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The dynamics of Canadian arctic fox populations

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The dynamics of Canadian arctic fox populations

by A. H. Macpherson

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Abstract

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Revenue from the trapping of arctic foxes is important to the economy of some northern communities. This study was undertaken to determine the cause of periodic population fluctuations in Keewatin and Franklin Districts, Northwest Territories, from 1958 to 1963.

Lemmings were found to be the major prey animals of arctic foxes. Fewer whelps survived in years when lemmings were scarce. Fighting among whelps is believed important in the reduction of litters. Survival of whelps in the first half year, rather than the number of litters produced in a given year, appeared to be the governing variable in population fluctuations.

Life table analysis suggests over half of a theoretical cohort (year-class) dies before weaning, and half the remainder in the next year. Less than 10 per cent of the cohort survives to the age of two.

Striking features of arctic fox breeding biology may be viewed as adaptations to the high latitude climatic regime and to dependence on an undiversified and fluctuating food base.

Cover
Top left — Adult white-phase arctic fox in summer pelage. T. C. Dauphiné
Top right — Young white-phase arctic fox. September 1955. S. D. MacDonald
Bottom left — Adult white-phase vixen in summer pelage. T. C. Dauphiné
Bottom right — Adult white-phase arctic fox showing complete winter pelage. S. D. MacDonald

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Introduction

The arctic fox (*Alopex lagopus* (L.)) is a small, compact fox, about the size of a domestic cat. Its breeding range extends over the whole of the arctic tundra zone of North America and Eurasia, and includes areas of alpine tundra in the mountains of Scandinavia. The arctic fox also breeds on the barren islands of the Arctic, North Atlantic, and North Pacific oceans, which it has presumably reached across drifting floe-ice.

The arctic fox has two colour phases, "white" and "blue". In summer the white fox becomes dark brown on the back, legs, tail and head, and whitish or yellowish on the underparts. It is pure white or nearly so in winter. The blue phase is more variable, from greyish or brownish to almost black, both in its winter and in its summer pelage. The proportions of the two colour phases vary greatly from place to place. Locally their proportions may also vary, through immigration, from year to year.

The beautiful and valuable pelt of the arctic fox attracted many of the first European explorers and traders into the lands that border the Arctic Ocean. In Canada alone, 10,000 to 68,000 arctic fox pelts are sold annually, a catch whose value at auction has been between $50,000 and $2,000,000 (Anon., 1962). The Eskimos and Indians who trap arctic foxes, and the small settlements at which they sell the pelts, have few other sources of income. In Canada, as in other northern countries, arctic fox populations vitally affect the settlement and economy of large, inhospitable areas.

Arctic fox populations are of great biological, as well as economic, interest. Monographs have been written on the species by Lavrov (1932), Boitzov (1937), and Braestrup (1941). Elton (1942) and Tchirkova (1951) have discussed the numerical fluctuations which arctic fox populations undergo. In addition, there are extensive notes on the arctic fox in the accounts of expedition members, biologists, traders, and other observers. There is also a considerable literature on its ranching and management.

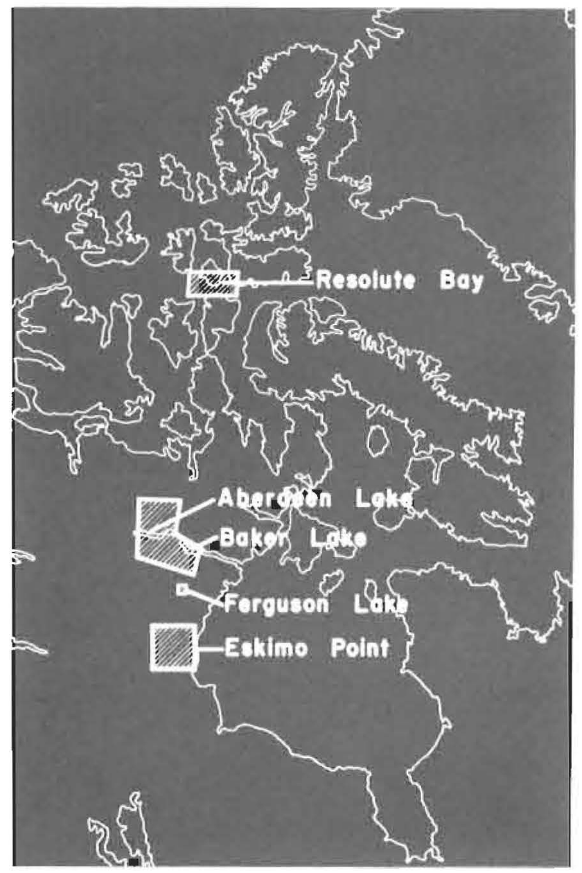
The objectives of the present study were to identify the factors important in determining arctic fox numbers in the wild, and to see whether a basis could be found for predicting trapping harvests. The results of earlier work helped in selecting the most important aspects of arctic fox population ecology for detailed study. These were age composition of the population, breeding performance in relation to age, whelp survival, and food availability.

The breeding biology of the species was investigated in central District of Keewatin in the summers of 1959 through 1963. The studies included annual surveys of fox dens, analyses of fox diets, estimations of lemming numbers, and counts of weaned fox litters.

The structure of arctic fox populations by sex and age in central District of Keewatin (Aberdeen Lake, Baker Lake, and Ferguson Lake), in the region of Eskimo Point, and around the high arctic settlement of Resolute Bay was investigated through periods of varying length by means of samples from the trapping harvests (Figure 1). The longest run of samples came from Resolute Bay, the first being collected in 1958 and the last in 1964.

In the following pages, the above studies are reported separately, and their results are then discussed in combination.

Figure 1 Map of northern North America showing the areas from which specimens or data were procured.



Dens and denning habitat of arctic foxes

The arctic fox normally whelps in underground breeding dens which are used for many years. The whelps are born in late spring, and the family is supported until the mid-summer weaning period almost exclusively by the dog-fox. The den is abandoned by the whelps in late summer, though according to trappers, who favour dens as trap locations, foxes may inhabit some dens all winter.

Previous work

The dens of arctic foxes in the tundra districts of the U.S.S.R. have been studied systematically by several biologists. Elsewhere they have had only passing mention. Danilov's (1958) excellent descriptions of dens and den sites are applicable to those of the central District of Keewatin and indeed to arctic Canada generally. Sdobnikov (1958) and Skrobov (1961) have also investigated den ecology and den distribution. Skrobov (1961a) has discussed the importance of arctic fox den surveys in forecasting annual trapping harvests.

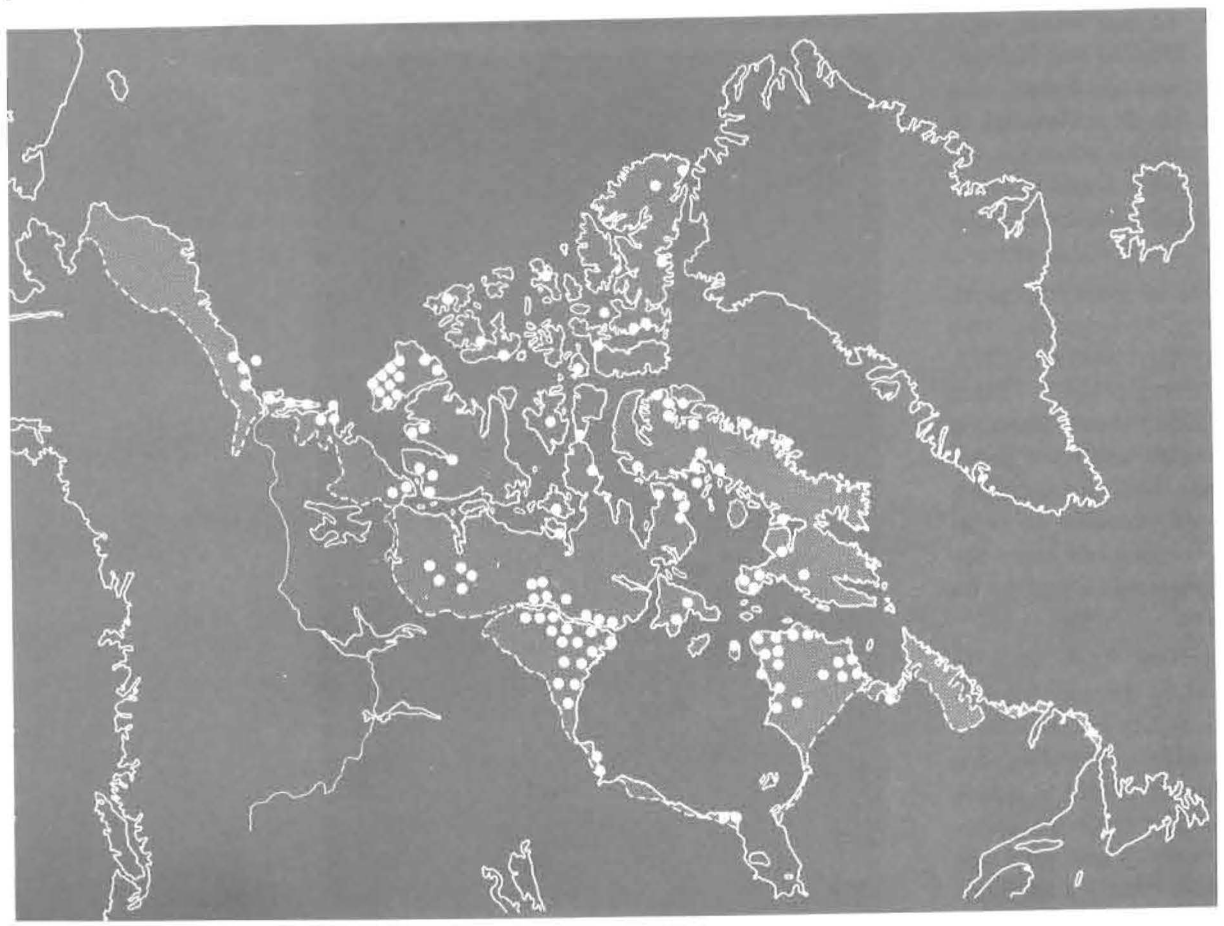
Materials and methods

The proposed work required a study area on which arctic fox dens were numerous, and an accurate foreknowledge of den locations. Inquiries made in the autumn of 1958 and later questionnaires provided the information for a map of known arctic fox den locations in Canada (Figure 2). In the spring and summer of 1959, parts of central District of Keewatin were searched by dog-sled, on foot, and by canoe from the settlement of Baker Lake. Several dens were examined, and the region of the Thelon–Dubawnt confluence was selected as the primary study area. Later in the same summer, low flying in light, single-engined aircraft was tested (on Victoria Island) as a method for surveying fox dens.

In the spring of 1960, camp was established at "Qiqiktalik",* on the north side of Aberdeen Lake near its western end (Figure 3). A small prefabricated building was erected to serve as a base. Later in 1960, and during the spring and summer of 1961, 1962, and 1963, nearby fox dens were observed. Other reported fox dens in the surrounding primary study area, around the lower course of Kazan River, and near Deep Rose Lake, south of Sinclair Falls on Back River, were examined (Figure 3).

*A local name without official status.

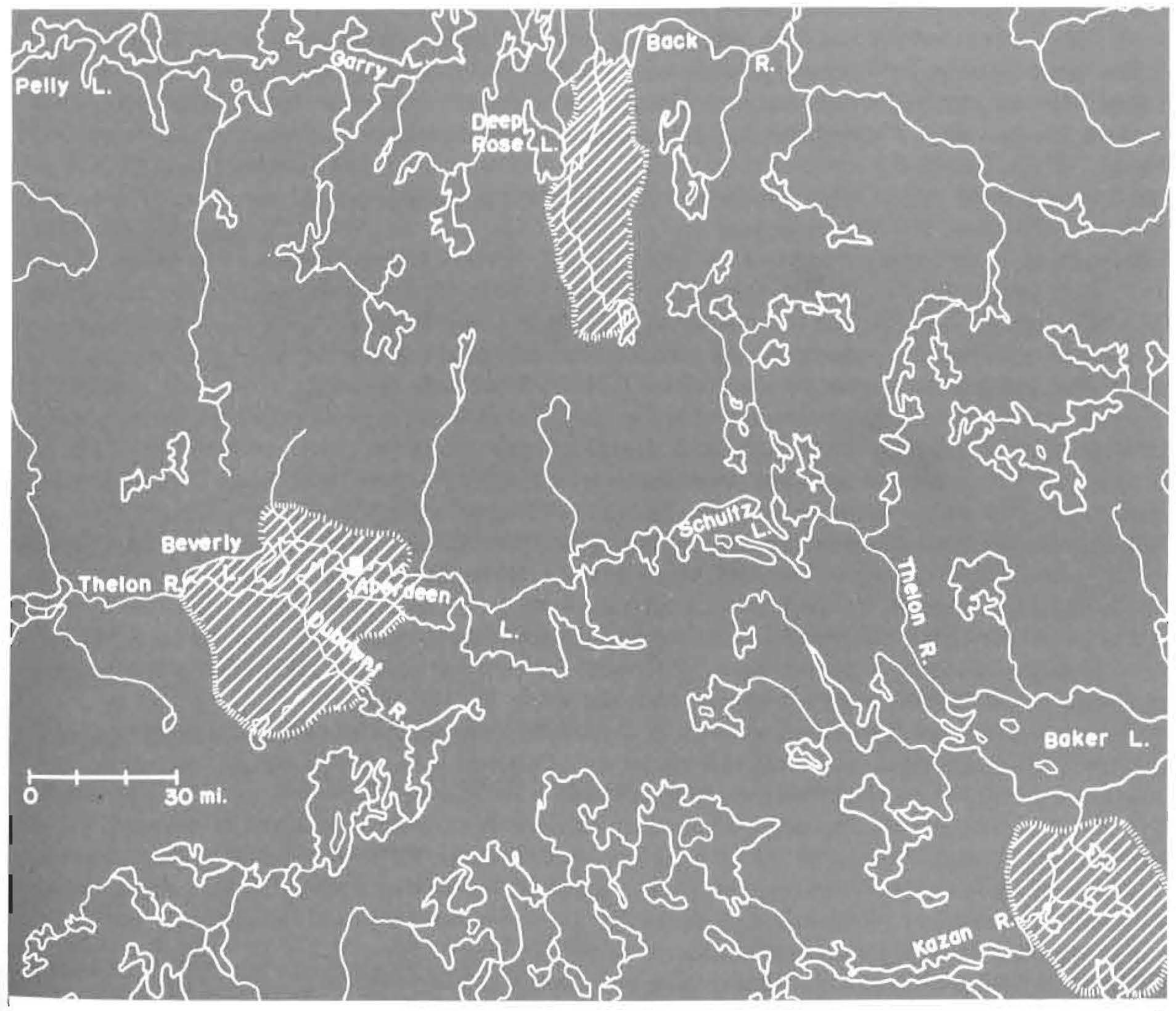
Figure 2 Den locations of the arctic fox in northern Canada. The breeding range of the species in North America probably extends over the entire arctic tundra zone (stippled).



The study area

The country in the vicinity of our cabin on Aberdeen Lake is low and rolling. On the north shore the land rises gently to hills some 10 miles inland. On the south side, the hills incline steeply from a narrow foreshore in a long series of wave-cut banks and beach terraces indicating post-glacial marine transgression: at the higher levels there are terraces said to have been formed by proglacial lakes (Bird, 1951). Exposed bedrock (sandstone) is very rare, the surface being composed of a thick layer of till which in places has been sorted to form expanses of sand or pebbles. The till is often thrown into oriented ridges and valleys, presumably by continental ice sheets. Prominent features of the landscape are sinuous eskers and esker-like hills but with bluff banks and truncated tops, as described by Clarke (1940) and Bird (1951). These and other re-sorted sandy deposits stand out sharply, owing to their lack of vegetation, from their surroundings. The lake and river banks are steep and actively eroding at promontories. Drainage is commonly poorly developed, except where streams run down through the sand and till, sometimes cutting deep, narrow canyons.

Figure 3 Study areas in central District of Keewatin.



The crests of the undulations and other dry places develop a characteristic plant association — a layer of moss capped with a mat of resilient black lichen penetrated here and there by a clump of feathery grass. The frost cracks in the humps often display a good growth of bake-apple berry. Marshy meadows occur in the dips with sphagnum, sedges, and dwarf birch the commonest plants. Tussocks, usually 12–18 inches high, are very numerous in the marshes. Occasional groups may be found up to 3 feet high, often associated with circular mud boils 10 feet or so in diameter, surrounded by rings 1 or 2 feet high bearing typical tussock vegetation. Intermediate habitats occur between the dips and the crests, on slopes and beach terraces, where the dominant species is commonly Labrador tea, with various berries, grasses, sedges, and lichens making up the remainder. A few stunted spruce trees grow in gullies and other favourable places near Beverly Lake, though trees are not common for another 20 miles or so up river; the tree line is 150 miles south of Aberdeen Lake. The most common woody plant is dwarf birch: it occurs most abundantly in damp, sheltered locations. In a few well-sheltered places, usually stream banks, heavy growths of willows up to 10 feet high may be found.

Other areas of fox den concentration, south of Sinclair Falls on Back River, and around the lower Kazan River, were visited annually on den surveys. Neither differed markedly in soil, topography, and vegetation from the main study area described briefly above at the west end of Aberdeen Lake. Areas of low den concentration, only casually or briefly examined during the study, included boulder fields, generally rocky country, broad areas of solifluction (usually thin sheets of unworked till, level or on long gentle slopes), areas of particularly confused drainage, and areas of sterile sand. Of the latter, a large tract stretching from Garry Lake south to the height of land bears little vegetation except lichen, and is practically devoid of lemmings (*Dicrostonyx torquatus* and *Lemmus sibiricus*), ground squirrels (*Spermophilus undulatus*), and arctic foxes.

Characteristics of denning habitat

Arctic fox dens were most common in sandy but well-vegetated areas of gentle slope. Places where numerous eskers or moraines overlooked broad valleys or river flats seemed the best occupied. Some differences between areas favoured by foxes and areas not favoured were readily apparent. Others were less obvious.

A stable surface deposit seems important to denning foxes. Areas in which solifluction features were widespread — patterned ground, mud boils, and earth slumps, for example — contained few fox dens. Large tracts of country, for example around the Marjorie Hills, had few fox dens, apparently because of the intensity of soil movement. Sites that appeared suitable for dens were present in such areas, and the scarcity of foxes may have been due to a scarcity of prey or to difficulty in obtaining it.

Fine, well-sorted silt and sand are favoured over clay, boulder clay, and rock debris. Where slabs of rock or boulders were common, fox dens were usually sparse. No fox dens were found in boulder fields or on talus, though potential den sites appeared numerous between the crevices in such places, and it may be that these render permanent den sites unnecessary. However, the pursuit of lemmings must be virtually futile among rockpiles with their abundant hiding places from which fugitives and their nests cannot be extricated.

The number of dens and their frequency of occupation

Altogether, 203 arctic fox dens were examined in the study areas during the 5 years in which surveys were made. The number newly found each year and the total number examined are shown for each survey in Table 1. Some were unoccupied, as shown by the absence of newly dug earth, few or no fresh droppings, and the absence of smell and moulted winter hair in the burrows. The presence of live ground squirrels or ermine (*Mustela erminea*) in fox dens was usually but not always evidence that arctic foxes were absent. Dens that were occupied early in the season, but abandoned before whelps would be expected to appear outside, showed evidence of occupancy such as winter hair and smell, but the heaps of excavated sand at their burrows were flattened and fresh sign was absent. Occupied dens were in general easily recognizable, even from the air, by the full and crumbly appearance of their sandheaps, which are added to continuously during the breeding and whelp-rearing season. Fox dens occupied exclusively by ground squirrels lacked rounded sandheaps at the burrow entrances. Alternatively, if foxes had recently abandoned a den, the sandheaps might be altered by ground squirrels, which quickly excavate shallow trenches through them.

Table 1 **Number and status of dens found in the study areas, central District of Keewatin, Northwest Territories, 1959–63**

Year	Dens newly found	Dens examined	Status: Occupied *and* abandoned	Status: Abandoned	Status: Not occupied
1959	19	19	19 (100%)	19	0
1960	95	113	45 (39.8%)	0	68
1961	54	163	102 (62.6%)	21	61
1962	22	169	47 (27.8%)	27	122
1963	13	188	66 (35.1%)	3	122

Of the 203 fox dens examined, 154 were occupied at least once during the 5-year study period. Only 19 dens were found in 1959, the first year of the study. The number examined in subsequent years ranged from 113 to 188. The proportion occupied and the proportion subsequently abandoned varied considerably from year to year. Chi-square tests showed the proportion occupied to be significantly greater* in 1961 than in any of the other years. It was also significantly greater in 1960 than in 1962 (*P* about .002). In 1963, it was intermediate between the values for 1960 and 1962, and the differences between the three are not significant.

Well over half the dens showing signs of recent occupancy that were examined in 1962 were abandoned, a significantly larger proportion than in any other year, excluding from consideration the small series visited in 1959. In the year with the next highest proportion of abandoned dens, 1961, approximately a fifth of recently occupied dens were abandoned. Significantly fewer (*P* about .002) were abandoned in 1960 and 1963, the difference between the proportions in the two seasons being insignificant.

The age of dens and associated changes in the frequency of use

Arctic fox dens in the study area range from single burrows to large, complex structures that are used and extended year after year. (For a more complete description of arctic fox dens see Danilov, 1958.) In the spring, when the dens are occupied, the ground is too hard frozen for foxes to tunnel, obliging them to use existing dens. It thus seems probable that breeding dens develop from temporary shelters dug in late summer.

Dens are excavated at the crests of slopes or banks, or on mounds, preferably in dry, light, sandy soil. The site appears to be chosen in part for its small accumulation of winter snow, good exposure to the sun in spring, protection from the severest summer winds, and elevation above the water and frost line. Up to 100 burrow entrances may be found in the largest dens, in various states of repair, and one or two new burrows may appear during the breeding season in an occupied den. Commonly, in old dens, part or all of the burrow system has collapsed entirely. Sometimes a den system appears to have moved along a ridge crest, as the older parts collapse and new burrows are dug at one end of the complex.

Fox droppings cause a dense mat of lush vegetation to develop around a well-used fox den. This mat may be visible over a mile away as a brilliant yellow-green patch amid the generally sere, brown and buff landscape. In contrast, the grasses around the burrows of ground squirrels appear blue-green. Among the abundant flowering plants at fox dens, cinquefoil, chickweed, and dandelions are some of the most conspicuous.

Authors have noted that fox dens differ considerably in size, complexity, and development, and that these differences relate to usage and age. Thus Sdobnikov (1958) speaks of complex and rudimentary dens, and Skrobov (1961) divides them as follows: recent (up to 10 entrances), middle-aged (from 11 to 25 entrances), and old (over 25 entrances). Skrobov's categorization is objective and appears useful, but the burrows are

*Here, and throughout the following pages when not otherwise stated, differences are considered significant when the probability of their being due to chance alone is one per cent or less.

difficult to count from the air, and a more subjective method, applicable to those dens in my series that were seen only from aircraft, was used in this study. Dens were classed as follows:

1. Youthful — no development of characteristic vegetation; burrows few; sand heaps the most conspicuous feature of the den (Figure 4).
2. Mature — well-developed; good mat of vegetation; no extensive area of collapsed burrows (Figure 5).
3. Old — large den site; many burrows; vegetation rich, with grasses becoming dominant; extensive area of collapsed burrows (Figure 6).
4. Senile — no longer active; burrows collapsed, producing a distinctive, hummocky appearance; covered with tall grasses (Figure 7).

Two dens were believed to have first been used by breeding foxes during the 5-year period, giving an increment of about 0.3 per cent per year. If we assume that the breeding population has not changed appreciably over the long term, the data suggest, very approximately, an average life-span of 330 years for each den. Den decrement figures are not available: one Stage 4 den remained unoccupied and completely inactive in the breeding seasons of 1960, 1961, and 1962, but was occupied in 1963. Some old fox dens had clearly been occupied by other species for many years. Wolves (*Canis lupus*) sometimes ruin active fox dens by digging out short, wide, breeding chambers, which may collapse, causing progressive erosion. Three active fox dens were taken over by wolves during the study period: one or more of them may still have been suitable for foxes afterwards. Occasionally, a grizzly bear (*Ursus arctos*) will dig out a fox den (two seen were so dug out), probably in search of ground squirrels. A den so treated is unlikely to attract foxes again.

The frequency distribution of arctic fox den stages (Table 2), however arbitrary the initial

Figure 4 Stage 1 fox den; lower Dubawnt River, July 1960; pilot Gordon Hornby in the background.

Figure 5 Stage 2 fox den; Deep Rose Lake, July 1962.

Figure 6 Stage 3 fox den; Dubawnt River, July 1963.

Figure 7 Aerial view of Stage 4 fox den; Kazan River, July 1960.

groupings, deserves some discussion. It approaches a normal distribution around the modal Stage 3, indicating that dens are in use for a long period, rarely becoming uninhabitable and rarely being replaced. The abruptness of the decline in number from Stage 3 to Stage 4 suggests either a peak of den digging, and hence of fox numbers, at some past epoch, or a rapid decline of the den from maturity through senescence to obscurity. The frequency of den use (sum of categories "occupied" and "abandoned") varies from stage to stage, declining from a peak of about once every 2 years for Stage 3 to once every 4 years for Stage 4. A decline in the frequency of den abandonment with increasing age is also evident from Table 2: one explanation might be that the most used dens are in the best places, hence the least subject to whelp mortality and its consequences, a subject to be discussed in more detail later on.

The density of dens

Arctic fox dens are nowhere very abundant in the Northwest Territories, and it is therefore necessary to survey large areas if data from a reasonable number of dens are desired. Furthermore, even practiced observers have difficulty in recognizing distant dens. Since it was not practicable to survey the whole of the large study areas intensively, the surveys made yielded only minimum estimates of the numbers of dens on the areas. The Aberdeen Lake study area was the most intensively surveyed of all those examined annually, mainly because of its proximity to our base camp, but also because it was the one best known to my trapper informants. I doubt if many dens in the area escaped our attention, and it is for this reason that the analysis of den distribution was carried further for the Aberdeen Lake area than for the other areas surveyed. Two of these, one near Deep Rose Lake, south of Sinclair Falls on Back River, and the other around the lower reaches of Kazan River, provide additional data (Figure 3). It is probable that on these areas relatively fewer of the existing dens were found. Table 3 shows features of the distribution of fox dens on the three areas, derived from measuring denning areas and distance between dens (by planimeter and caliper, using den locations recorded on 8-mile to the inch maps of the National Topographic Series). The mean density within the three study areas was 137 dens in 1,911 square miles, or one den in about 14 square miles (36 square kilometres).

Arctic fox dens appear to be more numerous in parts of the U.S.S.R. In the Bol'shezemel'skaya region, densities of from one to six dens per 10 square kilometres, or one den in approximately 0.6 to 4 square miles, have been recorded (Danilov, 1958; Skrobov, 1961). According to Dementyiev (1955), the upland tundra is the favourite denning habitat of the region, and bears an average density of about one den per 2.3 square miles. High densities were also found by Sdobnikov (1958) in the maritime tundra belt of Taimyr, where up to two dens per kilometre were recorded along the major river valleys that formed the favoured denning habitat. Boitzov (1937) quotes Tuomainen's estimate of the density of arctic fox dens of approximately one den per 50 square kilometres in Turukhansk region, which the latter investigated in 1926. Boitzov estimates a mean density of one den per 32 square kilometres for the whole tundra zone of the U.S.S.R., an estimate comparing closely with the one den per 36 square kilometres estimated for the Aberdeen Lake area.

Very high densities of breeding foxes, though coupled with small litters and high whelp mortality, are attained on the open island "ranches" of the North Pacific Ocean. Ashbrook and Walker (1925) indicate that up to 200 foxes can be maintained on an island ranch of 40 acres.

Table 2 The number of arctic fox dens found of each stage (age), and the relative frequency that dens of each stage were reported occupied, abandoned (occupied, but later vacated without evidence of whelps), and not occupied, on annual surveys. Totals for the breeding seasons of 1959 to 1963 inclusive, central District of Keewatin, Northwest Territories. The 203 dens found were visited annually an average of 3.3 times each

		Times reported						
	Total	Occupied		Abandoned		Not occupied		Total times
Stage	dens	No.	%	No.	%	No.	%	visited
1	21	17	28.3	10	16.7	33	55.0	60
2	64	79	35.4	34	15.2	110	49.3	223
3	87	90	32.0	23	8.2	168	59.8	281
4	31	21	21.4	4	4.1	73	74.5	98
Totals	203	207	31.3	71	10.7	384	58.0	662

Table 3 Features of arctic fox den distribution and dispersion on the study areas in central District of Keewatin

Region	Area, square miles	No. of dens	No. of square miles per den	R	c	Level of significance (P)
Aberdeen Lake	829	78	10.63	1.16	2.629	<.01
Deep Rose Lake	493	30	16.43	1.21	2.930	<.01
Kazan River	589	29	20.37	0.80	–2.059	<.05
All	1,911	137	13.94			

Note: The number shown is the maximum number found during the 5 years of the study. The Aberdeen Lake area was the one most intensively surveyed, though even there, some dens no doubt remained undiscovered. "R" is "the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbor" (Clark and Evans, 1954). "c" is the standard variate of the normal curve. The level of significance is that for the difference between the distribution and a random one of the same over-all density. Computations from Clark and Evans (1954).

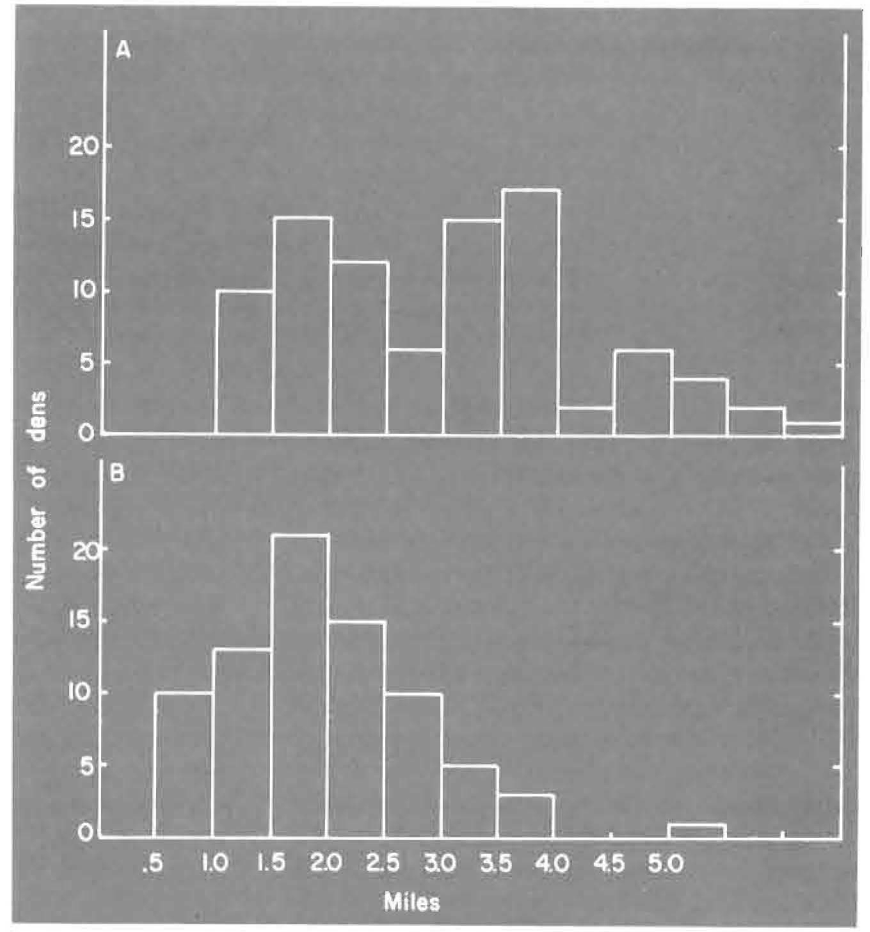


Figure 8 Distances between fox dens and their nearest neighbours in central District of Keewatin. A – between occupied dens, Aberdeen Lake study area, 1961–63; B – between all dens in the same study area, 1963.

The dispersion of dens

The statistical analysis of dispersion data in Table 3 is based on the design of Clark and Evans (1954). The mean of the distances between each den and its nearest neighbour is computed, as is the mean to be expected if dispersion were random. The ratio between the observed and expected means (R) indicates the departure of the dispersion pattern from a random pattern of the same density. If dispersion is random, R will equal 1. If there is no spacing, all the objects being at the same spot, R will equal zero. If spacing is maximal, and the objects are distributed in an even, hexagonal pattern, R will equal 2.1491. The significance of the difference between the means of observed and random dispersion patterns is obtained from the standard variate of the normal curve (c). When c = 2.58 or more, the

Table 4 Features of occupied arctic fox den dispersion in the Aberdeen Lake study area, 1961–63. Symbols as in Table 3

Year	Area, square miles	No. of dens	R	c	Level of significance (*P*)
1961	829	46	1.15	7.91	<.01
1962	829	23	1.11	0.43	>.05
1963	829	23	1.31	2.87	<.01
Combined	2487	92	1.18	3.28	<.01

probability that the difference between means is not significant is 1 per cent or less (Clark and Evans, 1954).

Not all dens used in the computations of Table 3 were occupied, and all the data included were obtained in 1963, when the location of every den in the final series was known. Den dispersion, as indicated by distance to nearest neighbour, was in each case significantly different from random ($P < .05$), the dens being in two areas more widely dispersed than would be the case if randomly placed, and in one area less so. Unfortunately, it is possible only to speculate on the differences between the landscape patterns of the three localities that might be responsible for differences in dispersion of fox dens.

The Aberdeen Lake area, being the best known, was used alone for the study of spatial relationships of occupied fox dens. The series included dens that were occupied in early summer but later abandoned. Data from the 3 years when most den locations were known, 1961–63, were combined, and the number of square miles tripled. The results (Table 4) indicate that, in 2 years out of 3 and also when all years are combined, fox dens were more widely spaced than they would probably have been if randomly dispersed, a finding suggestive of territoriality in denning foxes. On the other hand, there was no tendency toward more uniform dispersion with an increase in the breeding population, nor any significant difference between the R values ($P > .05$; $F = 0.594$, $N_1 = 78$, $N_2 = 92$) of the entire Aberdeen Lake series of 1963 and the combined occupied den series of 1961–63. Furthermore, spacing was by no means maximal. Under conditions of maximum dispersion, the calculated mean distance between occupied dens is 6 miles, and between all dens 3.8 miles. These distances were much greater than those observed, respectively, 3.1 miles and 2.1 miles. There is, however, a distinct tendency for denning foxes to keep their distance from each other. The minimum distance between occupied dens, irrespective of the density of occupied dens, was about 1 mile (Figure 8).

It must be concluded, therefore, that the number of occupied dens in the Aberdeen Lake study area is limited neither by habitat nor by territorial behaviour. Though the calculation does not therefore give a valid estimate of the extent of each territory, if the entire area is divided by the number of occupied fox dens, over 27 square miles were available, on the average, for the support of each family. This figure, or its equivalent of 70 square kilometres, may be compared with the figures 50 and 32 square kilometres quoted by Boitzov (1937).

Foods of the arctic fox and their relative importance

Previous work

The diet of the arctic fox has been examined systematically at both coastal and inland sites. All authors agree on the supreme importance of lemmings and other small mammals to inland arctic foxes, whose diet is well summed up by MacFarlane (1908) as "mice, lemmings, birds, and carrion". Foxes living on islands or near the sea may rely heavily on marine invertebrates, fish, seamammals, and sea-birds. Such diets have been analysed on the Commander Islands by Barabash-Nikiforov (1939) and on Kildin Island, Barents Sea, by Lavrov (1932). The propensity of arctic foxes to eat the remains of seals (mainly *Pusa hispida*) left on sea ice by polar bears (*Ursus maritimus*) is mentioned by several authors (*i.a.* Elton, 1927; Freuchen, 1935).

The food of an arctic fox population has rarely been analysed for a period of more than a single year. The exception is an analysis by Shibanoff (1951) of the diet of arctic fox whelps in 1946 and 1947, presumably on the Kanin Peninsula, U.S.S.R.

Much comparable work has been done on the foods of the red fox (*Vulpes vulpes*) in Scandinavia, Great Britain, and the United States of America. The results of several such studies, particularly as they concern the advantages and shortcomings of the various techniques, have been basic to the present analysis (see, for example, Scott and Klimstra, 1955; Lockie, 1959; Lund, 1962; Englund, 1965).

Materials and methods

Assessment of lemming numbers

Estimates of the relative size of the lemming population in the vicinity of base camp at Aberdeen Lake were obtained each year in mid-June and mid-July, by means of a standard line of snap-traps. Lemmings in the vicinity of Baker Lake were studied intensively during the same period by Krebs (1963, 1964, and *in litt.*), whose estimates are available for the period 1959 to 1962. My estimates of lemming numbers are discussed in an earlier publication, from which Table 5 and

Table 5 Lemming population indices, Aberdeen Lake standard trap line

	Dicrostonyx		*Lemmus*		Combined	
Year	June	July	June	July	June	July
1960	100	100	100	44	100	72
1961	121	81	24	13	74	48
1962	12	19	41	7	26	13
1963	36	43	33	11	34	27

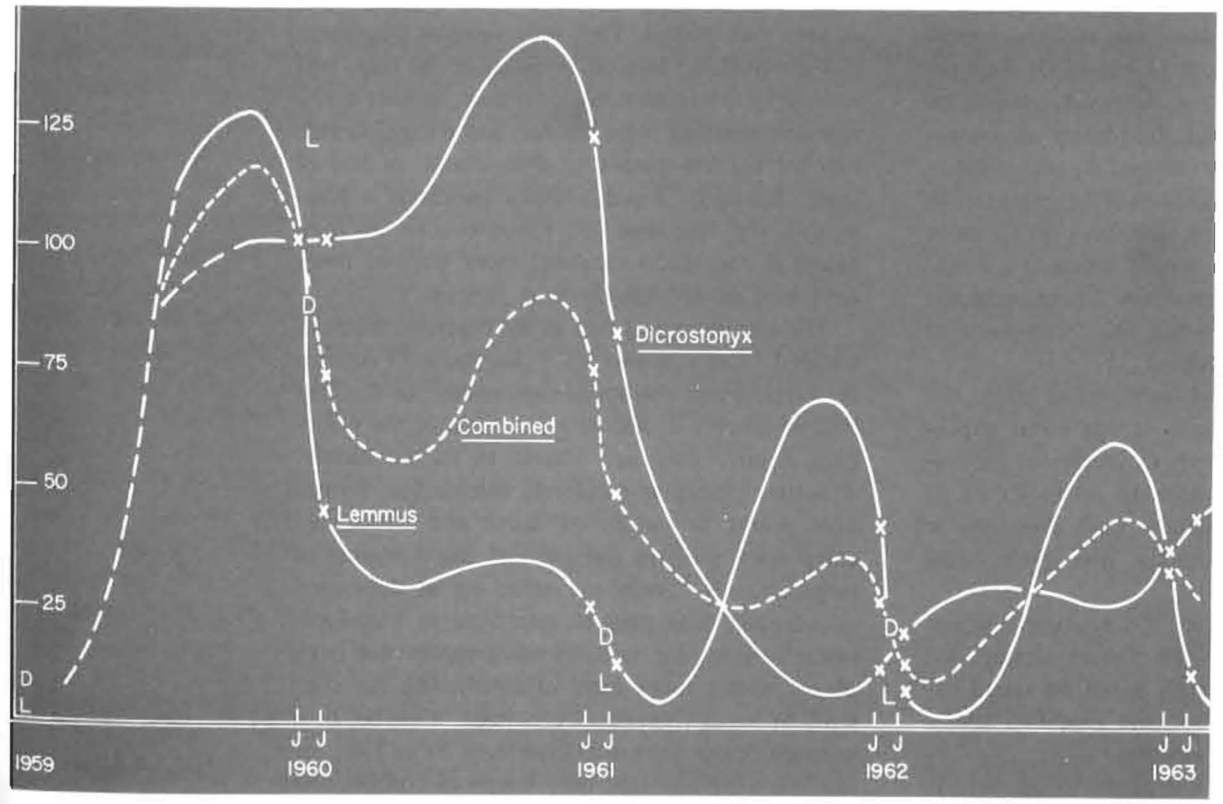


Figure 9 A hypothetical curve of changes in the number of trappable lemmings (*Dicrostonyx* and *Lemmus*) at the northwest corner of Aberdeen Lake, 1959–63, based on adjusted snap-trap indices. The indices are shown as "x's". For comparison, the relative abundance of the two species, according to Krebs (1963), 115 miles to the east at Baker Lake, is shown by an "L" for *Lemmus* and a "D" for *Dicrostonyx*.

Figure 9 are borrowed (Macpherson, 1966). Lemmings were very scarce in 1959, very abundant in 1960, declining through 1961 and 1962, and more numerous again in 1963.

Analysis of food remains

The main purpose of the food analyses performed was to find out what the arctic foxes of the study area ate during the breeding season, and how their diet was related to lemming abundance and to the reproductive success of the foxes. Most information came from the identification of food items in faecal pellets, classed according to their frequency of occurrence. Studies referred to above have shown that this method of analysis is unreliable for assessing the relative importance of large and small game and of vegetable and animal matter, the volumetric analysis of gut contents being the preferred method. However, foxes were neither abundant nor easily captured in the study area, and specimens therefore were not obtainable in the quantities that would be required. Although it is improbable, on evidence from red fox feeding trials (notably those of Lockie, 1959), that the diet of the foxes was exactly represented by the droppings analyses, most of the more common remains in the droppings were of items of comparable size — lemmings, birds, birds' eggs, and fish. There is thus no reason to believe that their proportions in the droppings differed appreciably from the proportions of the foods they represented in the diet. When, however, caribou or bee remains are included, frequency of occurrence figures convey less adequately the composition of the diet, for caribou may be expected to leave much fewer remains, and bees much more numerous remains, than would lemmings, birds' eggs, etc., per unit of meat eaten. These problems should be remembered when the "frequency of occurrence" tables are studied.

The droppings analysed were picked up on the study areas, mainly at dens. It was often impossible to relate the droppings to particular defecations, which might each include up to six or so separate pellets. Consequently, each dropping or pellet was analysed separately, and given equal weight in the summary.

Droppings were collected systematically whenever dens were examined. They were assessed for age on the following criteria based on timed exposure of fresh droppings, and modified somewhat in accordance with weather:

— up to 2 weeks old — bile pigments on surface, odour, mucous (slippery when wetted);

— 2 weeks to 1 month old — bile pigments inside but not on surface, no odour;

— 1 month to 2 months old — no bile pigments visible, hair fresh and tough, no green mould.

For examination, each dropping was washed in a fine-meshed sieve under bubbling water, until all its component materials were separated. A binocular loupe was used for identifying such objects as the incisors and cheek teeth of the two lemming species. A binocular microscope was used to identify smaller objects such as caribou hair, and the finer hairs of mammals were identified from resin impressions made as described by Williamson (1951).

A study of the winter diet of the arctic fox was made using gut contents obtained from samples of trappers' catches. The samples were first examined for parasites, then washed and examined dry for food remains.

The circumstances of capture of the trapped animals examined did not facilitate the study of diet. For the most part, arctic foxes taken by Eskimo trappers are caught by leg-hold steel traps, and the animals die from exposure or are killed by the trappers on one of their infrequent visits. The stomachs of trapped foxes frequently lack food contents altogether, and often contain parts of their own bodies. They may swallow fragments of their teeth broken off in biting at the trap, and sometimes parts of a mangled foot; almost every stomach contains some fox fur, and a considerable number contain pieces of skin, claws, or bits of bone. Similarly, Lund (1962) mentions a Norwegian red fox that had eaten two of its toes. Many of the tracts removed from trapped foxes contained no identifiable food remains.

The occurrence of bait in the digestive tracts of trapped foxes requires some discussion. Traps set for arctic foxes are not always baited. In the District of Keewatin, and in other parts of the Canadian Arctic, they are placed at such naturally attractive places as meat and fish caches, prominent points or cairns on lakes and rivers, old camp sites, garbage dumps, and the carcasses of large animals. Traps are often set at dens, and unoccupied dens may be improved as trap locations by bringing to them snow-blocks cut from places where foxes have urinated. The gut contents of foxes trapped at a carcass, a cache, or a garbage dump were not considered to be bait; for the following analysis, only lumps of blubber and meat without skin and hair were considered to be bait and excluded.

The remains of lemmings can never be considered other than indicative of natural feeding, but hair from caribou (*Rangifer tarandus*) or seals found in digestive tracts might come from carcasses, caches or garbage dumps, or from bait. From conversations with trappers, I believe that all such occurrences can be considered indicative of natural diets.

Finally, records were kept of the remains of food items found at occupied dens. Pieces of bone that appeared to date from previous years were not included in the tabulation.

Droppings at dens

Nearly 5,000 droppings were examined during the study, of which 4,653 were collected at breeding dens, and were used in the analysis. Summaries of the occurrences of identifiable food remains in droppings, segregated by date into groups representing periods of 2 weeks to a month, are given in Table 6. The data are shown graphically in Figure 10.

Lemmings (*Lemmus* and *Dicrostonyx*) predominated in the samples, constituting up to 90 per cent, and never less than 50 per cent, of identifiable occurrences. (Differences in the proportion of lemming remains identified to species between collections are due mainly to differences in experience and confidence between the assistants who helped me from time to time in examining the material.)

Birds and their eggs were next in importance; their frequency in the droppings generally increased during the period from May to July, and over the 4-year period ranged between 4 and 29 per cent. The remains of caribou, largely of fawns, were common in some years, with frequencies of up to nearly 15 per cent. The remains of other foods were scarce or lacking.

Arctic hare (*Lepus arcticus*) fur was identified in several 1960 and 1961 samples, but none was noted in the two following years. Fish (*Cristivomer* and *Lota*) remains were rarely found in droppings.

Insects were rare in the 1960 collection, but were a substantial proportion of the foods identified in later samples. The only ones of any importance were large bees (*Megabombus* sp.), the frequency of which varied between zero and 10.5 per cent. In 1962 and 1963, droppings were sometimes more than half composed of the remains of bees, indicating that the foxes were hunting the insects selectively, or perhaps digging out or lying in wait at nests. Berries also assumed greater importance in the later years of the study. Some of the 1962 and 1963 droppings would have been indistinguishable from those of geese, but for a little microtine hair between the skins and seeds of the berries or the packed leaf fragments. Moulting Canada geese (*Branta canadensis*) frequently graze the lush vegetation of fox dens, and there are often goose droppings even on occupied dens. *Empetrum* and *Rubus* were the usual berries found in fox droppings.

A wide variety of miscellaneous items was identified, but none occurred abundantly. An item which appeared fairly regularly was a black, amorphous material containing both vegetable fibre and microtine hairs. It was believed to be re-ingested droppings of caribou, with some other material. Foxes are said to eat caribou or reindeer droppings by such authors as Lavrov (1932), Dubrovskii (1937), and Pedersen (1959).

The frequency of lemming remains in the droppings decreased over the study period, undoubtedly owing to the concurrent decrease in lemming abundance. There is a marked correlation ($r_d = 0.954$; $P < .01$) between ranked lemming indices for each month and ranked frequencies of lemming remains in droppings. Means of grouped sample frequencies were used when more than one sample was available for the period represented by a single lemming index. The unranked data are plotted in Figure 11.

Thus the use made of lemmings by foxes varies with the abundance of lemmings as determined by snap-trapping. The percentage frequency of all other items combined in fox droppings obviously bears an inverse relationship to the percentage frequency of lemmings. When lemmings are scarce, foxes tend to feed more heavily on such foods as birds' eggs, insects, and even berries. Whether predation pressure on, for example, birds' eggs, is absolutely greater when lemmings are scarce is another question, and one which cannot be answered with the available data (but see Sdobnikov, 1958). It is my impression that droppings were harder to find in 1962 and 1963 than in 1960 and 1961, even at occupied dens, and that the fox population was obtaining very much less total food. On the other hand, rock ptarmigan (*Lagopus mutus*) were abundant

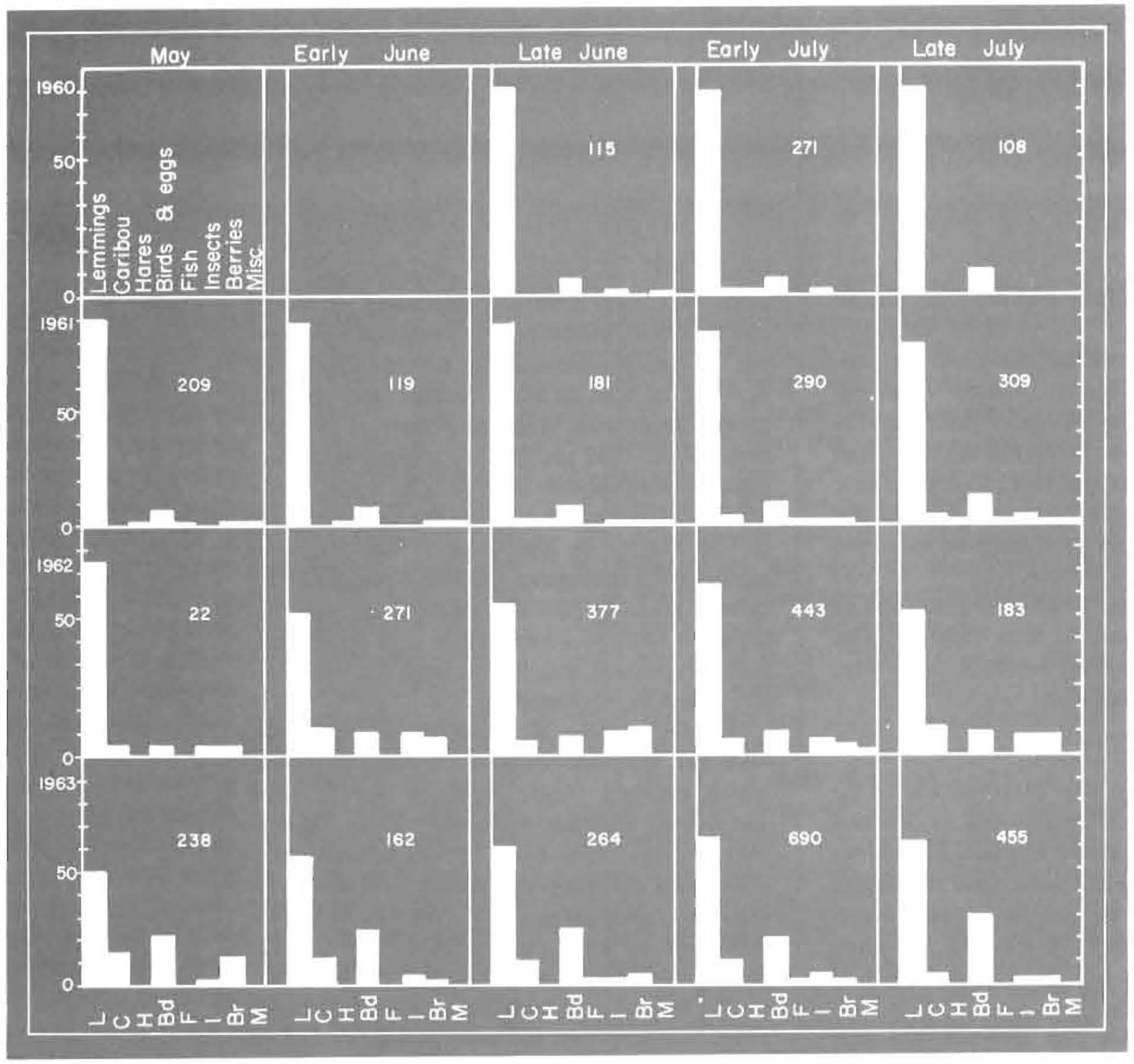


Figure 10 Histograms showing the proportions of various identifiable food remains in the droppings of arctic foxes in central District of Keewatin, 1960–63. The numbers on the graphs show the number of pellets in each sample.

Table 6 Percentage occurrences of food remains in the droppings of denning arctic foxes in central District of Keewatin, 1960–63

Year	Period	No. of pellets in sample	No. of occurrences of food items	D	L	UM	CL	C	H	Bd	F	I	Be	M
1960	Late June	115	134	49.3	39.6	1.5	90.4			7.5		1.5		0.7
	Early July	217	265	36.6	47.9	3.4	87.9	1.5	0.8	8.3		1.5		
	Late July	108	127	38.6	45.7	5.5	89.8			10.2				
1961	May	209	337	47.5	38.0	3.9	89.4		0.9	7.1	0.9		0.9	0.9
	Early June	119	155	54.8	31.0	1.9	87.7		1.3	8.4			0.6	1.9
	Late June	181	219	57.1	28.8	0.5	86.4	2.3	0.5	8.7		0.5	1.4	0.5
	Early July	290	347	42.1	36.6	4.9	83.6	3.5		9.8	0.6	2.3	0.3	
	Late July	309	413	32.0	38.0	6.8	76.8	3.9	0.2	12.1	1.0	4.6	0.7	0.7
1962	May	22	25	28.0	28.0	28.0	84.0	4.0		4.0		4.0	4.0	
	Early June	271	380	17.9	21.8	22.6	62.3	11.3		9.5		9.2	7.6	
	Late June	377	544	18.6	20.8	25.7	65.1	5.5		7.2		10.5	11.6	0.2
	Early July	443	551	20.5	29.8	23.6	73.9	5.6		9.6		6.5	3.6	0.7
	Late July	183	256	18.0	22.7	21.9	62.6	11.7		9.4		7.8	8.6	
1963	May	238	453	20.3	11.9	18.3	50.5	14.6		21.2		1.8	11.9	
	Early June	162	274	20.1	17.9	18.6	56.6	12.4		24.5		4.4	2.2	
	Late June	264	426	15.3	22.3	22.8	60.4	9.9		23.9	0.5	2.1	3.3	
	Early July	690	1030	19.8	20.4	24.6	64.8	9.3		20.1	0.3	3.3	2.2	
	Late July	455	685	13.0	19.1	30.8	62.9	3.6		28.9		2.9	1.5	0.1

Note: D = *Dicrostonyx*, L = *Lemmus*, UM = unidentified microtines (lemmings), CL = combined lemmings, C = caribou, H = hare, Bd = birds and eggs, F = fish, I = insects, Be = berries, M = miscellaneous.

on the study area only in 1960: they were least abundant in 1961 and 1962, and in 1963 appeared to have somewhat increased; that is, their numbers fluctuated concurrently with over-all lemming numbers.

Comparing the relative frequency of remains of the two lemming species of the region, the collared lemming (*Dicrostonyx*) and the brown lemming (*Lemmus*), with the indices of abundance established for them with the standard trap line, there was some indication that the foxes were consuming more individuals of the more abundant species (Figure 12).

By means of feeding trials, Lund (1962) found an aversion to the Norway lemming (*Lemmus lemmus*), a comparatively showy member of the genus, in Norwegian ranch red foxes. From the frequency of brown lemming remains in the droppings of the arctic fox in the District of Keewatin, it seems unlikely that our *Lemmus* is distasteful to the arctic fox.

The capacity of the red fox to switch to secondary prey species when its primary prey declines in abundance is well known, whether the primary prey be rabbits (Lever, 1959), small rodents (Englund, 1965), or vertebrate prey in general (Scott and Klimstra, 1955). Arctic foxes live in regions of lower biotic abundance, and it may be expected, as will appear, that a decline in lemming abundance profoundly affects fox production and numbers. Only in maritime areas may other food sources be abundant enough to mitigate the effects of a lemming scarcity (Manniche, 1910).

Food remains in digestive tracts

The numbers of digestive tracts examined, and of food remains identified from them, are shown in Table 7. The tracts came from foxes killed during the trapping season, which extends from November 5 to April 15, and the food remains are thus representative of winter diets only.

In a year of abundance such as 1960–61, lemmings made up a high proportion of total fox food in the District of Keewatin. When lemmings were scarcer, as in 1961–62, caribou remains were found more often. The latter were no doubt from carrion and from garbage at trappers' camps.

At Resolute Bay, in the District of Franklin, some 700 miles farther north than the inland study areas, there is only one species of lemming, and land mammals are much scarcer. There the remains of ringed seals, probably many of them left by polar bears (c.f. Elton, 1927; Lavrov, 1932; Freuchen, 1935; Kirpichnikov, 1937), formed a high proportion of the food remains found; seals and garbage became more frequent in the tracts as the frequency of lemmings decreased. No sea-mammal remains were found in Eskimo Point samples, also from a coastal locality. The difference is tentatively ascribed to the comparative abundance of polar bears at Resolute Bay, and their rarity in the vicinity of Eskimo

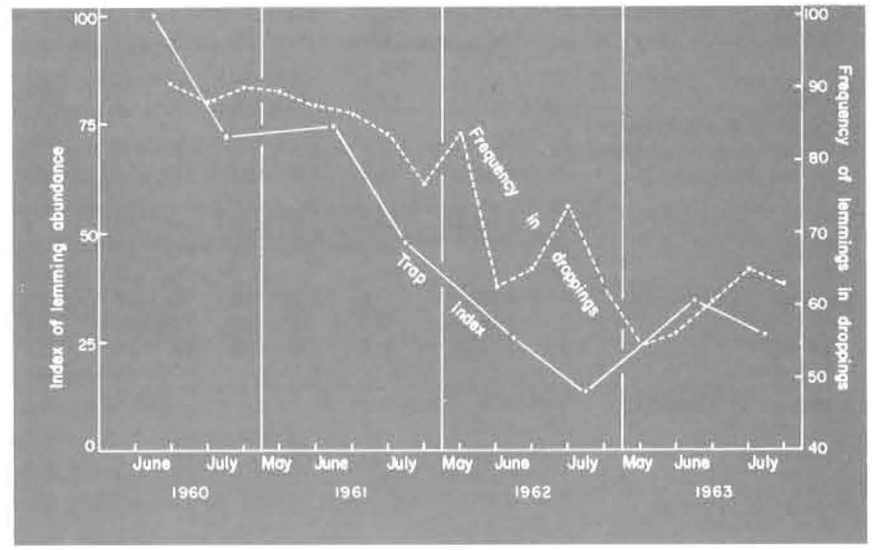


Figure 11 The proportion of all lemming remains to total food remains in the droppings of breeding arctic foxes, and contemporaneous indices of lemming abundance, central District of Keewatin, 1960–63.

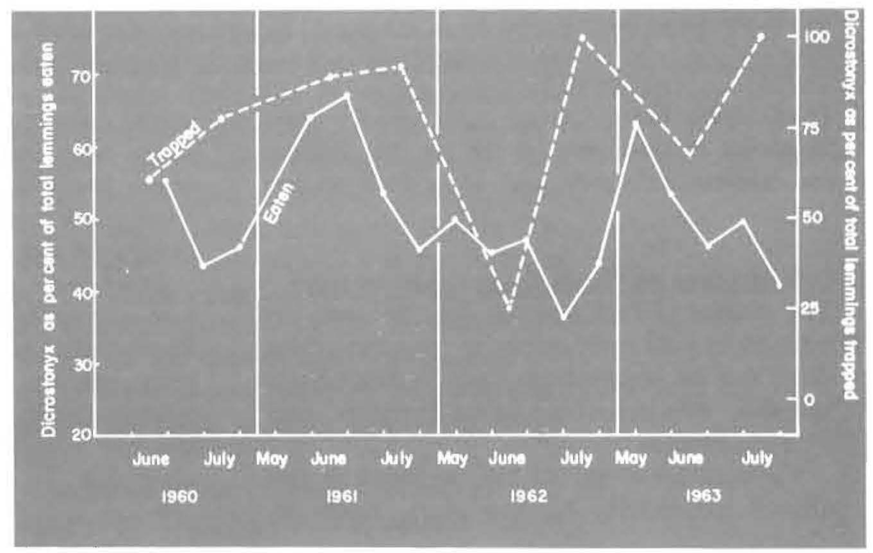


Figure 12 Contemporaneous changes in lemming species abundance at Aberdeen Lake, as determined by snap-trapping, and in the frequency of occurrence of lemming remains (by species) in the droppings of denning arctic foxes, 1960–63.

Table 7 Identifiable food remains in the digestive tracts of trapped arctic foxes

Place	Year	No. of tracts	D	L	CL	C	Birds	Seals	Garbage	Miscellaneous
District of Keewatin										
Inland: Baker L., Aberdeen	1958–59	5			2	4			1	
L. and Ferguson L.	1960–61	59	10	25	35	9			2	3 canid, 1 wolverine
	1961–62	36	8	15	23	25	1			2 wolverine
Total		100	18	40	60	37	1	0	3	6
Per cent					56	35	1		3	6
Coastal: Eskimo Pt.	1960–61	33	1	12	17	7				4 canid
	1961–62	84	1	20	21	41	13		15	1 fish
Total		117	2	32	38	48	13	0	15	5
Per cent					32	40	11	0	13	4
District of Franklin,										
Resolute B.	1958–59	15	4		4			4	1	1 hare
(Coastal)	1959–60	20	14		14		1	1		2 canid
	1960–61	100	27		27	10	5	10	4	1 marine algae and invertebrates
	1961–62	35	3		3	2		15	14	
Total		170	48	0	48	12	6	30	19	4
Per cent					40	10	5	25	16	3

Note: D = *Dicrostonyx*, L = *Lemmus*, CL = combined lemmings, C = caribou. "Canid" denotes hair of dog or wolf. Dead dogs could also be considered garbage. Wolves and wolverines, for the most part killed at poison bait, might best be considered carrion.

Point. Polar bears hunting seals usually leave fragments of their prey on the ice, but Eskimo seal hunters ordinarily haul away their victims intact.

Information on foods from other sources

The remains of food items at dens are generally believed to yield quite erroneous estimates of fox diets, and the observations given in Table 8 are included, with miscellaneous observations, only for completeness.

The numbers of animal remains found at dens differed considerably between years. Foxes appeared quite prodigal of food in 1960, when lemmings were most abundant, leaving lemming heads, stomachs, and even gravid uteri scattered around their dens. In 1961 and 1962, on the other hand, food remains were less common.

Foxes were frequently seen returning to the dens with food in their mouths, usually lemmings. Two breeding adult arctic foxes collected in other years, one on Prince of Wales Island and the other on Adelaide Peninsula, were carrying five and two lemmings respectively in their mouths when shot.

Table 8 The number of times that animal remains were found at dens, 1959–63. Only remains that appeared to be less than a year old were counted

Item	1959	1960	1961	1962	1963	Totals
Lemmus		(20)	(5)		(5)	(30)
Dicrostonyx		(9)	(1)		(3)	(12)
All lemmings		30	9		9	48
Caribou	4	5	3	1	3	16
Hare		2	1			3
Eggs		1		1		2
Waterfowl		2	2	1	4	9
Passerines		1			3	4
Other birds		3	2		3	8
Fish		2		1	1	4
Total all items						94

Age structure of arctic fox populations

Previous work

Several North American workers have studied aspects of the population dynamics of the red fox, *Vulpes vulpes*, and the gray fox, *Urocyon cinereoargenteus*, including Richards and Hine (1953), Layne and McKeon (1956), and Wood (1958). Only one arctic fox population has previously been studied systematically, and that in the U.S.S.R. The samples used came from an unspecified trapping area, and were analysed by Smirnov (1964) at Sverdlovsk. Techniques of age determination adequate for separating young-of-the-year, or whelps, from older red foxes are discussed by Reilly and Curren (1961). Few techniques for separating foxes of the older age classes are known. Wood (1958) aged gray foxes by tooth wear. His method was not applicable to the arctic foxes of the study area, whose teeth were found to wear very slowly. The methods that I used were developed from the work of Churcher (1957, 1960) on the red fox. Smirnov (1960) has developed another method based on the thickness of cemental deposition in the pulp cavities of the teeth, which he has used with success. In a footnote to a more recent paper, Smirnov (1964) says that he has been able to age arctic foxes by annuli in the cementum as well.

Materials

Most of the information obtained on the dynamics of arctic fox populations came from examination of samples from trappers' catches. The carcasses were, for the most part, examined in improvised laboratories at the settlements, but samples were occasionally shipped to Churchill or Ottawa for study. At some settlements a part-time curator of the samples was hired for the project.

I tried to get as many carcasses as possible, up to about 100, from both the early part of the trapping season, November and December, and the latter part, March and April. The skinned carcasses received from the trappers were, preferably, individually tagged with the date trapped, or, where it was unknown, kept in separate lots representing 2-week collecting periods. They were left frozen until they could be examined — sometimes as late as early June.

The carcasses were thawed in lots of up to 20 and subjected to post-mortem examination. Measurements were made, and organs and bones collected as necessary. Bones were later cleaned with dermestid beetles, and bleached and coated for examination. Nearly 1,000 specimens were so treated between 1958 and 1964.

Through the courtesy of Curator Edvard K. Barth, Zoological Museum of the University of Oslo, a collection of known-age blue fox carcasses was obtained from the experimental fox ranch of the Norwegian Agricultural College at Vollebeck, Norway, for the purpose of evaluating aging techniques.

Methods

The skulls and long bones of whelps killed in November and December are easily recognized by their open epiphyseal and basioccipital-basisphenoid sutures. Until arctic foxes are a year old these sutures are visible, and the presphenoid-basisphenoid suture is either open or visible. Arctic foxes in their first year of life are thus easily identified.

Several progressive changes take place in arctic foxes as they age, and all that could be identified were evaluated as bases for aging techniques. They included deposition of cementum on the roots of the teeth, increasing eye lens weight, bone accretion (as examined by measurement and weight, and by microscope and radiology), allometric cranial growth, and suture closure. The main criterion finally adopted was the degree of eruption of the upper canine teeth. The appearance of the canine tooth sockets, the state of certain sutures, and the condition of the cutting surfaces of the teeth were helpful in relegating questionable specimens to their most probable age classes.

The canine teeth of foxes continue to erupt through life. They progressively acquire cementum deposits on the roots, and at the same time their points become worn. Consequently, although the tooth changes little in length after the first half year of life, any fixed point on its surface moves gradually away from the root and toward the outer tip. As Churcher (1957, 1960) discovered in his study of the red fox, the proximal edge of the enamel forms such a fixed point, and the distance between it and a standard point on the edge of the alveolus is related to the age of the individual (Figure 13). The measurement was taken as shown on the anterolateral surfaces of both canine teeth, unless one was diseased or otherwise abnormal, in which case the single measurement was doubled. When the edge of the enamel was inconspicuous, it was revealed by

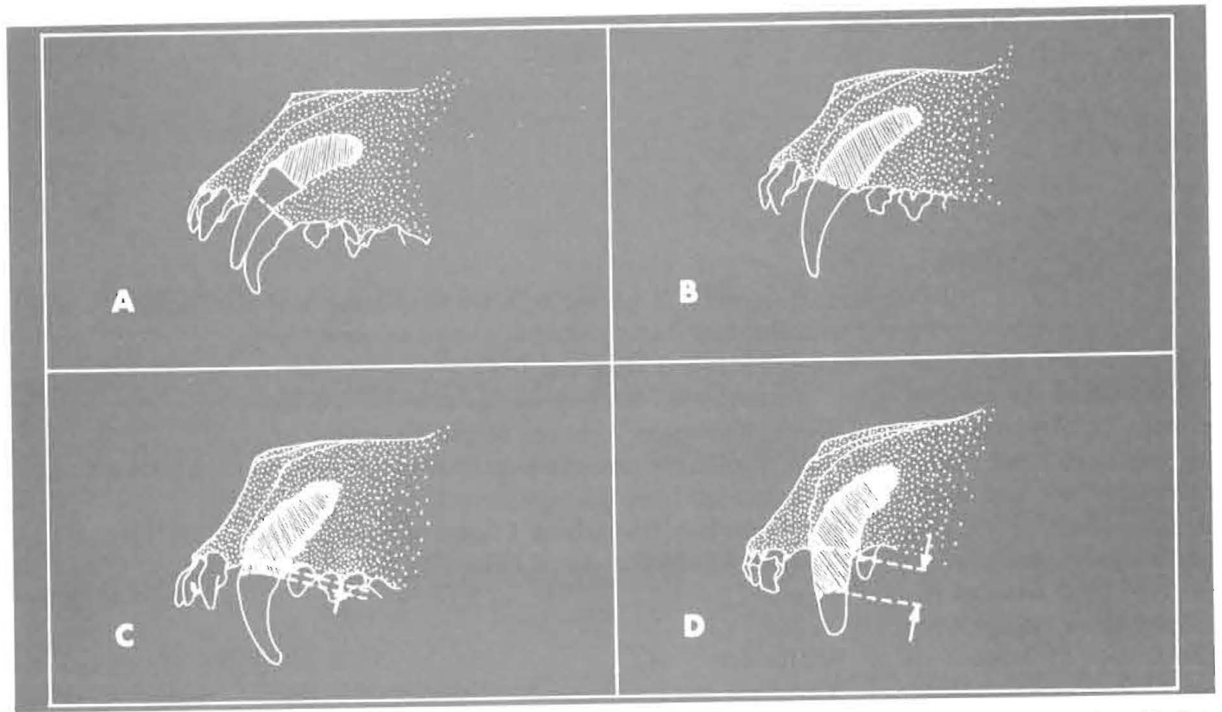


Figure 13 Stages in the eruption of the left upper canine tooth of the arctic fox. A – Whelp 3 months old (late August) with permanent upper canine erupting over the deciduous canine. B – Fox 6 months old (late November) with the boundary of the canine enamel coinciding with the edge of the alveolus. C – Fox 1½ years old (late November) with a band of dentine showing below the edge of the alveolus. D – An aged fox, perhaps 6 years old.

scratching with a knife, or by staining with alizarin, and routine skull preparation came to include the latter treatment.

The fact that arctic fox catches usually contain one dominant year-class or cohort made it possible to identify age classes up to 2½ years for November–December specimens, and up to 3 years for March–April specimens. That is, specimens of these ages were separable from specimens both a year younger and a year or more older. Plots of enamel height measurements for the males of Resolute Bay samples are shown in Figure 14. The females present a similar picture, but their enamel heights lag a few tenths of a millimetre behind those of the males. District of Keewatin foxes in successive samples yielded similar plots. Mean collection dates differed between successive samples: when specimens were abundant, it was possible to limit the sample period more than when the harvest was meagre. However, knowing the collection date of a sexed specimen, it was usually possible to assign it to its probable age class with confidence, particularly when, as was usually the case, alternate classes were scarce or absent in the sample. Other characters were, as stated, employed when a decision was impossible on the basis of enamel height alone.

The determination of age composition in samples does not by itself yield information on population structure, productivity, or survival. Methods of calculating the vital statistics of wild animal populations have been described and explained by Deevey (1947), and more recently by Quick (1963). The nature and representativeness of the sample must be considered. Such questions must be answered as: is it large enough? are all sex and age classes represented proportionally? Samples of trapped arctic foxes vary enormously in age composition, as has already been shown. It is clear that, even if samples from the trapping harvests are representative of the population from which they come, they are representative of it for a particular period only: a sample from the next trapping season is likely to display an utterly different picture. Consequently, averaging sample composition over a period of years cannot yield as full an understanding of population processes in these populations as in ones with more stable age compositions.

The method employed for the analysis of samples is substantially that of Smirnov (1964). Its basic feature is the treatment as a separate entity of the part of the population destined to die in traps. Thus samples are analysed, and the proportions of the different age groups in them extrapolated to each total kill represented. The portions of each year class that are caught in traps in successive years are accumulated, and their strength assessed through each trapping season in which they appear. The size and age composition of the "population" can thus be deduced for any trapping season for which the required data are available.

Smirnov apparently worked without data from the field on breeding success. In the present study such data were obtained for several of the years represented by specimen samples. Furthermore, he lacked information on age-specific reproductive rates. As will be shown, such data are necessary for the amalgamation of age structure analyses with uterine scar counts for the purpose of

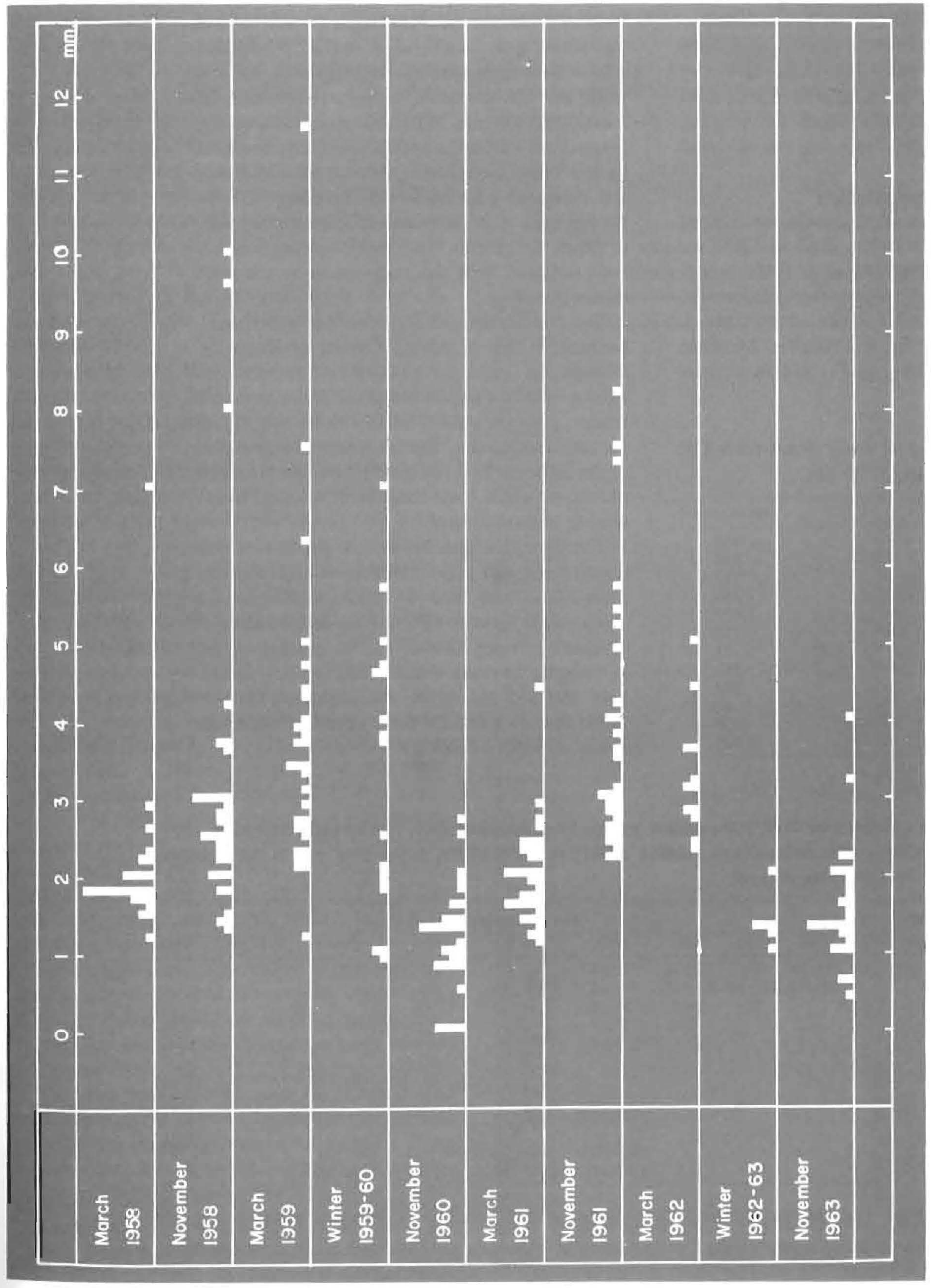


Figure 14 The frequency distribution of the sum of enamel height measurements from left and right upper canines, from male arctic foxes of successive Resolute Bay samples.

estimating differences in trap-proneness between whelps and older animals. They are also necessary for determining the effect of food abundance on breeding performance. In neither Smirnov's study nor in mine was an estimate of natural mortality obtained, a deficiency which has possibly introduced a considerable error into our analyses.

The Resolute Bay population

Of the settlements from which samples of trapped foxes were obtained, Resolute Bay produced the longest regular sampling period and the largest samples. This was due both to the excellent co-operation of the trappers, of our curator, Mr. J. Idlouk, and of the Royal Canadian Mounted Police members stationed there, and to characteristics of the community itself. All the trappers lived in the settlement and brought in their catches for skinning at home; also, caribou, fish, and marine mammals were available for man and dog food, and fox carcasses were rarely needed for meat. The climate kept the specimens solidly frozen until late in the spring, and frequent flights by the Royal Canadian Air Force permitted easy and inexpensive access at will. Sampling from the kill has been more successful at Resolute Bay than at other settlements, and more information has been obtained from this region than by the same means elsewhere.

The country around Resolute Bay differs markedly from that in central District of Keewatin. Though the land is far more barren, the sea provides a wealth of animal life absent from the inland tundra, and contributes heavily to the support of the local arctic foxes. The frequency of occurrence of the different food remains in the digestive tracts of trapped arctic foxes from various localities has already been discussed.

The Resolute Bay arctic fox population was sampled through seven consecutive trapping seasons, 1957–58 to 1963–64, during which time the catch varied between 40 and 825, and the samples obtained between 13 and 182. A general decline in trapping harvests occurred during the period, here ascribed to social and economic factors rather than to a decline in the abundance or availability of foxes (Table 9).

Table 9 The number of arctic foxes traded at Resolute Bay, 1953–65

Year	Pelts traded
1953–54	156
1954–55	335
1955–56	763
1956–57	380
1957–58	825
1958–59	738
1959–60	57
1960–61	282
1961–62	382
1962–63	40
1963–64	210
1964–65	405

Table 10 Arctic fox catches and their composition by age from Resolute Bay, Northwest Territories, 1957–58 to 1963–64, with estimates of relative cohort size and of the population size at the beginning of each of four trapping seasons

Season	Number caught	Size of sample	Year of birth 1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
1957–58	825	60	14±14	14±14	0	27±22	770±27						
1958–59	738	182		52±14	28±10	85±17	503±26	69±16					
1959–60	57	31			0	9±4	26±5	9±4	13±4				
1960–61	282	143				0	2±1	0	4±1	276±3			
1961–62	382	140					27±8	30±9	30±9	292±14	3±3		
1962–63	40	13						0	0	0	0	40	
1963–64	210	45							0	5±2	9±6	0	196±8
Total number trapped by cohort							1328±39	108±19	47±10	573±14			
Minimum population at start of season							1557±55 (1957–58)	840±41 (1958–59)	150±17 (1959–60)	666±21 (1960–61)			

Note: Standard errors of age class sizes are calculated from the formula $\sqrt{\frac{pq}{n}}$ where p = per cent of sample in age class, $q = 100 - p$, n = number of specimens in sample. Standard errors of cohort and population estimates are calculated from the formula $\sqrt{\Sigma x^2}$ where x = number of foxes per standard error in each of the individual age classes summed.

In all, 614* foxes were examined from Resolute Bay. The sex ratio, 290 males to 321 females over-all, did not differ significantly from 100:100 (chi-square = 1.57), though the individual sample ratios varied within wide limits. The widest deviation from the expected ratio is found in the late winter sample of 1958–59, in which were 33 males and 61 females (chi-square = 8.34). The missing males were, according to sample information, not caught in later years, and the reason for the preponderance of females remains obscure.

The analysis of age composition is shown in tabular form (Table 10), following the model of Smirnov (1964).

It may be seen that sample age composition changes drastically from one trapping season to the next. The proportion of specimens in the first age class (i.e., young of the year) shows a particularly marked fluctuation, from less than 1 per cent of the total sample to 100 per cent. Generally speaking, a heavy catch of whelps one year is followed the next year by a heavy catch of yearlings, and the large cohorts which these catches represent are also recognizable in later catches.

In the table, sample age composition has been extrapolated to the entire catch of each trapping season, and the total catches from four cohorts have been summed under the years 1957 to 1960 (the last may be slightly underestimated as no sample was available for 1964–65). From the sample data, it seems probable that the 1956 cohort was smaller than that of 1957 but larger than that of 1958, that the 1961 cohort was smaller than that of 1959, and that the 1963 cohort was similar in size to that of 1956. They may thus be ranked as follows: (1) 1957; (2) 1960; (3) 1956, 1963; (4) 1958, 1962; (5) 1959; (6) 1961.

No demonstrable correlation exists between ranked cohort size and harvest size (${}^{r}d = .46$; $P > .1$). This is largely the result of high catches of yearlings and 2-year-olds in years when whelps are scarce.

The data may also be used to calculate the minimum number of arctic foxes at the beginning of each trapping season, that is, the numbers alive each autumn that were caught in the following and in subsequent seasons. The calculation is performed by adding to the catch of the year in question the number of animals in subsequent catches belonging to cohorts born before the trapping season began. To these estimates are affixed standard errors calculated from the sum of the squares of the standard errors for the segments of

*Three of these were withdrawn from the sex ratio samples because of contradictions in the recording of their sex.

Table 11 The number of arctic foxes traded at Baker Lake, 1917–18 to 1964–65

Year	Pelts traded
1917–18	2,653
1918–19	2,386
1919–20	1,910
1920–21	945
1921–22	2,247
1922–23	4,458
1923–24	1,167
1924–25	1,735
1925–26	715
1926–27	1,408
1927–28	495
1928–29	256
1929–30	2,033
1930–31	843
1931–32	1,255
1932–33	538
1933–34	1,320
1934–35	1,512
1935–36	543
1936–37	1,317
1937–38	2,766
1938–39	2,900
1939–40	1,520
1940–41	3,844
1941–42	2,602
1942–43	2,147
1943–44	2,115
1944–45	1,479
1945–46	3,544
1946–47	3,431
1947–48	1,615
1948–49	939
1949–50	2,255
1950–51	2,904
1951–52	2,161
1952–53	973
1953–54	2,055
1954–55	3,022
1955–56	767
1956–57	1,248
1957–58	1,104
1958–59	767
1959–60	377
1960–61	1,855
1961–62	903
1962–63	303
1963–64	1,231
1964–65	724

Note: Trading statistics from Hudson's Bay Company post records, after T. H. Butters (1961), and Northern Administration Branch records (A. M. Millican, *in litt.*)

Table 12 **Arctic fox catches and their composition by age from central District of Keewatin, Northwest Territories, 1958–59 to 1962–63, with estimates of relative cohort size and of the population size at the beginning of each of four trapping seasons. The standard error calculations are explained under Table 10**

Season	Number caught	Size of sample	Year of birth 1954	1955	1956	1957	1958	1959	1960	1961	1962
1958–59	767	32	96±45	24±23	55±33	551±61	55±33				
1959–60	377	21		36±24	36±24	108±37	0	197±41			
1960–61	1,855	163			68±27	45±23	0	80±29	1662±45		
1961–62	903	39				23±23	0	116±47	764±52	0	
1962–63	303	82					11±6	22±9	255±12	11±6	4±4
Total number trapped by cohort							66±37	>415±69	>2681±70		
Minimum population at start of season							1108±113	>742±96	>3046±99		

the catches that were analysed by age groups. These figures constitute our best estimates of the size of the population yielding annual harvests to the trappers of Resolute Bay. It must be repeated, however, that the estimates are based only on the numbers of foxes trapped, and foxes dying of other causes are not taken into account.

The Keewatin population

Samples from local fox catches were not as easily obtained at Keewatin settlements as at Resolute Bay. The people of the area were undergoing a period of social upheaval (Vallee, 1962; Brack and McIntosh, 1963). The local Eskimos depended on barren-ground caribou until the early 1950's, when caribou were becoming much less abundant. They have since been abandoning their scattered camps, and moving to Baker Lake and the settlements of the Hudson Bay coast. Factors in this movement have been the decline in number of the barren-ground caribou and attraction to the amenities of the settlements. Trapping is carried on in an increasingly casual manner. The places from which samples were obtained included Baker Lake and satellite trapping camps at Ferguson Lake and Aberdeen Lake. Samples from the three areas were combined for the following analysis.

Catches in the study period ranged from 303 to 1,855 (Table 11), and samples from 21 to 144. The harvest of 1963–64 was a heavy one and, since no large proportion of it could be ascribed to older cohorts, production was evidently good in the spring of 1963 (see also litter counts, in a later section). Though sample evidence is lacking, the cohort may be ranked in order of size with the others, on the above evidence, as follows: (1) 1960; (2) 1963; (3) 1957; (4) 1958, 1959; (5) 1961, 1962. The correlation between Baker Lake and Resolute Bay cohort sizes as ranked from 1957 to 1963 was not significant (r_d = .786, P > .1), the only major discrepancy being between the 1957 cohorts, which are comparatively poorly known owing to lack of a 1957–58 Baker Lake sample.

The samples obtained included 166 males and 171 females, a ratio not differing significantly from 100:100 (chi-square = .1, P about .75), though greater disproportions exist, on either side, in the 1958–59 and 1962–63 samples. As for the Resolute Bay population, it does not seem possible to explain these changes in sex ratio among harvest samples.

Calculations were made (Table 12) of the minimum population size for the period before each trapping season began, ignoring, as before, the possibility of natural mortality. That for 1958 was based on 5 years' data, and those for later years on shorter series. Thus for the season following 1959 the series lacks the fifth year's catch of the 1959 cohort. Fifth year catches are, however, small in proportion to earlier yields of cohorts. For the season following 1960, the above catch, and the probably much larger fourth year catch of the 1960 cohort, are both missing, and the estimate is indeed minimal. It is evident from the calculations, however, that the population at the beginning of the trapping season varied between four-fold and five-fold between successive years — to about the same degree, in fact, as the catches.

The reproductive success of the arctic fox and its determinants

Introduction

The factors implicated in varying reproductive success required identification and assessment. The size of any cohort obviously depended on several variables, including the abundance of breeding stock, differences in performance between animals of different ages, and the age composition of the population. It was necessary to obtain data on as many of these variables as possible, in order to make comparisons between years and between places.

The size and age composition of breeding populations have already been discussed, from the analysis of harvest samples. The proportion of dens occupied was assessed annually for the Keewatin population. Litter size, and the proportion of vixens of various ages breeding, were obtainable by examining the uteri of vixens from the trapping samples. Finally, litters could be counted directly around the time of weaning, when the whelps would emerge to play at the surface of the dens.

Data from reproductive tracts

Materials and methods

The age of reproductive maturity and the proportion of females of different ages bearing litters could be determined from samples of the trapping harvests. Variation in litter size with age could not be determined directly, for digging out litters from the deep, solidly frozen dens of the region was impossible. Evidence of litter size, however, remains for several months in the uterus of a post-partal vixen, and this information also could be obtained from harvest samples. The pigmented placental scars of arctic foxes are easily visible through the thin-walled resting uterus, particularly when it is stretched between the fingers and held against the light. The main difficulty encountered in the study was to collect adequate data. Large samples of carcasses were never easy to obtain, and usually, as has been shown, some age classes were poorly represented in, or absent from, particular samples. This greatly limited the number of opportunities for testing for differences in placental scar counts between localities, years, and age classes.

A series of vixens of known reproductive history, killed late in 1962, was obtained from the Norwegian Agricultural College, Vollebeck, through the kindness of Curator Edvard K. Barth, University Zoological Museum, Oslo. Their breeding records are shown in Table 13. The data indicate that placental scars do not appear in the uterus before the arctic fox vixen has bred, that breeding may occur at the age of a year, and that, in this particular sample, placental scar counts closely resembled actual litter sizes. Some of the discrepancies shown in the table between litter sizes and scar counts can probably be attributed

Table 13 **Evaluation of placental scars as indicators of number of whelps in last litter**

Number of specimens	Age (yrs.)	Reproductive history	Placental scars	Appearance of uterus
18	½	None	None	Virgin
1	1½	Weak oestrus, no copulation	None	Virgin
1	1½	Bore 13 whelps previous June (1962)	14	Thick
1	1½	Bore 12 whelps previous June (1962)	12	Thick
1	2½	Bore 8 whelps 1961, none 1962	?	Full of pigmented matter
1	2½	Bore 8 whelps 1961, none 1962	?	Some implantation sites could be distinguished but not counted
1	2½	Bore 10 and 14 whelps 1961 and 1962	?	Full of pigmented matter
1	2½	Bore 12 whelps 1961, none 1962	12	Right horn shrivelled; ovary atrophied
1	2½	Bore 13 and 14 whelps 1961 and 1962	12	Right horn damaged by lesion
1	2½	Bore 15 and 10 whelps 1961 and 1962	10	Plus 2 lighter scars in each horn
1	3½	Bore 12, 12 and 15 whelps, 1960–62	15	
1	3½	Bore 14, 14 and 15 whelps, 1960–62	15	Plus 2 lighter scars in each horn
1	3½	Bore 9, 15 and 9 whelps, 1960–62	9	
1	3½	Bore 5, 11 and 10 whelps, 1960–62	11	
1	4½	Bore 10, 8; aborted 12; bore 10, 1959–62	?	Full of pigmented matter
1	4½	Bore 7; aborted no. ?; bore 10 and 5, 1959–62	5	
Average size of last litter 11.5			11.5	Average number of placental scars (n = 10)

Note: Vixens of known reproductive history from Norwegian Agricultural College, Vollebeck, courtesy of Edvard K. Barth.

Table 14 Frequency distribution of placental scar counts from vixens of various ages taken by trappers at Franklin and Keewatin localities, 1957–58 to 1962–63. The ages given are those of the animals at the last breeding season before their deaths

Place	Age	Year	Number of placental scars 2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Resolute Bay	1	1957–58										1										
		1958–59					1	3	2	2	2	2	1									
		1959–60										1										
		1961–62					4		1	4	4	2	2	3	1	1	1	2				
	2	1958–59							2	1			1	1	2	1						
		1959–60	1		1	1		1	1													
		1961–62					1		1			1	1			1						
	3+	1957–58														1						
		1958–59							2	1	4	1	2	1	1			1				
		1959–60							1													
		1961–62										1	3	3	1		1					
Central Keewatin	1	1958–59							1													
		1960–61											1	1								
		1961–62							1	2	2	2	1	1			1					1
	2	1958–59							1													
		1961–62												1			1					
		1962–63					1			1		2	1									
	3+	1958–59								1												
Eskimo Point	1	1961–62								1	1	1	1		1							
		1962–63							1	1				1								
	2	1962–63						1	1	1												
	3+	1962–63							1	1												
Totals			1		1	1	7	5	16	16	13	14	14	12	6	4	4	3				1

to reproductive disorders: poor or irregular reproductive performance had been recorded for the vixens in question, and reproductive difficulties probably led to their selection for killing and pelting. It also should be noted that placental scars seemed generally less distinct and discrete in the ranch vixens than in those from trapping harvests.

Other students of fox biology have found placental scar counts to be reasonably accurate indicators of the number of whelps per litter. Smirnov (1964) relied on arctic fox scar counts for estimating fertility. Wood (1958) and Layne (1958) found no significant differences between mean embryo and scar counts in gray foxes from the southeastern United States and southern Illinois, though in both red and gray foxes from New York State scar counts tended to be somewhat higher than embryo counts from comparable samples (Layne and McKeon, 1956).

Arctic fox placental scars ("pigmented areas") are described and figured by McEwen and Scott (1956).

The proportion of vixens bearing placental scars
The occurrence and number of placental scars in the uteri of vixens from the districts of Franklin and Keewatin are shown as frequency distributions in Table 14 and again summarized in Tables 15 and 16.

The available data are insufficient to test for differences in the proportion of vixens parous between different places, but within the same age classes and in the same years. It will be remembered that a correlation could not be established between the ranked cohort sizes for Resolute Bay and Keewatin populations. It might be that, if all variables were properly quantified (in particular, there are no indices of lemming abundance for Resolute Bay), the comparisons should be made, not for the same years, but for different years in the series for which the populations were investigated. The few comparisons that were possible were made between age groups and between years. The significance of difference* was obtain-

*As before, the 99 per cent level is meant, unless otherwise stated.

Table 15 The occurrence and number of placental scars in the uteri of trapped foxes from District of Franklin, 1958–59 to 1963–64

Place	Year	Age at last breeding season	No.	No. bearing scars: No.	No. bearing scars: Per cent (if N ≧ 5)	Mean no. of scars (ital. if N ≧ 5) ± S.E.$_{\bar{x}}$ (if N ≧ 7)
Resolute Bay	1957–58	1	2	1		11
		2	0			
		3+	1	1		15
	1958–59	1	77	15	19.5	*8.85* ± 0.517
		2	11	9	81.8	*11.63* ± 1.017
		3+	17	17	100.0	*11.08* ± 0.702
	1959–60	1	1	1		11
		2	7	5	71.4	*5.2*
		3+	1	1		8
	1960–61	1	0			
		2	0			
		3+	0			
	1961–62	1	59	25	42.4	*10.88* ± 0.664
		2	7	5	71.4	*10.4*
		3+	10	10	100.0	*12.9* ± 0.485
	1962–63	1	0			
		2	0			
		3+	0			
	1963–64	1	0			
		2	0			
		3+	1	0		

Table 16 The occurrence and number of placental scars in the uteri of trapped foxes from District of Keewatin, 1958–59 to 1962–63

Place	Year	Age at last breeding season	No.	No. bearing scars: No.	No. bearing scars: Per cent (if N ≧ 5)	Mean no. of scars (ital. if N ≧ 5) ± S.E.$_{\bar{x}}$ (if N ≧ 7)
Central Keewatin	1958–59	1	14	1		8
		2	2	1		8
		3+	3	1		9
	1959–60	1	3	3?		
		2	0			
		3+	1	1		
	1960–61	1	5	3		12.5
		2	0			
		3+	2	0		
	1961–62	1	17	12	70.6	*11.82* ± 1.135
		2	2	2		14.5
		3+	0			
	1962–63	1	3	0		
		2	42	5	11.9	*9.8*
		3+	1	0		
Eskimo Point	1961–62	1	9	6	66.7	*11.2*
		2	0			
		3+	0			
	1962–63	1	21	3	14.3	10
		2	13	3		8
		3+	2	2		8.5

ed from chi-square calculations and from four-by-four contingency tables, following the method of Mainland *et al.* (1956).

Using data from all samples (all places, all years), no significant difference was detectable in the proportions of vixens bearing scars dating from the first and second springs after birth. Of these, about one-third (34 per cent) bore scars. Of the vixens that were 3 years old or older at the last breeding season, some 85 per cent had bred, a significantly greater proportion than was found in the more youthful age classes. No differences in reproductive performance between ages within the 3-year and older group could be sought owing to the lack of a method of separating the older age classes.

Testing for differences within age groups and between years, it was found that significantly more Resolute Bay 1-year-olds bore scars in 1961–62 than in 1958–59. The corresponding 2-year-old and older vixens showed no such differences. The paucity of the data prevented more such comparisons being made.

Combining age groups and testing for differences between years, significantly more vixens from central District of Keewatin and Eskimo Point bore placental scars in 1961–62 than in 1958–59 or 1962–63, and the same was true of all vixens combined, though not of the Resolute Bay samples alone. The 1- and 2-year-olds were responsible for most of the differences between years.

The findings may be summarized as follows, for the years, places, and age groups investigated. About a third of the vixens bred in each of their first and second years, and about five-sixths in each of their later years. Such data as are available indicate variations in these proportions between years, particularly in 1- and 2-year-old vixens.

A high proportion of 1-year-old vixens bred in the spring of 1961. These were part of the large cohort of 1960. A lower proportion bred in 1958 (central Keewatin) and 1962 (Eskimo Point): these were from smaller cohorts. The available data thus suggest that 1- and 2-year-old vixens breed only once, in their first year if from a large cohort, and in their second if from a small one.

The production of a particular season does not necessarily follow on the proportion of young vixens breeding, for 1961 was a year of very low production both at Resolute Bay and in central District of Keewatin.

The number of placental scars

Analysis of variance was performed for each series (separated according to year and age of vixen) consisting of eight or more placental scar counts. No significant differences were detected between the means at even the 95 per cent level. Thus, although assumptions regarding the nature of the frequency distribution of the counts are unwarranted, it seems evident that their means vary significantly neither with age nor with year.

The mean of scar counts from the vixens of all samples was 10.576 ± 0.2834 (N = 118; $S.D._{\bar{x}} = 3.0788$).

Clarke (1940) was told at Fort Reliance that the number of embryos in arctic foxes varies from year to year. If so, it is possible that uterine resorbtion may be an important factor in some years. Tchirkova's (1951) observation that litter size varied annually with food supply could also concern only resorbtion. I obtained no evidence for variation in litter size between years, though, as shown below, the mean size of *weaned* litters was found to vary greatly.

Data from observations at dens

In the course of the field studies in central District of Keewatin, many observations were made on the foxes, their dens, and their ecological circumstances. Those concerning the proportion of dens occupied, the proportion subsequently abandoned, and weaned litter size relate directly to production. The available data on these subjects are discussed in the following sections.

Proportions of dens occupied and abandoned

Disregarding the 1959 data, which were obtained from a small and poorly distributed sample, the proportion of dens occupied (including those later abandoned) varied materially (Table 17). In 1961, the proportion occupied was significantly higher than in any other year, and, among the years of lower den occupancy, more dens were occupied in 1960 than in 1962. The proportion occupied in 1963 was intermediate between those of 1960 and 1962, and differed significantly from neither.

The proportion of dens occupied but abandoned before the end of the denning season also varied. Again excluding the 1959 data, significantly more were abandoned in 1962 than in any other year. The years of lowest den abandonment, 1960 and 1963, showed no significant difference. Otherwise, all years showed significant differences

in the proportion abandoned. Most den abandonment occurred in the first weeks of July, though a few dens were abandoned in June, and one in early August (Table 18).

The number of weaned whelps per litter

It was not possible to obtain direct information on litter size at birth (see above), but about mid-July the whelps would emerge, and could be seen on fine days at the surface. At first they confined their excursions to depressions at the burrow entrances, where they sat blinking in the sun. Later they could be seen romping and playing around the whole den site, and it was then, in the latter half of July, that they could best be counted. Whelps of the younger litters were at this time still suckling, but even the smallest voraciously devoured the prey that the dog fox delivered to the den, at intervals throughout the day and night.

In only 3 of the 5 years were fox litters seen, in 1960, 1961, and 1963. In 1959, opportunities for viewing whelps were rare, for few dens were found. In 1962, however, dens were watched successively for many days without a single whelp being observed. The data obtained are given in full in Table 19 and in summary in Table 20. It seems unlikely that anything other than loss of the entire litter could have been responsible for the absence of whelps at dens occupied only by pairs of adults, and for the total abandonment of dens occupied at the beginning of the whelping period. The effect of abandonment has been treated separately. The number of dens at which adults were seen alone was small enough to neglect. "Zero" counts are therefore not included in the litter size statistics.

Weaned litter means varied from 9.7 whelps in 1960 to 4.6 in 1961, with the intermediate figure of 7.2 in 1963. The differences between the 1961 mean and the other two are significant.

Placental scar counts from vixens breeding in the years for which counts of weaned litters are available were discussed above (see Tables 15 and 16). There is no evidence of a relationship between variations in weaned litter counts and

Table 17 **Occupation of dens and abandonment of occupied dens in central District of Keewatin, 1959–63**

Year	No. of dens examined	Occupied through denning season		Occupied but abandoned before end of denning season	
		No.	Per cent	No.	Per cent
1959	19	0	0	19	100
1960	113	45	39.8	0	0
1961	163	81	49.7	21	20.6
1962	169	20	11.8	27	57.4
1963	188	63	33.5	3	4.5

Table 18 **Abandonment of arctic fox dens, by approximate date, in central District of Keewatin, 1960–63**

Year	May	June			July			August
		Early	Mid	Late	Early	Mid	Late	Early
1960	0	0	0	0	0	0	0	0
1961	0	0	0	1	4	1	0	0
1962	0	0	1	1	9	4	3	1
1963	0	2	0	0	1	1	0	0
Total	0	2	1	2	14	6	3	1

Table 19 Counts of weaned arctic fox litters, central District of Keewatin, 1959–63

Den	1959	1960	1961	1962	1963
	Year				
16	0	7	5	0	0?
18	0	0	0	0	10
19	0	14	8	0	11
21	0	4?	2?	0	9
27		10	7	0	6
30		11	?	0	0?
31		0	5	0	0
32		0	3	0	0
47		?	5	0	?
53		4	3	0	4
68		?	?	?	4
102		?	?	0	10
110		?	7	0	?
128		?	1?	0	?
129		?	4	0	5
130		0	0	0	8
131		12	0	0	0
154		?	0	0	5
162		?	2	0	0
164		?	2	0	0

Note: A blank means the den was not seen, and a zero that it was uninhabited by whelps. A question mark shows that the den may have been occupied but the number of whelps in it was not ascertained.

placental scar counts. The former are for the most part considerably smaller than the latter. Scar counts in Keewatin vixens, dating from the 1961 breeding season, when the mean of weaned litter counts was 4.6, averaged about 12. The mean of all placental scar counts was 10.6 per parous vixen (N = 118), and that of all weaned litters was 6.7 (N = 27). It is evident that the average litter suffers a considerable reduction between implantation or birth, and weaning. Since the number of placental scars did not vary significantly from year to year, and weaned litter counts did, the scale of reduction in the litters obviously varied from year to year. This process, and later mortality of whelps occurring before the commencement of the trapping season, together seem to be responsible in themselves for most of the observed variation in arctic fox numbers and the age composition of their populations. It is discussed further in later sections.

Causes of whelp mortality

Little direct evidence was secured on the causes of whelp mortality. Food scarcity seems the most probable factor, particularly in view of the relationship between the scale of mortality and the abundance of lemmings discussed in a later section. Though actual starvation may play a part, the available evidence suggests that food shortage operates in a less direct manner.

Six dead whelps were found at one den, and one at another, during the study. I visited the former den on June 29, 1961, with the intention of digging out and tagging the whelps. Despite the fact that the den was selected for its apparent shallowness and ease of digging, several hours of work with a post-hole auger resulted in unravelling only the central portion. Four of the six dead whelps were found outside the den and two inside. Inspection of the rather emaciated carcasses showed that death was due in all cases to a fracture at the base of the cranium and severe internal hemorrhage. On July 12, the three surviving whelps were seen at the den and counted.

The carcasses of 40 collared lemmings and one brown lemming, all adult or nearly adult, were found in the major galleries, mostly about 2 feet from the entrances. Some were far from fresh.

Two live whelps of about the same size as the survivors of the above litter in mid-July were brought south in early August 1961, and released into an outside pen. A few days later, the larger and more aggressive of the two killed his sibling. Post-mortem examination revealed a broken base of the skull and extensive hemorrhage, both inside and outside the cranium; the whelp's appearance when skinned was identical to that of the whelp shown in Figure 15. The stronger one had caught it by the upper jaw and shaken it to death.

Table 20 Some data on the sizes of weaned arctic fox litters

Year	No.	Range	$\overline{X} \pm$ S.E.	S.D. $\pm$ S.E.	C.V. $\pm$ S.E.
1959	4	0	0		
1960	6	4–14	9.667 ± 1.476	3.615 ± 1.044	37.394 ± 10.795
1961	11	2–8	4.636 ± 0.622	2.063 ± 0.440	44.487 ± 9.485
1962	19	0	0		
1963	10	4–11	7.200 ± 0.854	2.699 ± 0.604	37.499 ± 8.385

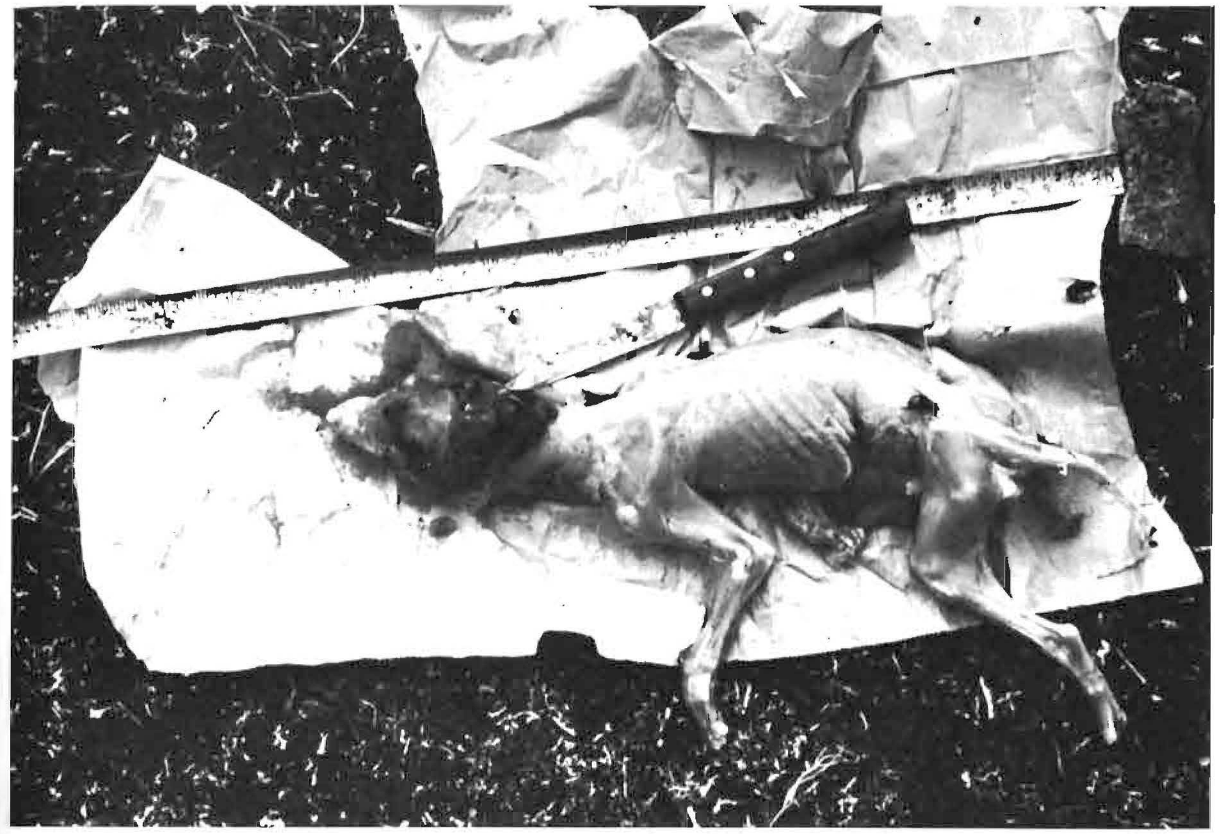


Figure 15 A fox whelp found dead and skinned to show the cause of death: trauma, including fracture, at the base of the cranium. June 30, 1961, Aberdeen Lake.

The captive whelps had quarrelled only once before, when a white rat was introduced into their cage. The larger one immediately seized it and carried it squeaking into the "den" (a cylindrical fibre container about 18 x 36 inches with the top off). From there, while killing and eating the rat, he kept up a continual snarling. When the smaller whelp entered the den, the larger dropped his prey, attacked it furiously, and drove it out. The next morning I found that the smaller one was still not permitted into the den, and therefore had to put a second container into the cage. It thus seems probable that jealousy over prey (or food?) was responsible for the death of the captive. That the deaths of the wild whelps were brought about by similar injuries suggests that they also were killed by siblings.

Injuries to the facial parts of arctic fox skulls, made by the grip that seems to have been fatal in the encounter between the captives, were frequently noted in the specimens from the catches. Sixty-seven, or 20.3 per cent, of 330 Keewatin specimens bore marks of puncture wounds on the face or palate.

Hypotheses

Changes from year to year in reproductive success were evidently responsible for much of the variability in arctic fox numbers. An effort was therefore made to identify and analyse the factors that most affected reproductive success.

Many hypotheses have been elaborated to relate variations in fox populations to one or more environmental variables, including, *i.a.,* sunspots and fertility agents in plants, acting supposedly through their effects on lemming populations, and hypothalamic stimulation caused by cumulative sightings of prey. Only those based on scholarly evaluations of observations, preferably systematic, and on actual ecological investigations will be discussed.

Charles Elton has written voluminously on the 4-year fox cycles in Ungava and elsewhere (Elton, 1942). The data upon which his conclusions are based are traders' records and diary extracts, some more than a century old, and many of questionable accuracy. The feature of rodent cycles of greatest import to foxes and other predators was in his view the decline: the years of bumper fox harvests coincided most often not with the year of peak vole populations, but with the year following the herbivore peak. It is starving foxes then, that fall prey to trappers, and starving snowy owls that emigrate to the Temperate Zone. Elton identifies this "quadrennial driving hunger" as "a master factor influencing the fur returns. . ." (1942; 278, 331). The "Canadian Arctic Wild Life Enquiry", a questionnaire survey undertaken annually between 1935–36 and 1947–48 by interested agencies in Ottawa, and analysed by D. and H. Chitty and their colleagues at the Bureau of Animal Population, Oxford, gave further evidence of a relationship between fox and lemming numbers. The relationship was variable, however, some fox peaks apparently coinciding with lemming peaks, and others lagging by 1 or even 2 years. It was owing to the impossibility of reaching conclusions on the dynamics of the cycle with such data that the enquiry was finally terminated. The arctic fox cycle was, by the end of the enquiry, determined to be a result of the lemming cycle, and the periodic disappearance of lemmings was evidently considered the major factor responsible for high fox yields (Chitty, 1950).

F. W. Braestrup, in his exhaustive compilation of observations on the natural history of the arctic fox, and analysis of Greenland records (1941), demonstrated a cyclic fluctuation in the catch from northeast Greenland, in comparison to west Greenland, where no tendency for a 4-year rhythm was discernible. In northeast Greenland, the arctic fox depends on lemmings: in west Greenland it cannot, for rodents are entirely absent. The cycles in abundance of foxes in northeast Greenland corresponded to those of the lemmings, with maximum fox catches in the winters following lemming maxima. By an impressive accumulation of evidence, Braestrup showed that foxes depending on lemmings raised about twice as many whelps per litter as those which lived on the coast, preying mostly on marine animals and birds. Whether the litters of the latter are actually smaller, or whether they lose more whelps before weaning, has not yet been ascertained.

Attempts to develop methods of forecasting arctic fox harvests were made by A. F. Tchirkova between 1944 and 1949 for the All-Union Scientific Research Institute of the Trapping Industry of the U.S.S.R. Masses of data were accumulated from correspondents. A preliminary report (Tchirkova, 1951) stressed the importance of abundant food to fox production in any given season, particularly of lemming abundance during the preceding autumn. The abundance of lemmings determined the level of nutrition of the foxes, and this in turn governed the proportion breeding and the sizes of their litters. This conclusion might appear to account, at least in part, for the coincidence of peak fox catches with the years following peak lemming abundance (Elton, 1942; Chitty, 1950). However, in the final report of the survey, Tchirkova (1955) did not repeat her earlier conclusion, but proposed more intensive studies.

By discussing the above conclusions and hypotheses in context, I do not mean to imply that the material upon which each of the investigations was based, and that of the present study, were all derived from similar populations undergoing similar processes. I intend rather to show what has been done, and what previous ideas might relate to the dynamic process under investigation. In the same vein, an important hypothesis by A. O. Gross (1947) on the reasons for snowy owl (*Nyctea scandiaca*) invasions in New England should be considered.

Gross noted that snowy owls lay large clutches, of from 6 to 8 or even 13 eggs. When lemmings are scarce much starvation occurs among the owlets, with ordinarily only two or three reaching maturity (see also Murie, 1929). When lemmings are abundant, on the other hand, most or all of the young survive. Following such a successful breeding season, when the lemmings decline, the owls invade the Temperate Zone in large numbers. Gross states, then, that there are two main operative factors in the invasion, ". . . first, the great increase of the Snowy Owl population; and, second, the abrupt disappearance of their chief food, the lemmings". For another species, the tawny owl (*Strix aluco*), Southern (1959) has shown that the maximum variation from year to year in the number of young fledged per nest may exceed the variation in clutch size.

The importance to arctic fox population fluctuations of the second factor, abrupt disappearance of lemmings, was not thoroughly evaluated in the present study, the lemming decline, in fact, being not "abrupt" but rather gradual, from a high in 1960 to a low in 1962. It may possibly have been operative, however, in the increased catches of older foxes in the winters following those yielding high proportions of whelps. As is shown below, the importance of the first factor (high reproductive success), which is made possible by an abundance of food during the breeding season, is very great. The point made by Dymond (1947) and Lack (1954; 212), that it is the declines which need explaining and not the increases, is not at issue, though there seems no *a priori* reason for considering the capacity of a population to increase beyond its usual limit more understandable than its corresponding capacity to sink below normal abundance. What matters in the present study, at least, is the identification and assessment of the causative factors.

What causes cyclic fluctuations in the abundance of lemmings is another problem. The reader is referred to Marsden (1964) for a discussion of the subject, and to Krebs (1963) for an analysis of population processes in the lemmings of Baker Lake in the years 1959 to 1962.

Factors identified in the present study

In this section, I propose to survey briefly the information secured on factors influencing fox numbers, including the biological limitations of the animal in nature, and the limiting factors of its habitat.

The arctic fox is sexually mature in its first rutting season, at the age of about 9 months. As previously discussed, only about a third of the 1- and 2-year-old vixens breed in a given year, whereas some five-sixths of those 3 years old or older do. The proportion breeding varies between years, but appears unrelated to any other variable examined in the study.

The animals mate and the pairs occupy widely scattered breeding dens in late winter. Each pair raises a single litter, which is born about late May and weaned about the third week in July. The whelps disperse from the den after mid-August. Litter size at birth, estimated from placental scar counts, averages 10.6, and varies consistently neither with year nor with age of vixen.

Other features of breeding biology vary more obviously between years. The major variables identified are summarized in Table 21.

The catch of the preceding winter may be used as an estimate of abundance in early spring, when the arctic fox mates and occupies its breeding den. In the 4 years for which reliable data are available, the catch varied by a factor of six. The proportion of dens occupied, however, varied by a

Table 21 Summary of data on lemming abundance, fox numbers and production, 1960–63, District of Keewatin (see also Table 24)

Factor	1960	1961	1962	1963	Source
Catch preceding winter	377	1855	903	303	Table 11
Dens occupied (per cent)	39.8	62.6	27.8	35.1	Table 17*
Dens abandoned (per cent)	0	20.6	57.4	4.5	Table 17
Weaned litter size	9.7	4.6	0	7.2	Table 20
Whelp production per 100 dens	386	229	0	241	Calculated
Lemming abundance	v. high	high	v. low	low	Table 5

*In Table 17, dens abandoned during the breeding season are not listed in the "occupied" column, as they are here.

factor of little more than two, though it was highest in the year following the highest catch. Between zero and 57 per cent of the occupied dens were abandoned during the summer, during the 4 years. The size of weaned litters appears related to the scale of den abandonment (Figure 16), abandonment evidently occurring when a litter is reduced to zero. This idea is borne out by the result of a rank correlation test (r_d equals 1.0; $P < .05$ for one-tailed test), inverting rank order of den abandonment percentages. It seems evident that den abandonment and litter reduction are in themselves responsible for by far the larger part of the variability in whelp production between years. Indeed, both weaned litter means and den abandonment percentages (inverted) give significant rank correlations (as above) with the extrapolated size of the harvest of whelps in the subsequent trapping season.

What factors are responsible for litter reduction and den abandonment? The obvious possibility is variability in the predator's food supply, of which lemmings provide the mainstay. The year of highest whelp production (highest weaned litter size, lowest scale of den abandonment) was also that of highest lemming abundance, and the year of lowest whelp production was also the year of lowest lemming abundance. Dr. P. R. Grant of McGill University, on reviewing the data, has suggested (pers. communication) that the abundance of potential breeders may also produce some indirect effects. In the breeding seasons following the highest catches (1961 and 1962) den abandonment was heaviest and litter size least, suggesting competitive interaction. This hypothesis is particularly appealing with respect to the 1961 data, a year in which production was poor in spite of an abundance of lemmings. On the other hand, breeding dens are so widely scattered, and breeding foxes so scarce in the study area, that serious interaction and competition for food in the breeding season can hardly be considered a possibility. My own explanation for the conflicting data for 1961 is that lemmings decreased rapidly during the summer, but more slowly near my base camp, where they were sampled, than over most of the study area. It is interesting to note that unusually large numbers of young foxes were attracted to Keewatin settlements in the early autumn of that year, but that few were caught after the trapping season opened in November. A sample I secured of 33 arctic foxes shot as a public health measure

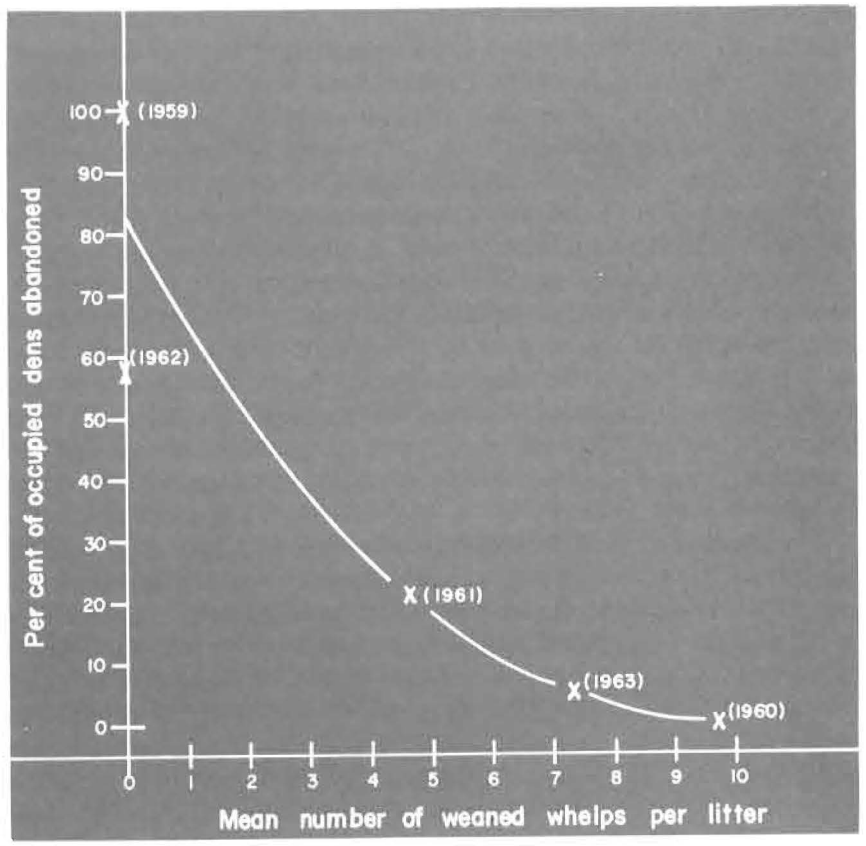


Figure 16 The relationship of mean weaned litter size and the proportion of dens abandoned for the years 1960–63, central District of Keewatin.

in October 1961, at Baker Lake, were all young of the year.

Litter reduction and den abandonment are no doubt causally related (directly through starvation or indirectly through aggression) to food scarcity, and in particular to a scarcity of lemmings. No statistical correlation can be established, however, the lemming index being unexpectedly low in 1963, or unexpectedly high in 1961, in relation to weaned litter means, den abandonment, and the sizes of the fox cohorts produced. In my opinion, failure to establish a correlation may be attributed to the continuation of the lemming decline of 1961 after the period chosen for estimating lemming abundance, to the short run of data (only 4 years), and to the possible inadequacy of the standard line index as a measure of lemming abundance in the vast area of central District of Keewatin rather than to independent variation in lemming numbers and fox whelp survival.

My tentative conclusions on the problem of population fluctuation in the arctic fox may be summarized as follows. Breeding populations vary

by a factor of less than three. This factor is derived from den occupancy figures, and thus, if it may safely be assumed that all vixens occupying dens are pregnant or parous, the factor covers all variations in reproductive potential inherent in the variations in age structure of the breeding population and of the year-specific fecundity of the 1- and 2-year-olds. These variations, then, fail to account for changes in production or cohort size, which in central Keewatin between 1958 and 1960 varied by a factor of about 40, summing cohorts, or from zero to over 1,600, if the number of whelps in the catch is taken alone (Table 12). It is evident that litter reduction and den abandonment are the overriding determinants of cohort size, and it is believed that the scale of these is determined by the relative scarcity of lemmings, with sibling aggression the proximate cause of some, at least, of the reduction.

Estimates of population and production

Age structure and numbers

Estimates of population size, and of the forces of production and repression to which the population is subject, may be based on the age structure of the catches, den occupancy, proportion of vixens parous, and weaned litter sizes, though it is necessary, as stated before, to assume either that natural mortality (other than inferred whelp mortality) is insignificant, or that trapping mortality is representative of total mortality (with the same reservation). The second of these assumptions is in my opinion reasonable. As a first step, it is necessary to examine the differences between whelps and older animals in their vulnerability to trapping.

In the seven catches from Resolute Bay, taken between 1957–58 and 1963–64, extrapolations from sample data (Table 10) give whelp to adult ratios varying from 100:0 and 100:2 to 1:100. It is evident that there are years (1957–58, 1960–61, 1962–63, 1963–64) in which whelps are caught far in excess of the number that could have been raised by the animals of older generations in the same catches. In other years 1958–59, 1959–60, 1961–62), the number of whelps caught could reasonably have been produced by the adults in the catches. It is self-evident that although the age compositions of the latter years could be representative of the age compositions of the populations at the time, those of the former years cannot be so considered. In only one year (1960–61) of the five (1958–59 to 1962–63) for which samples were available from central District of Keewatin (Table 12) were whelps found in excess of the number that could have been produced by adults in the sample extrapolation.

At least two hypotheses could be made to explain the overabundance of whelps in the catches of certain years. One is that many were born elsewhere, and another is that whelps are far more prone to capture than adults. Neither accounts, however, for another feature of the age compositions, namely that more animals of the older age classes tend to be found in the catches following a year of high whelp abundance.

A somewhat more elaborate hypothesis is needed to account for both these striking features of catch age composition. Certain assumptions must be made concerning winter food abundance and territoriality, subjects upon which satisfactory data are lacking. The hypothesis is as follows. In a year of high whelp abundance, the adults are relatively scarce, and remain in occupation of their breeding territories. The whelps, on the other hand, are numerous, and few of them enjoy the possession of settled territories. They may also be harried out of the territories of the adults, and thereby kept on the move. The traps take the settled adults in whose territories they happen to have been set, but for the most part they catch the wandering, harried whelps. Consequently whelps are vastly over-represented in the catches of such years.

At the beginning of the next year's trapping season, if few young survive, the most numerous fox cohort is between 1 and 2 years old. Its members are presumably competitive with older foxes; hence competition for territories and food is at its peak. At the same time, the abundance of lemmings, which favoured whelp survival the previous year, is likely to have declined. With food scarcity, adult foxes wander more widely than they did the year before. All age classes are mobile, none having the survival advantage of a sedentary life.

The above explanation is frankly hypothetical. The differences in sample age compositions, however, are such that some process of the kind described is obviously affecting trap-proneness differentially in relation to the size of the whelp cohort. The hypothesis is supported by a comparison of the Resolute Bay and central Keewatin age composition extrapolations, which shows that adult foxes are proportionally more numerous in the catches of the mainland study area, where dens are far more abundant than on the high arctic islands.

There is no reason to believe that arctic foxes between the ages of 1 and 2 years are more trap-prone than older foxes. Indeed, on general considerations of the relationship between age-specific reproductive potentials and survival rates (Figure 17), it would seem unlikely that such a disadvantage could be perpetuated. If this assumption is correct, mean age composition and survival calculations may be based on the proportions of all foxes other than whelps (i.e., all older than 1.0 year) in the trapping catches (Tables 22 and 23).

Production

Estimates of total weaned whelp production per 100 dens may be calculated from den occupancy, den abandonment, and mean weaned litter size as shown in Table 24.

These estimates agree with estimates of the number of whelps in subsequent catches (Table 12) only in that both show 1960 as the year of

Table 22 Arctic foxes over a year old alive in the central District of Keewatin population in October 1958, 1959, and 1960 (data from Table 12)

	Individuals alive				
Year (October)	1 to 2 years	2 to 3 years	3 to 4 years	Over 4 years	Total
1958	727	159	60	96	1,042
1959	11	176	104	36	327
1960	218	11	68	68	365
Totals	956	346	232	200	1,734

Table 23 Arctic foxes over a year old alive in the Resolute Bay population in October 1957 to 1960 (data from Table 10)

	Individuals alive				
Year (October)	1–2 years	2–3 years	3–4 years	Over 4 years	Total
1957	121	28	66	14	229
1958	558	94	28	52	732
1959	39	55	9	0	103
1960	34	30	29	0	93
Totals	752	207	132	66	1,157

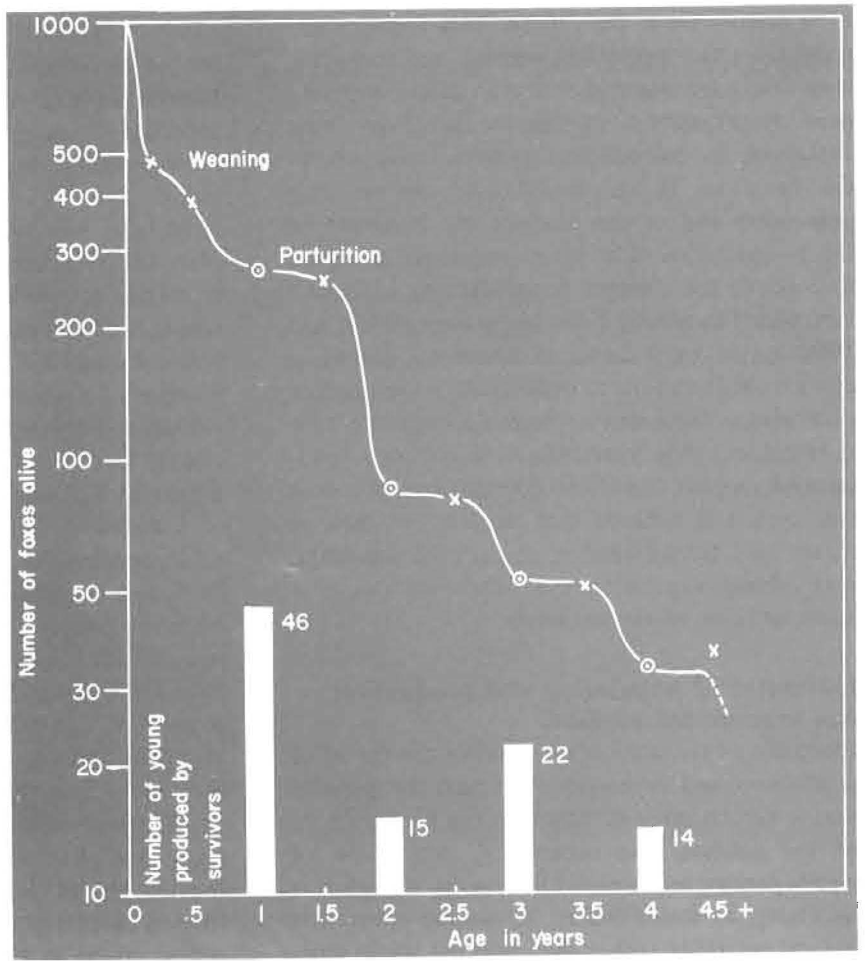


Figure 17 A curve of survivorship for arctic foxes in the Northwest Territories, from the l_x means of Table 25. The histograms below the curve show the number of litters in the expected reproductive contribution of the cohort at each age.

Table 24 Estimated whelp production per 100 dens, computed for 1959–63 inclusive, in central District of Keewatin. Data from Tables 17 and 21

Year	Per cent of dens occupied	Per cent of these abandoned	Average weaned litter number	Per cent of dens producing litters	Total production per 100 dens
1959	100	100	0	0	0
1960	39.8	0	9.7	39.8	386
1961	62.6	20.6	4.6	49.7	229
1962	27.8	57.4	0	11.8	0
1963	35.1	4.5	7.2	33.5	241

Table 25 Life table for the arctic fox in the Northwest Territories, based on data from reproductive tracts, den surveys, weaned litter counts, and harvest samples, detailed elsewhere in this report

x	d_x	l_x	$1,000q_x$	L_x	e_x
Age (yrs.)	Number dying in age interval out of 1,000 born	Number surviving at beginning of age interval out of 1,000 born	Mortality rate per 1,000 alive at beginning of age interval	Number alive between ages x and x + 1	Expectation of life, or mean life remaining to those attaining age interval (yrs.)
0 –0.5	609	1,000	609.0	695.5	1.30
0.5–1.5	135	391	345.3	323.5	1.54
1.5–2.5	176	256	687.5	168.0	1.09
2.5–3.5	27	80	337.5	66.5	1.39
3.5–4.5	17	53	320.8	44.5	0.50
4.5+	36	36	1,000.0	18.0	unknown

highest production and 1962 as a year of very low production. In 1961, despite fair production, and a heavy influx of young foxes into the settlements in September, no whelps were identified in the (admittedly small) sample from central Keewatin. However, young foxes were being shot at Baker Lake before the trapping season began (I examined 33 frozen carcasses the following spring), in the belief that they were starving and diseased, and hence a menace to public health. At Eskimo Point, Cpl. Bob Ward, R.C.M. Police, took moving pictures of foxes scavenging at the settlement in groups of a dozen or so. Most disappeared before their coats were prime and the Eskimos had set their traps. During the summer of 1961, an abrupt decline in lemming abundance was recorded at Aberdeen Lake. This decline evidently caused continued whelp mortality past the time of weaning, and up to the beginning of winter.

Life table

The figures obtained seem suitable for tentative life table analysis, although the samples are smaller than desirable and there are many possibilities of error. Of these, one is occasioned by our inability to estimate natural mortality after the age of one-half year. Even a preliminary life table is useful, however, in that it brings together in one format all the data gathered in various ways on age composition and mortality (Table 25). The derivation of the figures is outlined in Table 26.

The upper part of the table is based, necessarily, on the central Keewatin breeding studies. The age composition of the adult part of the population (a year or more old) had been estimated from both Keewatin and Resolute Bay samples. The adult age structures estimated for the two areas differed very little, and the means of the two were used as a basis for the life table calculations.

Table 26 Calculations of life table data (see text)

Age	Year	Mean litter count	Dens abandoned (per cent)	No. of litters	No. of weaned whelps
Birth (ca. May 25)	1,000 whelps or $\frac{\text{no. of whelps}}{\text{mean placental scar counts}}$ = 94.55 litters				
Weaning (2.5 mo.)	1	9.7	0.0	94.6	914
	2	4.6	20.7	94.6–20.7%	346
	3	0.0	57.4	–	0
	4	7.2	4.5	94.6–4.5%	650
	Total				1,910
	Mean				478
October 31 (5 mo.)	Total weaned whelps less year 2, divided by total years = 391				

October 31 (Older age classes)	Keewatin: From Table 22	Keewatin: Reduced to	Resolute Bay: From Table 23	Resolute Bay: Reduced to	Mean
1.5 yrs.	956	223	752	288	256
2.5 yrs.	346	81	207	79	80
3.5 yrs.	232	54	132	51	53
4.5 yrs.	200	47	66	25	36

Placental scar counts are used for estimating mean number of whelps born per litter, and the average of all annual means, each previously corrected for den abandonment, for estimating mid-summer whelp numbers. Little information is available on mortality among cubs after weaning and before the trapping season. Only in 1961, or in 1 year out of 4, did autumn mortality appear important; in that year the number of whelps per breeding pair dropped from 4.6 to zero (see above). There seems little chance of such an event unless preceded by heavy litter reduction, as in 1961, when the weaned litters averaged only half the mean placental scar count. An estimate of mortality at this stage can thus best be made by recalculating the mean cohort size from den occupancy and abandonment and mean weaned litter counts, giving that of 1961 a value of zero.

It was next necessary to fit together the two segments of the life table, separately calculated from field production data and sample age composition estimates. Assuming negligible adult mortality between whelping and the beginning of the trapping season, the problem is reduced to finding the number of foxes, of the age composition and age-specific reproductive performance determined from catch samples, required to produce 1,000 whelps, or 94.6 litters.

Figure 17 shows survivorship in the theoretical cohort of the life table. The curve is of the "positively skewed rectangular" type, indicating heavy mortality in the first and lighter mortality in the later parts of life. The reproductive contributions of the cohort at successive breeding seasons are indicated below the curve. Most foxes over 6 months old no doubt die in the winter months, when food is difficult to obtain and the trappers are active. Seasonal differences in mortality rates are represented subjectively on the survival curve by changes in the slope of the line connecting the l_x estimates. A vertical line running through the histograms to the circled points on the curve marking parturition dates would represent an estimate of the number of foxes of the cohort available for reproduction at each age. The histograms represent the estimated fraction that are breeding vixens, and therefore the number of litters expected from the cohort at each age. If the estimates were sufficiently accurate, and the intrinsic rate of natural increase in the population equal to unity, the sum of the litters produced by the cohort multiplied by mean litter size would exactly equal the initial size of the cohort, or 1000. In fact, the quotient is 1026, and therefore close to the expected figure.

Adaptive features of the arctic fox breeding cycle

Morphologically, the arctic fox exemplifies arctic adaptation in its reduced limbs, snout, and ears, its dense, warm winter coat, and the whiteness of its winter pelage. It comes as no surprise to learn of its magnificent physiological adaptations to a cold environment (Scholander *et al.*, 1950). One is tempted to seek evidence of adaptation to arctic conditions in its reproductive characteristics as well, in particular, in the comparatively large size of the average arctic fox litter.

A general decrease in the length of the growing season occurs as one moves northward from southern North America, central to the range of the gray fox, through the Temperate Zone occupied by the red fox, to the Arctic-Alpine Zone, where the arctic fox predominates. Other related species (the last two not always accepted by modern taxonomists) are the swift fox (*V. velox*), the Pribilof Islands fox (*A. pribilofensis*), and the Commander Islands fox (*A. beringensis*). Lord (1960) found a positive regression between their median embryo counts and the median latitudes of their ranges, but the correlation coefficient he calculated was not significant.

The island arctic foxes live under unusual circumstances, and direct comparisons between their litter sizes and those of continental populations do not appear justified in this context. The climate of the North Pacific islands is much milder than that at similar latitudes in central North America, and the natural foods of the foxes there are related less to the production of the land than to the bounty of the sea. The observation of Braestrup (1941), that litter size differs between lemming-based and marine-based arctic fox populations, has already been mentioned. The red and gray fox litter sizes in the published reports referred to by Lord (1960) are shown plotted against latitude in Figure 18 (see Table 27 for data and references). Only embryo counts and placental scar counts, alone or in combination, are included, and data on island foxes have been omitted.

As Lord pointed out, the red fox data show a negative slope, and the gray fox data have a similar tendency. Looking only at the means of litter counts and latitudes for each species, however, it is evident that the farther north a species lives the larger is its mean litter size.

Lord (1960) ascribes the tendency for litter size in closely related species to increase with latitude to severe winter mortality and consequent sparsity of breeding populations. I am in substantial agreement with Lord's hypothesis, though preferring to view large litters as a consequence of heightened seasonal contrast in food resources rather than of winter mortality as such.

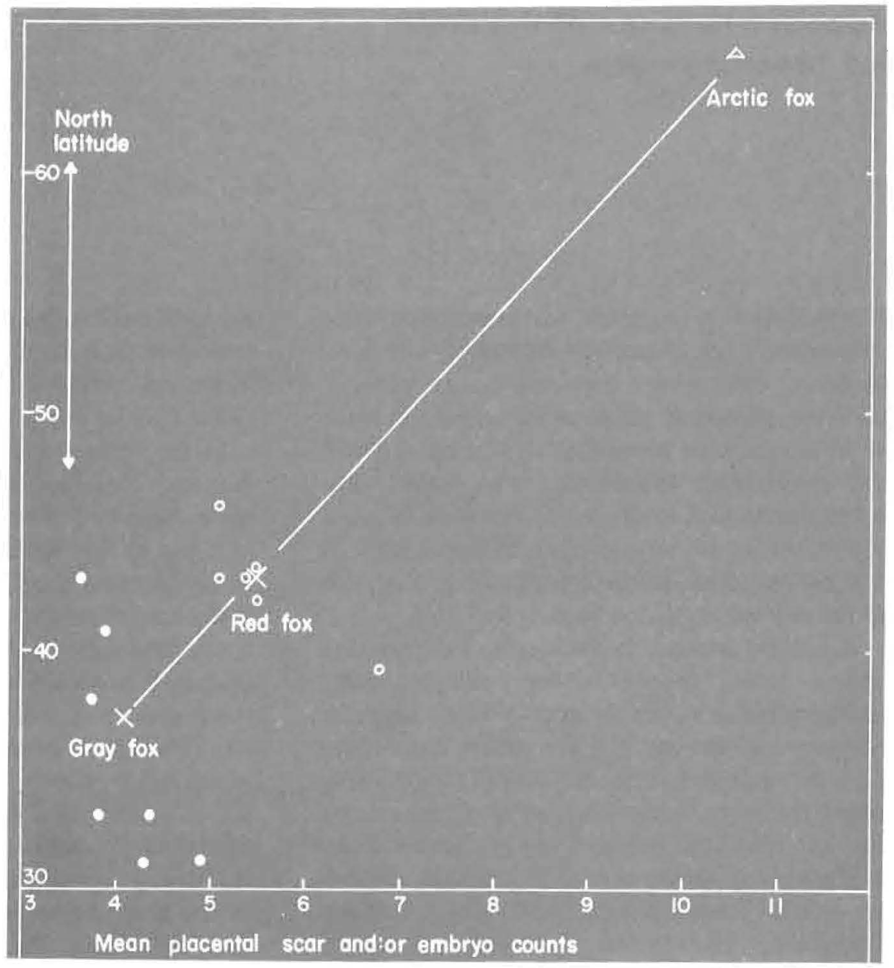
In the winter, life is precarious for the arctic fox, and mortality may be severe. In summer, life is comparatively easy. Lemmings that wintered in dense drifts where they were able to feed securely in tunnels on frozen plants are now more easily caught as they scamper on the surface or cower in shallow crevices. Birds, insects, fish, and even caribou on the mainland, are all available in much greater abundance in summer than in winter. This time of plenty is necessarily also the time of whelping. Lack (1954) postulates that litter size is adaptively adjusted so as to make for the maximum production of viable young per breeding pair. It presumably, then, relates essentially to the breeding season, when food is comparatively abundant. Breeding populations, on the other hand, are composed of the survivors of one or more rigorous winter seasons, and are consequently small. Farther south, with less contrast between summer and winter food resources, there is a smaller food surplus available in summer, over the needs of the breeding population, for the raising of young. The same point, in regard to clutch size in birds, has recently been made by Lack (1965), quoting Ashmole (1961).

While other prey, such as birds and caribou, may be vital to the maintenance of arctic foxes in years of scarcity, lemming abundance appears to be the *sine qua non* of high reproductive success. As noted above, Braestrup (1941) shows that smaller fox litters are the rule where lemmings are absent, and larger where they are present.

The arctic fox displays other reproductive features which may be viewed as adaptations to a cycling microtine prey population. At the same time, although cycling microtines are not confined to the Arctic, complete dependence upon them for production by a predator may be. There are few alternate prey species in terrestrial arctic ecosystems, and none, evidently, that can support a tolerable level of breeding success by arctic foxes.

Arctic fox vixens breed comparatively rarely in their first and second years. This is apparently in marked contrast to Temperate Zone red and gray fox vixens (Layne and McKeon, 1956; Wood, 1958). It is unfortunate that more data could not be obtained on associated factors. The ermine,

Figure 18 Gray fox (*Urocyon*), red fox (*Vulpes*), and arctic fox (*Alopex*) litter sizes in relation to latitude. The "x's" represent the means of all localities.



Mustela erminea, has been shown to exhibit an immature yearling stage in arctic Canada (Macpherson and Manning, 1958), in contrast to Temperate Zone representatives of the same species. Whether delayed maturity is an adaptation to arctic life, or whether it is an adaptation to dependence on a cycling prey species, is open to question. Assuming selection for maximum production of viable young (Lack, 1954; *pace* Wynne-Edwards, 1962), delayed maturity under the conditions reported here might be of selective value. Most arctic foxes destined to survive their first winters are born in years of lemming abundance, and it is unlikely that the following year, or even the year after, will bring another such bumper season. Breeding in the first or second years of life may thus be non-advantageous: it may result only in the production of whelps with very little chance of survival to breeding age. Though non-advantageous or neutral characteristics no doubt may suffer by selection, it is possible that early breeding in the arctic fox is actively selected against by a small margin owing to the risks and energy drain of parenthood being counter-balanced so rarely by the production of descendants.

The efficacy of the arrangements for the reduction of litter size in the species appears remarkable. Gross (1947) calls attention to the enormous size variation between nestlings in the snowy owl, and points out how it may contribute to the rapid decline and death of the smaller nestlings if food is short, with the waste of food to doomed young minimized. No such extreme size variation was noted in sibling arctic foxes. Perhaps part, at least, of the same role is played in the arctic fox by a precocious development of a hierarchy of aggression in the litter.

Table 27 Litter size and latitude in North American foxes (*Urocyon*, *Vulpes*, and *Alopex*)

Species	Place	Approximate latitude	Mean litter size (embryos and/or placental scars)	Authority
Gray fox	Georgia-Florida	31° N.	4.9 (embryos) 4.3 (scars)	Wood (1958)
	Alabama	33	3.8	Sullivan (1956)
	S. Illinois	38	3.8	Layne (1958)
	S.W. Wisconsin	42	3.9	Richards and Hine (1953)
	New York State	43	4.4	Layne and McKeon (1956)
	New York State	43	3.7	Sheldon (1949)
Red fox	S. Michigan	42° N.	5.5	Schofield (1958)
	New York State	43	5.4	Sheldon (1949)
	New York State	43	5.4	Layne and McKeon (1956)
	S.W. Wisconsin	43	5.1	Richards and Hine (1953)
	N. Michigan	46	4.6	Schofield (1958)
	Indiana	40	6.8	Hoffman and Kirkpatrick (1954)
Arctic fox (continental)	Franklin-Keewatin	65° N.	10.6	This study

Suggestions for management of continental arctic fox populations

The habitat of the arctic fox seems unlikely to be affected greatly by exploitive industries and expanding human settlement for the next few decades. It also seems improbable, in view of present trends, that Canadian arctic fox populations will, in the same period, be exposed to heavier trapping pressures than they now withstand. The red fox appears to be widening its range into the arctic zone, both in the U.S.S.R. (Skrobov, 1959) and Canada (Macpherson, 1964), but the effect of its spread on arctic fox populations is questionable, and the possibility of effective measures against it highly problematical.

When arctic fox fur is in fashion, the trapper can obtain $30 or more for a single pelt, but when it is in disrepute he may be lucky to obtain a sixth the price. If and when the value of the fur makes management economic, there are certain measures that could be taken with benefit. These include the protection of breeding adults before whelping, the capture and feeding of whelps before their fur becomes prime, and the replacement of the steel trap by one that kills the fox before it has a chance to escape, or that keeps its pelt safe from predators, or that does both.

Trappers favour fox dens as trap locations. Throughout the District of Keewatin, and in many other parts of the Canadian Arctic, a large proportion of the catch is taken at fox dens in late winter and spring. Fox dens within a few hours' travel of Baker Lake raise few whelps and appear to be falling into disuse, due, I believe, to heavy trapping pressure by hunters from the settlement. Farther afield, den occupancy is greater: there traps are likely to be sprung earlier, so that the people can leave to sell their fur and move to the settlement or to other locations for the summer. Den trapping continued late in the spring preceding a good lemming year may well result in reduced catches for the trappers in the following winter.

The fate of the central Keewatin whelps born in 1961 has been described above. When they over-ran the settlements in early autumn, their pelts were valueless. The same situation is well known in the trapping regions of the U.S.S.R., but there, according to Lavrov (1932), the trappers catch the animals and put them in stout wooden hutches, to which they keep them confined until their pelts are prime. Indeed, when the prices warrant the necessary effort, and where the cost of fox food is not prohibitive, whelps might be caught in summer at the dens, and kept until midwinter, as Lavrov says is done in various parts of the U.S.S.R.* Alternatively, food may be provided at the dens (see Shereshevskiĭ and Petrîaev, 1949).

Trappers always lose a few trapped foxes: some tear their toes or feet away and escape, and the frozen bodies of others are ravaged by predators, including other foxes. In the U.S.S.R., Greenland, and Svalbard, according to Lavrov (1932) and Pedersen (1959), it is customary to catch the arctic fox in box or deadfall traps. The use of such cumbersome structures is unlikely to be revived in the Canadian Arctic, however, unless an increased demand for arctic fox pelts occurs, bringing with it a demand for a registered trapping area, a sense of trap-line ownership, and a wish by the individual trapper to improve his trap-line.

In the meantime, inefficiently exploited as its populations may be, the arctic fox continues to form the basis for one of the most important industries of the Canadian tundra.

*Mr. T. H. Manning has informed me that whelps have been caught and kept until prime, experimentally, at Pangnirtung and on the west coast of Hudson Bay, in the late 1930's. The practice was presumably found to be uneconomic at that time.

Summary

Canadian populations of the panarctic species *Alopex lagopus* (L.) are of considerable economic importance and biological interest. The factors concerned in the wide fluctuations in abundance that they display were studied from 1958 to 1964 in the districts of Keewatin and Franklin, Northwest Territories.

Over 200 arctic fox dens were found, and between 100 and 200 were examined annually, between 1960 and 1963, in central District of Keewatin, a low-arctic area of sandy surface sediments and low relief. Breeding arctic foxes appeared to be territorial in that they never denned less than a mile apart, but other features of den dispersion suggest that they failed to fill their breeding habitat. The dens are often ancient, perhaps lasting for several centuries. Only one-quarter to three-quarters were occupied each year. "Old" (Stage 3) dens were occupied more frequently than "youthful" or "mature" (Stages 1 and 2) and "senile" (Stage 4) dens. Average density of occupied dens on the study area was lower (one per 27 square miles) than reports suggest is the case in important denning regions of the U.S.S.R.

Lemmings formed by far the largest component of the diet of breeding arctic foxes, averaging up to 90 per cent and never below 50 per cent of total food remains in droppings, analysed by semi-monthly periods in the breeding seasons of 1960 to 1963. The frequency of lemming remains in droppings tended to vary with the abundance of lemmings as determined by snap-trapping. Other foods eaten were birds and their eggs, caribou, fish, insects, and berries. Lemmings were also important in winter diets, as shown by analyses of digestive tract contents from trapped animals. The remains identified included those of caribou, seal, and other carrion.

Semi-annual samples of carcasses from the trapping harvests were collected and examined. The age of each carcass was determined, mainly by skull suture closure and canine tooth eruption. The samples were found to vary in age composition, to the extent that inferred variations in breeding success were large enough to account for observed fluctuations in trapping harvests. Extrapolations were made from sample age compositions, and, summing these, estimates were obtained of cohort sizes and of the minimum population before each of several trapping seasons. These estimates failed to take account of natural mortality, on which data are lacking.

Post-mortem examinations of vixens revealed differences in the proportions breeding, related to age and also to year. These differences failed to account for differences in whelp production from year to year. Placental scar counts varied consistently neither with age nor with year, the mean being about 10.6.

The scale of reduction in mean litter size, and associated den abandonment, varied greatly. In one year both were trivial, and in another not a single whelp appeared to have been raised. There was evidence that lemming abundance in the breeding season governed the survival of fox whelps, and thereby the abundance of arctic foxes in each age class in any trapping season. The little evidence obtained suggests that litter reduction is in part the result of sibling strife.

Further examination of sample age composition in the light of the data on production revealed inconsistencies in the ratios of whelps to potential parents in the catches. These are considered indicative of greater trap-proneness in whelps than in adults, at least in the trapping seasons following summers of high whelp production. If natural mortality past the age at which whelps are first trapped may be assumed proportionate to trapping mortality, a life table may be based on the figures calculated for adult age composition, production, and whelp mortality. This gives a survival curve of the "negatively skewed rectangular" type.

Adaptive features of the breeding cycle include, as an adaptation to the arctic environment, the relatively high litter size. They include also, as adaptations to fluctuating prey abundance, but of special importance in view of reduced high-latitude species diversity, relatively infrequent breeding on the part of young vixens, and an efficient mechanism for litter reduction. The latter is perhaps activated through the precocious development of dominance hierarchy among siblings.

Measures that might be introduced, if and when the value of the arctic fox as a fur animal warrants intensive management, include cessation of spring den trapping, and the raising of whelps by hand until their fur is prime. Present trapping practices could be improved by the adoption of a trap that kills the fox immediately and protects its pelt from damage by predators.

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Les populations canadiennes de l'espèce panarctique appelée renard arctique (*Alopex lagopus* L.) sont à la fois d'une importance économique et d'un vif intérêt biologique. Les facteurs dont dépendent les fluctuations de leur nombre ont été étudiés de 1958 à 1964 dans les districts de Franklin et de Keewatin (Territoires du Nord-Ouest).

De 1960 à 1963, on a trouvé plus de 200 tanières de renards arctiques et on en a examiné de 100 à 200, chaque année, dans le district central de Keewatin, région arctique basse, peu accidentée et recouverte de sédiments sableux. Il semble que les renards arctiques reproducteurs se réservent un certain territoire, puisqu'ils construisent toujours leurs tanières à un mille environ de distance les unes des autres; cependant, d'autres aspects de la répartition des tanières laissent croire qu'ils n'occupent pas tout le territoire disponible. Les tanières sont souvent anciennes, ayant même parfois plusieurs siècles d'existence. La proportion des tanières occupées chaque année varie du quart aux trois quarts. Ils occupaient plus fréquemment les tanières très anciennes (stade 3) que les tanières récentes ou anciennes (stades 1 et 2) et les tanières les plus anciennes (stade 4). Le nombre des tanières occupées dans la région étudiée était inférieur (une par 27 milles carrés) à celui que des relevés avaient indiqué à propos de certaines régions de l'URSS.

Les lemmings constituent l'élément le plus important du régime alimentaire des renards arctiques en période de reproduction; ils peuvent représenter jusqu'à 90 p. 100 et jamais moins de 50 p. 100 de l'ensemble global des restes de nourriture dans la fiente qui fut analysée deux fois par mois pendant les saisons de reproduction des années 1960 à 1963. La quantité des restes de lemmings dans les fientes avait tendance à varier avec le nombre des lemmings évalué par piégeage. Les renards se nourrissent aussi d'oiseaux et de leurs œufs, de caribou, de poisson, d'insectes et de baies. De plus, les lemmings constituent un élément important du régime d'hiver des renards, comme l'indique l'analyse des restes trouvés dans le tube digestif des animaux pris au piège. Parmi les restes identifiés, mentionnons ceux du caribou, du phoque et d'autres viandes putréfiées.

On a recueilli et étudié, deux fois par année, des échantillons de carcasses d'animaux pris au piège. L'âge de chacune des carcasses fut déterminé surtout par l'étude de la suture crânienne et l'éruption de la dent canine. On a constaté que

la composition des échantillons par catégorie d'âge variait au point que les fluctuations attribuées, par voie de déduction, au succès de la reproduction étaient assez élevées pour expliquer celles du nombre d'animaux pris au piège. Des extrapolations ont été faites à partir de la composition des échantillons par catégorie d'âge. Celles-ci permettaient, en résumé, d'obtenir une estimation de l'importance des cohortes et de leur population minimum avant chacune des saisons de piégeage. Ces estimations ne tiennent pas compte de la mortalité naturelle sur laquelle les données font défaut.

Les autopsies pratiquées sur des femelles ont révélé l'existence de différences dans le rythme de reproduction, suivant l'âge et l'année. Ces différences n'expliquent pas cependant les fluctuations de la mise bas d'année en année. Le compte des cicatrices placentaires n'a pas révélé de variations constantes selon l'âge ou l'année, la moyenne étant d'environ 10.6.

Le taux de réduction du nombre moyen des petits de chaque portée, ainsi que l'abandon des tanières qui en résulte, accusait d'importantes fluctuations. Au cours d'une année, les deux éléments étaient négligeables, alors que, au cours d'une autre année, il semblait qu'aucun petit n'avait été élevé. Il y a des raisons de croire que l'abondance des lemmings pendant la saison de reproduction détermine le taux de survivance des renardeaux, et partant, l'abondance des renards arctiques dans chaque catégorie d'âge, quelle que soit l'année de piégeage. L'insuffisance des données obtenues porte à croire que la diminution des portées résulte en partie des combats que se livrent les renardeaux.

Un examen plus approfondi de la composition des échantillons par catégorie d'âge, à la lumière des données sur la reproduction, révèle une disproportion entre la quantité de petits et de bêtes capables de reproduction qui sont pris au piège. Il semble en effet, que les renardeaux se laissent plus facilement prendre au piège que les adultes, du moins lorsque l'été qui précède la saison de piégeage à été marqué par une production élevée de petits. En supposant que la mortalité naturelle chez les animaux ayant dépassé l'âge qu'ont les petits qui se font prendre au piège, est proportionnelle à celle des animaux pris au piège, on peut fonder un tableau de longévité sur les chiffres calculés d'après la catégorie d'âge des adultes, la production et le taux de mortalité des petits. L'on obtient ainsi une courbe de survivance de type «négativement asymétrique et rectangulaire».

L'une des conséquences de l'adaptation du cycle de reproduction aux conditions rigoureuses de l'Arctique, c'est que les portées y sont relativement nombreuses. Il faut noter également, pour ce qui est de l'adaptation à l'abondance variable des proies, mais d'une importance particulière en raison de la diversité réduite des espèces dans les latitudes élevées, un ralentissement relatif du rythme de reproduction chez les jeunes renardes et un mécanisme efficace pour la réduction des portées. Ce dernier phénomène est peut-être accentué du fait de l'apparition précoce de tendances dominatrices chez certains petits.

Si jamais la fourrure du renard arctique acquiert une valeur qui justifie l'intensification des mesures de conservation, il faudrait notamment interdire le piégeage tout près des tanières, au printemps, et recourir au biberon pour élever les petits jusqu'à ce que leur fourrure soit à son meilleur. On pourrait aussi améliorer les méthodes actuelles de piégeage en adoptant un piège qui tue le renard immédiatement et protège la fourrure contre les dommages effectués par les prédateurs.

РЕЗЮМЕ

Популяции канадских панарктических видов Alopex lagopus (L.) представляет значительную хозяйственную ценность и биологический интерес. Причины широких колебаний численности песца в районах Киуатин и Франклин в Северо-Западных территориях изучались с 1958 по 1964 год.

Было установлено свыше 200 логовищ песца. В центральном районе Киуатин ежегодно изучалось от 100 до 200 логовищ в период между 1960 и 1963 гг. Район этот низко-арктический, представляет собой отложения с песчаной поверхностью и низким рельефом. Размножающийся песец придерживается определенной территории, и логовища его никогда не находятся на расстоянии меньше мили одно от другого. Однако, иные характерные черты распространения логовищ наводят нас на мысль о том, что песец не использует полностью свою территорию расплода: логовища в большинстве случаев старые, просуществовали, должно быть, несколько столетий. Во время наших исследований только от одной четвертой до трех четвертых их занимались песцом каждый год. "Старые" логовища (третий период) занимались более часто, чем "недавние", или "выдержанные" (первый и второй периоды), и "дряхлые" (четвертый период). Средняя плотность занятых логовищ на изученной территории была один песец на 27 кв. миль. Доклады указывают на то, что эта плотность меньше плотности важных логовищ песца в СССР.

Наиболее многочисленными животными, которыми питается песец (в среднем до 90%, и ни в коем случае не меньше 50% от всех отходов, найденных в помете, который изучался два раза в месяц в период расплода от 1960 до 1963 г.), были лемминги. Частота остатков в помете имела тенденцию изменяться в зависимости от изобилия леммингов, подсчет которых производился путем их ловли капканами. Песец питался еще птицами и их яйцами, карибу, рыбой, насекомыми и ягодами. Лемминги были также важной пищей зимой, о чем можно судить по анализу содержимого в пищеварительном канале, содержащем животных, пойманных капканами. Обнаруженные остатки включали погибших карибу, котиков и других животных, мясо которых разложилось.

Собирались и изучались образцы каркасов животных, пойманных во время заготовки пушнины. Возраст каждого каркаса определялся главным образом по зарастанию швов черепа и прорезыванию клыков. Было установлено, что образцы отличались в возрастном отношении в такой степени, что вариации успешного расплода, к чему мы пришли после изучения, были довольно значительными, чтобы объяснить замеченные изменения в заготовках пушнины. Экстраполяции приготовлялись из образцов возрастного состава; суммируя этот состав, устанавливались размеры когорт и минимальной популяции наперед, до каждого из нескольких сезонов заготовки песца. Однако, при такого рода определениях не учитывалось естественную смертность, о которой нет никаких данных.

Исследования после смерти лисиц указывают на разницу в пропорциях размножения, которая зависит и от возраста и от года. Из этой разницы невозможно было учесть разницу расплода щенков из года в год. Подсчеты послеродовых шрамов последовательно не изменялись, будь-ли в отношении возраста, или года, и среднее число было приблизительно 10,6.

Шкала уменьшения среднего размера помета и сопровождаемый уход песца из логовищ довольно непостоянная. В одном году эта шкала уменьшения и уход песца из логовищ были незначительны, а в другом казалось, что ни одного щенка не было выращено. Было ясно, что изобилие леммингов во время сезона расплода являлось главным фактором, влияющим на выживание щенков (и таким образом на изобилие песца в каждой возрастной группе любого периода заготовки этого животного). Незначительное доказательство в нашем распоряжении наводит нас на мысль о том, что уменьшение числа пометов является частично результатом борьбы за существование щенков одного и того же вывода.

Дальнейшее исследование образцов возрастного состава в свете данных о размножении песца выявило непостоянность про-

порций щенков к возможным родителям, пойманным во время заготовки. Непостоянства эти считаются показательными для щенков, которые гораздо чаще попадаются в капканы, чем взрослые песцы (в крайнем случае во время периода заготовки песца после значительного вывода щенков летом). Если принять естественную смертность песца (после возраста, когда он становится взрослым и впервые попадает в ловушки) как пропорциональную смертности от попадания в ловушки, тогда можно составить таблицу его жизни на основании чисел, подсчитанных для взрослых песцов, его численность и смертность щенков. Это дает кривую выживаемости типа "отрицательный скошенный прямоугольник".

Как приспособление к арктическим условиям, черты приспособления цикла размножения включают сравнительно значительный размер помета. Они также включают относительно редкий расплод, наблюдаемый у молодых лисиц, и успешное средство для уменьшения помета. Эти черты — это приспособление к изменчивому изобилию объектов питания, которое играет очень важную роль в жизни песца ввиду уменьшенного разнообразия видов, встречаемых в высоких широтах. Уменьшение это, должно быть, активируется посредством предосторожного развития иерархии доминирования среди щенков одних и тех же родителей.

Мероприятия, которые можно бы ввести (только в том случае, если значение песца как пушного зверя будет гарантировать его усиленную эксплуатацию), включают прекращение весенней заготовки песца в его логовищах, а также выращивание молодняка человеком, пока его мех не станет превосходным. Настоящую заготовку можно улучшить путем переключения на использование капканов, которые убивали бы песца немедленно и в то же самое время сохраняли его мех от повреждений другими хищными животными.

Canadian Wildlife Service
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