.6030	N.s.
Nova Scotia	56	0.311	0.0197	*
Northwest Territories	59	0.484	0.0001	**
Newfoundland	28	0.397	0.0364	*
Ontario	59	0.369	0.0040	*
P.E.I.	49	-0.088	0.5480	N.s.
Quebec	59	0.251	0.0548	N.s.
Saskatchewan	59	0.321	0.0132	*
Yukon	59	0.021	0.8764	N.s.

fox price ratio in the late 1950s to early 1960s, at a time when climatic variations were small, may explain the absence of temporal correlation between climate and the ratio of arctic to red foxes in the trading figures since the 1930s.

Changes in Eurasia

Between 1900 and 1926 the arctic fox population of Fennoscandia declined drastically (Lönnberg 1927). The consensus is that this decrease was due to over-harvest (Haglund and Nilsson 1977). Despite protection since 1928, 1930 and 1940 in Sweden, Norway and Finland, respectively, the population has failed to recover (Hersteinsson et al. 1989).

We suggest that over-exploitation alone was not responsible for the drastic decline in arctic fox numbers in Fennoscandia at the beginning of this century. Rather the concerted effect of overhunting and invasion by red foxes into the tundra biome together precipitated the decline. After the arctic fox was protected we believe that competition with red foxes for a niche, by then altered due to ameliorated climate, is a sufficient condition for the failure of arctic foxes to return to their former numbers. Decimation of the wolf population in Fennoscandia during the 19th century (Haglund 1975) does not coincide with the reduction in arctic fox numbers.

From geo-climatic considerations we predict that red foxes would initially oust arctic foxes from milder coastal regions where they were quite common in the 1880's (Collett 1912). The arctic species would retain inland, mountainous strongholds. No data are available on the relative coastal and inland distribution of arctic foxes following the population decline, but Johnsen (1947) provides corroborative evidence for this prediction. He states that in comparison to the white morph the blue variety was regarded formerly as much scarcer in the south than in the north (where it made up 17–20% of the arctic fox population). By the 1940's, however, blue foxes made up approximately 1% of the arctic foxes in the north as well as in the south (Munsterhjelm 1946, quoted by Pulliainen 1965). The blue morph is generally associated with coastal habitats (Braestrup 1941, Hersteinsson 1989). We conclude that arctic foxes were largely expelled from coastal regions by red foxes, and became confined to zones where the white phase prevails due to its adaptation to winter snow. A recent increase in the proportion of the blue morph among arctic foxes in southern Norway may be due to influx of genes from escaped farm-bred blue foxes (Frafjord 1989).

In the USSR, Skrobov (1960, 1961) claims that red foxes have been invading the tundra during this century, driving the arctic foxes away from parts of their range. These red foxes mainly inhabit the flood terraces of rivers, areas which have a higher than average primary productivity (Rodin et al. 1975).

Discussion

We have demonstrated spatial and temporal variations in the abundance of red and arctic foxes that fulfil the predictions of our hypothesis. Nonetheless, we are mindful of the dangers of inferring causation from correlative evidence. Although there is clear coincidence in the changes observed in climate, flora and fauna, there have been other changes during the same period, such as the incidence of rabies, alteration in livestock husbandry, forestry, human settlements and hunting practices. Furthermore, the interpretation of hunting statistics is notoriously complex (e.g. Usher and Wenzel 1987). In this case the relationship between pelt prices and the ratio of arctic to red foxes in the catch suggests that, at least since the 1930s, the trading figures may present a distorted version of the harvest and, in turn, of the populations. This relationship might arise if hunters: (1) stockpile pelts of the less valuable species until prices recover, (2) concentrate their efforts on localities where the more valuable species predominates, (3) selectively hunt the more valuable species from any given area. Any or all of these confounding factors might operate, but we think they are listed in order of diminishing plausibility. Nonetheless, an excellent correspondence is frequently observed between species diversity, abundance and geo-climatic features (e.g. MacArthur 1972), and in this case our hypothesis does appear to be strongly supported.

Our argument rests as much on the similarities between red and arctic foxes as on their differences. It hinges upon the energetic consequences of the difference in body size between two otherwise very similar species. The red fox's larger size simply makes it too expensive to operate in environments with low primary and secondary productivity, such as the arctic tundra. Our review (1982) of the great similarities between these two species leads us to consider that in ecological terms the arctic fox is, for practical purposes, a small red fox in white (or blue) clothing. This, we suggest, is also how the red fox reacts to the arctic fox when they meet beyond the constraining influence of environmental paucity; then the larger species dominates the smaller in direct competition. The strain (*sensu* Welden and Slauson 1986) suffered by red foxes due to food shortage far outweighs that caused by competition with arctic foxes near their northern distribution limits, while the strain suffered by arctic foxes due to competition with red foxes, in areas where the latter are numerous, will outweigh any benefit of higher food availability. A parallel case is found in the altitudinal zonation of chipmunk species, *Eutamias*, in the mountains of western Alberta (Brown 1971, Heller 1971, Sheppard 1971).

We suggest that arctic foxes have evolved a body size close to optimal for their niche in the Arctic. Red foxes, trying to settle there would have to compete for the same prey, due to the low diversity of prey species. However, because of their larger body size, their net

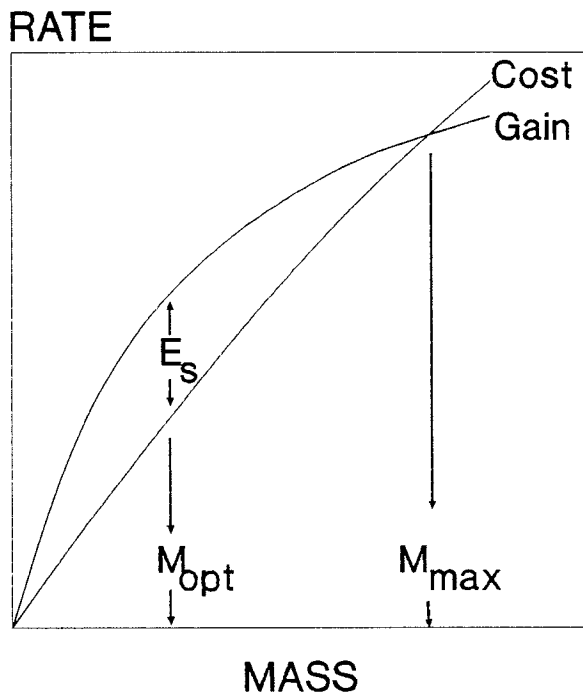


Fig. 8. Schematization (adapted from Werner and Gilliam 1984) of metabolic cost and gain curves for foxes in the Arctic. M_{max} is the maximum size attainable on the given resource, E_s is the surplus energy available for growth and reproduction, and M_{opt} is the size at which surplus energy is maximised. Cost curve: $E_m = kM^\delta$; where M = mass, δ = constant that averages 0.75 across species, k = species-specific constant which depends on factors such as temperature and activity. Gain curve: $E_g = hM^\tau$; where h and τ are fitted constants that are habitat and species-specific. Surplus energy: $E_s = hM^\tau - kM^\delta$.

foraging gain would be too low for reproduction and survival except in years of rodent abundance. This situation is schematized in Fig. 8, which is adapted from Werner and Gilliam's (1984) analysis of the costs and benefits of body size. While the metabolic cost curve would remain similar in most years, the gain curve will change from year to year, according to food availability. We assume that the arctic fox's mass is close to optimal (M_{opt}) in years of rodent abundance, and their surplus energy (E_s), which can be channelled into reproduction, is maximised. Indeed, their reproductive output is enormous in such years, with weaned litter sizes averaging 9–10 cubs (Macpherson 1969). In contrast, their reproduction fails totally over large areas when rodents are scarce, whereupon arctic foxes may emigrate en masse, usually southwards (Skrobov 1961, Bannikov 1970, Wrigley and Hatch 1976) or out onto the sea-ice (Chesmore 1975). Red foxes, too, could breed when rodents abound, although their surplus energy might be lower than that of arctic foxes, but when rodents were scarce their E_s would be negative, resulting in starvation and death. We propose, therefore, that extinction of red foxes during rodent minima accounts for their absence

or rarity in the northern tundra, despite their capacity to breed there during rodent maxima. The dispersal distances necessary to compensate for such extinctions would be prohibitive.

We propose that this argument can be extended to other pairs of similar canid species, such as Red, Rüppell's (*Vulpes ruppelli* Schinz) and Blanford's fox (*Vulpes cana* Blanford) in deserts, where we predict that equivalent interactions between body size, secondary productivity and competition will similarly affect their geographical distributions.

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