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Observations on the ecology of arctic foxes *Alopex lagopus* in Eqalummiut Nunaat, West Greenland

J. D. S. Birks and N. Penford

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Birks. J. D. S. and Penford, N. 1990. Observations on the ecology of arctic foxes *Alopex lagopus* in Eqalummiut Nunaat, West Greenland. – Meddr Grønland, Bioscience 32, 28 pp. Copenhagen 1990–3–27.

Information on diet, home range and activity of arctic foxes *Alopex lagopus* was collected by radio-tracking and faecal analysis in Eqalummiut Nunaat, West Greenland during spring and summer 1984. The study aimed to investigate the feeding ecology of foxes in an area where »traditional« prey such as lemmings *Dicrostonyx groenlandicus* and coastal food sources are absent.

Foxes were found to be heavily dependent on abundant caribou *Rangifer tarandus* carrion, and invertebrates found in the layer of soil above the the permafrost. Scat analysis and behavioural observations showed that foxes were quick to modify their foraging to exploit seasonal changes in food availability, and preyed heavily on nesting birds, mainly passerines, when these became available. Mean home range size of two radio-tagged female foxes was 11.7 km^2. It was thought that fox density was unusually high due to the abundance of caribou carrion as a result of the exceptionally long preceding winter.

The incidence of food caches was investigated and it was found that most were unearthed in June, after the thaw and just before passerine prey became abundant. White-fronted goose eggs and caribou carrion were the items most frequently found at unearthed caches.

Observations and radio-tracking revealed that foxes predominated in lowland areas, generally avoiding plateau areas above 500 m, where passerines and caribou carrion were scarce. Foxes were found to be 50% more numerous on the study area in 1984 than in 1979, and this was felt to be related to differences in the availability of caribou carrion. Foxes were found to be major predators of the eggs of Greenland White-fronted geese.

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Key words: Arctic fox, West Greenland, diet, behaviour, radio-tracking, caribou carrion, range size, colour morphs.

Introduction

The arctic fox *Alopex lagopus* is a circumpolar predator, occurring in tundra latitudes. It is common in central West Greenland, but very little is known about its ecology in this area, except for the work of Braestrup (1941). This area is of particular interest due to the absence of lemmings *Dicrostonyx groenlandicus* and other forms of prey which form a major resource to arctic foxes throughout most of the rest of their range. The aims of this study were to collect information on diet, home range and activity patterns of arctic foxes, using scat analysis and radio-tracking as an autecological study and also to investigate the influence of arctic foxes on other species, particularly Greenland white-fronted geese *Anser albifrons flavirostris*.

The study took place between 5th May and 11th August 1984 and was part of an expedition to investigate aspects of the ecology of the Greenland white-fronted goose.

Study area

The study was carried out in Eqalummiut Nunaat, central West Greenland (67°30'N, 50°30' W), which lies some 120 km north of the Arctic Circle (Figure 1). Eqalummiut Nunaat comprises 750 km^2 of predominantly upland tundra at the western edge of the Greenland ice sheet. It is bounded to the north and south by two large meltwater valleys which join to form the southern branch of Nassuttooq (Nordre Strømfjord) which continues westwards for 120 km to the Davis Strait.

Our observations on arctic foxes were concentrated in

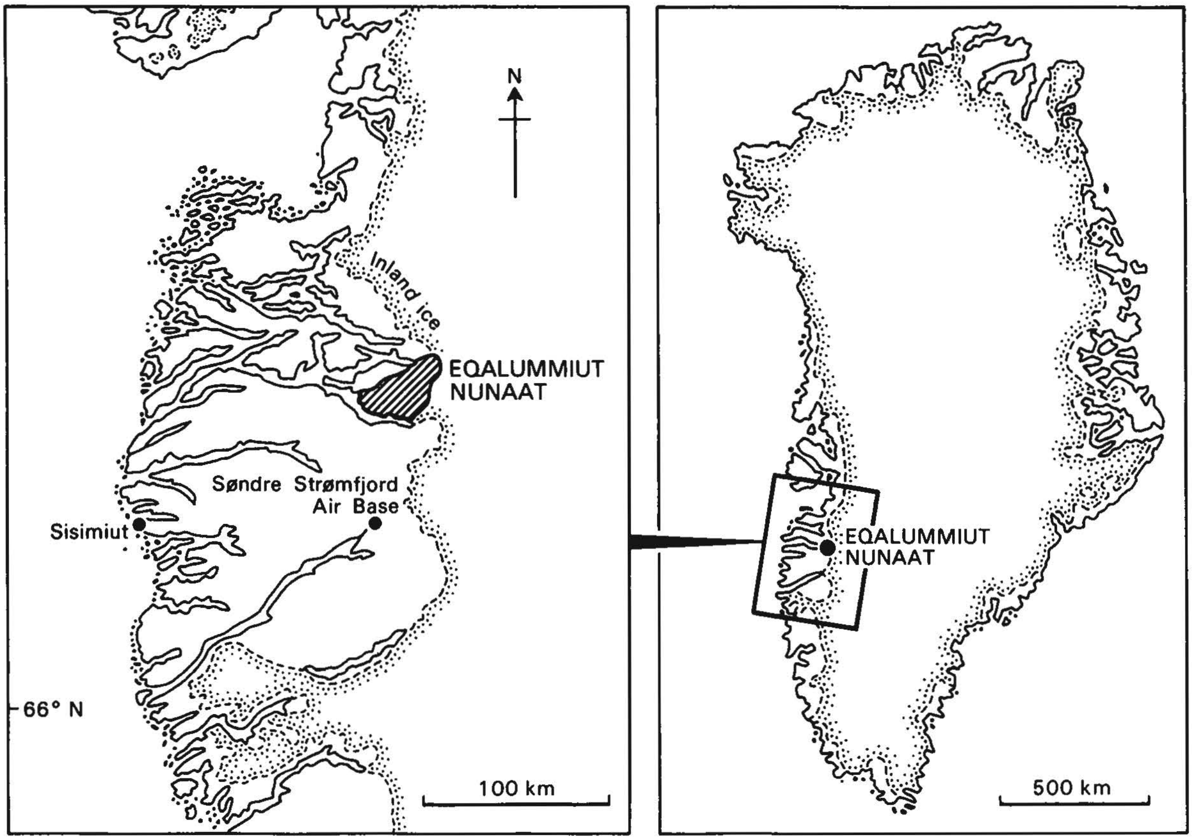


Figure 1. The location of the Greenland white-fronted goose study area, Eqalummiut Nunaat, West Greenland.

an area of approximately 44 km^2 in the southern, lower-lying half of Eqalummiut Nunaat (Figures 2 and 3). The altitude of this area ranges from 0–627 m above sea level, although most of the work was undertaken below 200 m.

Vegetation and climate.

Lowland plant communities are dominated by *Calamagrostis lapponica* grassland with a variety of herbs such as *Stellaria longipes* and *Cerastium alpinum*. Variations in aspect and drainage result in the replacement of this community by shrub vegetation, with *Salix glauca* flourishing on south-facing slopes and along streamsides, whilst *Betula nana* and *Ledum palustre* dominate slopes with a more northerly aspect.

At higher altitudes, particularly above 400 m, dry plateau vegetation occurs with species characteristic of low arctic heath, such as *Dryas integrifolia* and *Vaccinium uliginosum*. Bare ground is abundant in these areas of thin soil; rock outcrops and boulder fields are also a common feature. Further details of the vegetation communities of the area are presented by Fox (1981).

Lakes and pools are frequent in this landscape of periglacial features and impeded drainage. These wetlands, together with associated marshes and streams, were frozen and easily traversable by arctic foxes at the start of the study in early May. However, after a thaw at the beginning of June, some of the features became significant obstacles.

The proximity of the study area to the Greenland ice cap ensures that it experiences a stable "continental" climate, characterised by high pressure systems which lead to high summer temperatures, low humidity and low precipitation.

Local weather conditions during the study period.

During the 14 week study the weather varied considerably, with 100% snow cover in early May, progressing through thaw to high daytime temperatures in July and ending with the return of new snow in August. Table 1 summarises the main climatic changes divided into four sample periods. The study began on 5th May 1984 when meteorological recordings commenced; hence, there are no meteorological data for period 1 but scats collected at this time can be assigned to conditions of 100% snow cover pre-dating the study, with sub-zero temperatures occurring on all days. The thaw was exceptionally late in 1984, and comparison with data from a previous study (Fox and Stroud 1981; Fox *et al.* 1987)

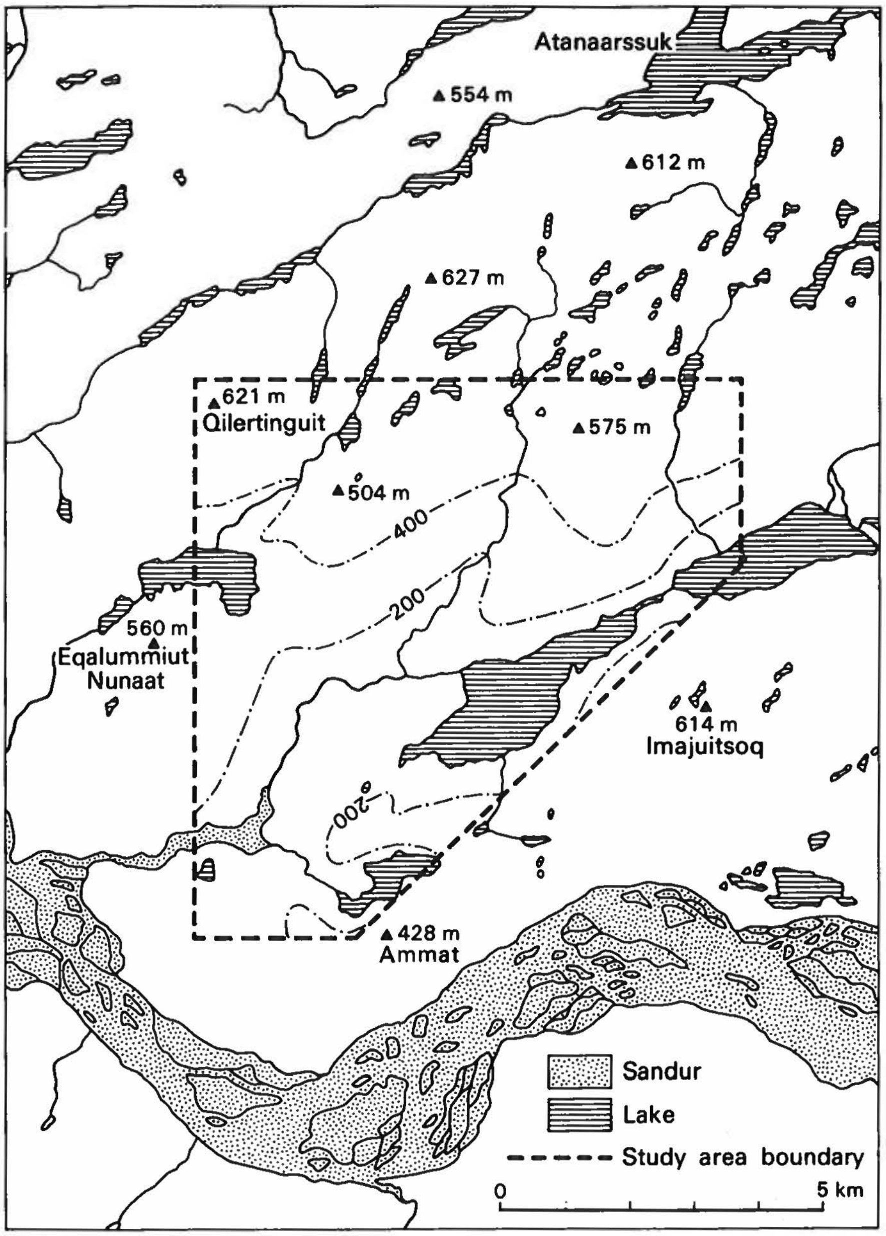


Figure 2. The arctic fox study area, comprising approximately 44 km² in the central southern part of Eqalummiut Nunaat (c.f Figure 1).

suggests that it occurred three weeks later than in most years, with high snow cover persisting through much of period 2. The very gradual thaw during this period increased rapidly between 2nd and 6th June when a strong föhn wind from the ice cap melted the remaining snow, releasing large volumes of meltwater into newly thawed rivers, and resulted in many lowland areas becoming marshy.

Following the thaw a typical stable continental climate ensued through period 3, with little cloud cover and maximum daytime ground temperatures of 25°C. Throughout the study there was little precipitation owing to the prevailing anticyclonic conditions; there was increasingly changeable weather in period 4 with sleet and rain showers turning to snow towards the end of the study in mid-August.

Arctic fox prey availability.

A notable ecological feature of the study area is the absence of prey items that form a major part of arctic fox diet in other areas of the Arctic. For example, lemmings (*Lemmus* and *Dicrostonyx* spp.) are absent from this area and from all of west Greenland (Braestrup 1941); there were seldom any opportunities for regular scavenging of marine foods or human refuse

Figure 3. Part of the study area following the thaw in June 1984.

since the nearest open coastline lies 60 km to the west and the nearest permanent human settlement some 60 km to the south of the study area. Greenlanders visit the area each summer for hunting and fishing and may provide a source of discarded food for a short period (late July-Sept.). The expedition was also the source of a small amount of food that foxes scavenged. No colonies of breeding seabirds lay within the study area, the nearest being on cliffs some 10 km to the west.

Other mammals occurring in the study area were caribou *Rangifer tarandus groenlandicus* and arctic hares *Lepus timidus*. Potential avian prey included ptarmigan *Lagopus mutus*, one of the few resident birds, together with a number of summer visitors. Of these the passerines were most abundant, with high breeding densities of Lapland buntings *Calcarius lapponicus* (Fox *et al.* 1987) and redpolls *Carduelis flammea* in the lowland areas, and numerous pairs of wheatears *Oenanthe oenanthe* and snow buntings *Plectrophenax nivalis* associated with rocky areas. Larger ground-nesting birds included mallard *Anas platyrhynchos*, longtailed duck *Clangula hyemalis*, Greenland white-fronted goose *Anser albifrons flavirostris*, and red-necked phalarope *Phalaropus lobatus* (Fox and Stroud 1981).

Arctic char *Salvelinus alpinus* and three-spined stickleback *Gasterostus aculeatus* were present in the main river and some of the lowland lakes in the study area. A few specimens of the latter species were found dead at the margin of the river during the spring break-up of the ice.

An annotated list of invertebrates collected from Eqalummiut Nunaat has been published previously (Bell 1981).

Arctic fox diet

Methods

Collection and treatment of droppings

Arctic fox droppings or "scats" were collected from the study area between 5th May and 11th August 1984. The collection date, location and site of deposition (e.g."on a prominent rock" or "at caribou carcass") were recorded for each scat. Scats were classified as either "fresh" or "recent" according to the estimated time since deposition. Fresh scats had a strong odour and were often shiny, a feature which was less pronounced in recent scats. Scats which were obviously old (> 1 month), such as those which showed signs of leaching or bleaching of the upper surface, were rejected.

By revisiting productive collecting areas regularly it was possible to maximise the samples of scats of known age. Scats were air-dried and stored individually in paper bags containing naptha crystals to prevent attack by coprophagous insects.

Faecal analysis

The air-dried scats were weighed individually to the nearest 0.01g, and then teased apart beneath a ×40 binocular microscope to reveal the undigested remains of prey. Individual hairs and feathers were examined at high power (×100) to identify mammalian and avian prey using the keys of Day (1966) and Kennedy and Carbyn (1981). In many cases remains of birds and mammals were identified by reference to a collection of fur and feathers from known potential prey species in the study area.

Fragments of eggshell in droppings did not normally allow identification of the bird species from which they originated, due to absence of pigment and loss of substance resulting from the passage through the acid medium of the stomach. However, fragments of eggshell were usually large enough to indicate, from their apparent thickness and degree of curvature, their approximate size when whole. On this basis egg remains found in scats were categorised as either "large" or "small", with the eggs of ptarmigan representing the lower end of the "large" category.

Fish remains were identified by reference to Webb's (undated) key. Insect remains occurred in many scats as chitinous fragments of pupal cases, or the head capsules and "skins" of larvae. These remains were submitted to entomologists for identification (J. Böcher and D. Sheppard pers. comm.).

Remains of scavenged "human" food in scats were identified by the fragments of paper or polythene associated with them.

Additional sources of dietary information

In addition to the collection and analysis of fox faeces, accessory information on the foxes' diet was gathered in the field. Records were made of all predation attempts witnessed while watching foxes; all prey remains found at fox resting places and at unearthed caches were recorded; notes were also made of evidence of fox activity at caribou carcasses.

Presentation of results

The majority of the information on fox diet presented here is derived from the analysis of scats which could be assigned to four samples corresponding to distinct stages within the period of study (Table 1).

Information on the relative contributions of different foods to the overall diet, as indicated by faecal analysis, is presented in three forms in this paper. In order to make these data comparable with other studies, increase accuracy and ease statistical analysis, we have adopted three forms of presentation, as follows:

A) "Percentage occurrence": the relative frequency of occurrence of each food category (species or taxonomic group) expressed as a percentage of all food occurrences in that sample.
B) "Percentage bulk": the relative estimated bulk of the undigested remains of each food category expressed as a percentage of the total bulk of the sample. For each scat the relative volume of each food category was estimated to the nearest 10%, and was subsequently used to calculate the estimated bulk of each food by using the weight of the scat as a guide (bulk = estimated volume × scat weight). Bulk values were summed for each food and for all foods for the derivation of percentage bulk.
C) "Percentage of scats": the proportion of scats in which a particular food category was recorded.

The "percentage bulk" form of presentation is generally regarded as the most accurate indicator of the relative contributions of different foods to the diet, because it addresses the problem of a lack of volumetric weighting inherent in the alternative forms. However, even the "percentage bulk" presentation can benefit from further refinement.

Some analysts of the diet of polyphagous carnivores have attempted to derive conversion factors for different foods, to correct for errors arising from the differential digestibility of foods when quantitative data are

Table 1. Details of the sample periods used in the analysis of temporal changes in the diet of arctic foxes during 1984.

Sample Period	No. of scats	Period covered	Prevailing weather conditions	Comments
1	83	Up to 5th May	100% snow cover recent snowfall	Recent scats from snow surface during first 3 days of study
2	115	6th May- 6th June	Slow thaw; 27 days with min temp <0°C Min temp −18°C Max temp 16°C	Covers main arrival period of migrant birds prior to nesting
3	67	7th June- 8th July	Post thaw; 5% snow cover; 9 days with min temps <0°C Min temp −2°C Max temp +25°C	Nesting period of avian prey
4	64	9th July- 11th August	1 day with min temp <0°C; Min temp −1°C Max temp +24°C	Late nesting, fledging and moulting period of avian prey

derived from the relative amounts of undigested remains in droppings (e.g. Lockie 1959; Wise *et al.* 1981). This technique, involving feeding trials with captive animals, was not applicable to this study. It is accepted, therefore, that the data presented here contain some unavoidable inaccuracies. For example, the dietary importance of items which leave little undigested material relative to their original volume, such as eggs, will be somewhat under-estimated by "percentage bulk" values as used here.

Results

Scat collection sites

A total of 329 fox scats from Eqalummiut Nunaat was collected and analysed. The sites of collection were recorded for 311 of these, and the information is summarized in Figure 4. It should be stressed that the search for scats was not random, but was concentrated upon those features of the terrain which proved productive. Figure 4 should not, therefore, be regarded as a precise frequency distribution of scat deposition sites used by arctic foxes, but it is thought to show some of those sites which were preferred.

The four most productive types of collecting site accounted for 84.9% of all scats collected. Although more scats were found beneath overhanging rocks than at any other site, there was a marked decline in the "productivity" of this category of collecting site as the study progressed (Table 2). This may reflect a reduction in the use by foxes of such sheltered sites as resting places as weather conditions ameliorated. It is interesting to note that foxes developed the habit of depositing scats at the sites of snares set to catch the animals for radio-tracking. Approximately one third of scats, during samples 3 and 4, were collected from such sites.

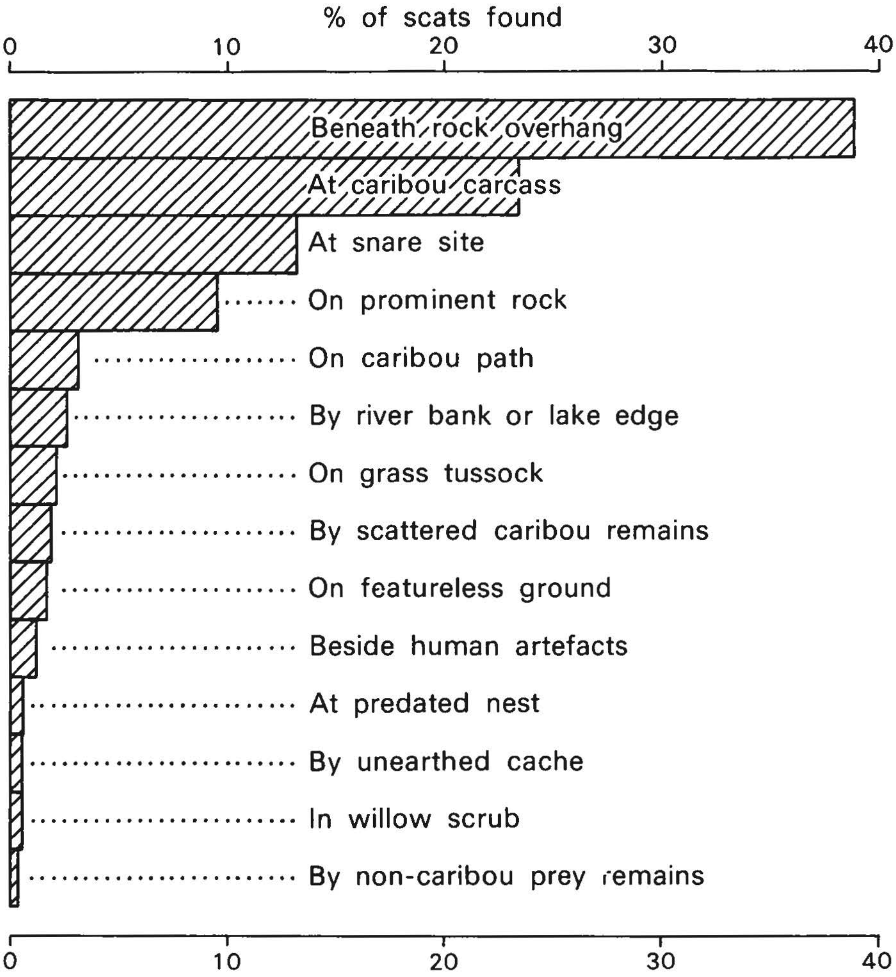


Figure 4. The percentage of arctic fox scats (n = 311) collected from different types of deposition site in Eqalummiut Nunaat during the study period (5th May – 11th August 1984).

Table 2. Temporal changes in the percentage of scats collected from the 4 main sites of deposition (see Figure 4).

Collecting site	Scat sample period 1	2	3	4
Beneath overhanging rocks	80.5	45.2	5.1	0.0
At caribou carcass	6.1	34.8	25.4	21.0
At snare site	0.0	6.1	33.9	32.3
On prominent rock	8.5	4.3	15.2	14.5
Other sites	4.9	9.6	20.4	32.2

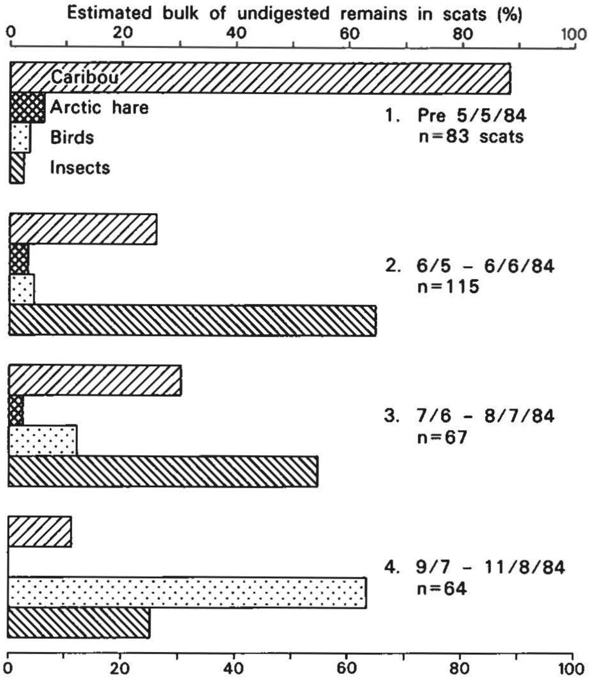


Figure 5. Temporal changes in consumption by foxes of the main prey groups, as indicated by the analysis of scats collected over 4 sample periods (minor prey groups are omitted from this figure).

The food of arctic foxes as indicated by faecal analysis

The results of the faecal analysis are presented in Table 3 and summarized graphically in Figure 5. Each food category is considered separately below.

Caribou

Caribou was the most important item in the overall diet of the foxes during this study. The abundance in the study area of carcasses of caribou which had died during the winter of 1983/84 was remarkable, as was the contribution which this food made to the foxes' diet.

Caribou consumption was greatest in the period covered by scat sample 1 (Figure 5), when snow cover was complete and few migrant birds were present on the study area. During this period caribou comprised more than 90% (bulk) of undigested remains in fox scats, mostly in the form of fur. Small chips of bone, pieces of caribou skin and hoof were present in a minority of droppings, and one scat appeared to contain macerated vegetation from a caribou stomach in association with caribou fur.

The quantity of caribou carrion consumed by foxes was much reduced after the onset of a gradual thaw and a concomitant increase in the extent of exposed ground (Figure 5, samples 2 – 4). Examination of caribou carcasses at this stage suggested that over 95% of the available flesh had already been consumed (Figure 6). Foxes were the main scavengers involved, although there was evidence that a few ravens *Corvus corax* also fed at caribou carcasses.

Foxes continued to feed on caribou throughout the study period. However, this form of foraging clearly

Table 3. The food of arctic foxes during spring and summer 1984, as indicated by the analysis of 329 scats collected over 4 sample periods (defined in Table 1). The data are presented as A. % occurrence: B. % bulk: C. % of scats (see text for details of analysis and presentation).

FOOD TYPE	Sample period 1 A	B	C	Sample period 2 A	B	C	Sample period 3 A	B	C	Sample period 4 A	B	C	Overall diet A	B	C
Caribou *Rangifer tarandus*	80.0	90.8	96.4	42.6	27.3	74.8	33.1	27.4	61.2	17.3	10.8	26.6	42.7	47.2	68.1
Arctic hare *Lepus timidus*	4.0	5.7	4.8	1.0	0.3	1.7	0.6	0.7	1.5				1.3	2.2	2.1
Arctic fox *Alopex lagopus*										1.0	1.2	1.6	0.2	0.1	0.3
Galliforme birds				0.5	0.1	0.9							0.2	0.1	0.3
Passeriforme birds	3.0	2.1	3.6	5.9	3.1	10.4	6.5	5.7	11.9	28.6	42.4	43.7	9.7	7.0	15.5
Unidentified birds				1.5	0.6	2.6	4.8	5.6	9.0	17.3	20.1	26.6	5.0	3.2	7.9
Birds' eggs				2.5	0.8	4.3	8.9	0.4	16.4	1.0	0.1	1.6	3.2	0.2	5.2
Arctic char *Salvelinus alpinus*							3.2	1.3	6.0				0.8	0.2	1.2
Insects	13.0	1.4	15.7	46.0	67.9	80.9	41.9	58.4	77.6	34.7	25.5	53.1	36.6	39.7	58.3
Scavenged "human" food							0.6	0.3	1.5				0.2	0.1	0.3

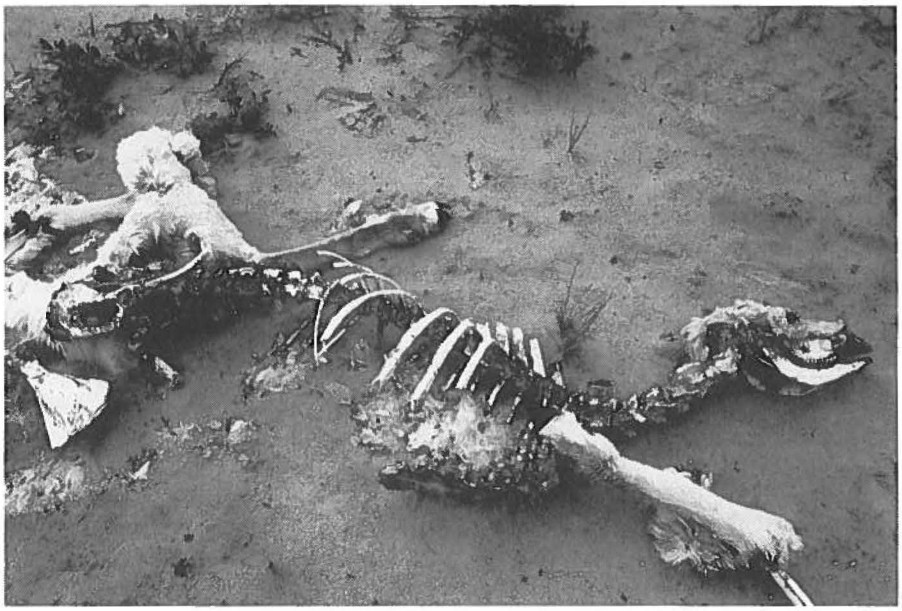


Figure 6. Caribou carcass from the 1983/84 winter preceeding the study. Most of the flesh had been removed by arctic foxes when the photograph was taken in July 1984.

became less important with time because progressively fewer scats contained caribou remains, and of those which did, fewer consisted predominantly of caribou remains (Figure 7). This was confirmed by radio-tracking observations of foraging behaviour, discussed below. This reflected both the decline in availability of caribou carrion, as well as the appearance of alternative food following snow melt and the arrival of migrant birds.

Arctic hare

Athough arctic hares were commonly seen on the study area, they were only of minor importance as prey to the foxes. Hare remains were found in seven of the 329 scats analysed, and these amounted to 2.2% (bulk) of the overall diet. As in the case of caribou, arctic hares contributed more to the foxes' diet in the earlier samples analysed (Figure 5).

Arctic fox

Arctic fox fur was frequently identified in scats, but other fox remains were absent. This was assumed to represent fur ingested during grooming. Figure 8 shows the changing incidence of fox fur present in scats from the four samples. The pattern suggests that moulting, as indicated by the level of fur ingestion, reached a peak towards the end of the study period, when over a quarter of the scats contained fox fur. This was confirmed by observations, which indicated that moulting proceeded slowly initially, then increased rapidly during July.

There was one instance of a scat from sample 4 which was largely composed of fox fur attached to a piece of skin. Further evidence of cannibalism arose from the discovery, on 31st May 1984, of the remains of an adult arctic fox which appeared to have largely been consumed by other foxes.

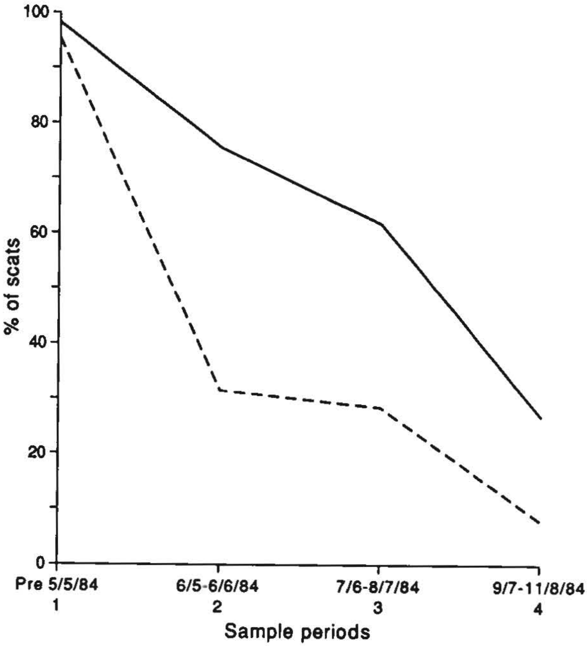


Figure 7. The declining importance of caribou carrion in arctic fox diet during the study. Solid line represents percentage of fox scats containing caribou remains; broken line represents percentage of fox scats in which caribou remains comprised >50% of the scat volume.

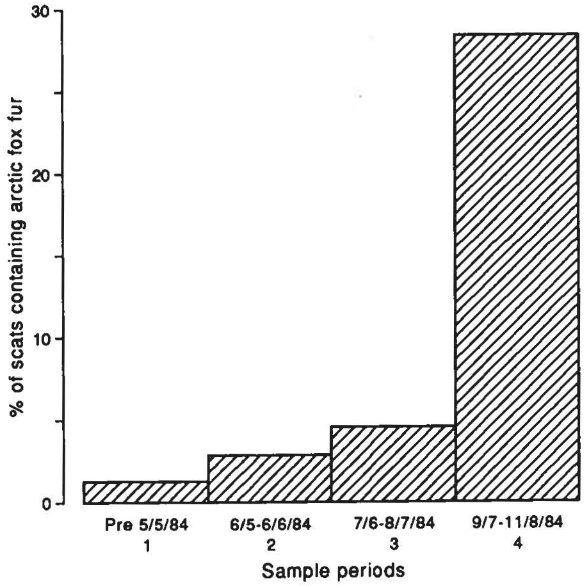


Figure 8. The changing incidence of scats containing fox fur through the 4 sample periods, indicating progress of moult of arctic foxes.

Birds

Birds were the most important prey during the period covered by sample 4 (9th July – 11th August), which corresponded with the fledging of young birds and moult in adults (Figure 5). Passeriformes appeared to experience the highest levels of fox predation in all samples (Table 3). The size and colour of Passeriforme feathers in scats suggested that snow buntings were the predominant identifiable bird species eaten by foxes in the early days of the study, whilst Lapland buntings predominated in the latter two samples. This correlates with the changing relative abundance of these species: snow buntings tended to arrive first in the study area, but were later joined by large numbers of Lapland buntings which nested at high densities in the short tundra vegetation (Fox *et al.* 1987).

The remains of Galliformes, solely represented by the ptarmigan in Greenland, were only recorded once in scats in this study. This is somewhat surprising in view of the ptarmigans' sedentary habits and widespread occurrence in the study area.

Approximately one third of bird remains found in scats could not be identified because of the absence of characteristic "downy" barbules on the feathers. These barbules do not occur on the plumage of juvenile birds, so the peak in the proportion of unidentifiable remains in sample 3 (Figure 9) suggests that much of the bird predation consisted of nestlings at this time.

Despite the presence, and availability to foxes, of members of the Anseriformes on the study area, feath-

Table 4. A summary of observed or suggested interactions between arctic foxes and some other vertebrates encountered in the study area.

Species	Summary of interactions observed
Arctic hare *Lepus timidus*	No predation attempts by foxes observed. Foxes often seen foraging within 100 m of hares (in full view), yet no interest was shown. Hares did not normally display alarm, but often remained alert and occasionally fled a short distance when a fox approached within 50 m.
Greenland white-fronted goose *Anser albifrons flavirostris*	No observations of attempted predation by foxes on adult geese. Foxes often foraged within 100 m of geese feeding on lowland marshes in May and June. Geese tended to remain alert when a fox was within 50 m. Egg predation was apparently common, with one fox seen carrying and then eating a fresh goose egg in early June. A total of 5 goose nests was apparently predated by foxes out of 6 nests known in 1984. A fox was twice observed to pass watchfully within 25 m of a nest on which a female goose was sitting, suggesting that successful egg predation may depend upon the absence of the adult geese (Stroud 1982).
Great northern diver *Gavia immer*	On three occasions foxes were seen to visit the bank of a lake adjacent to the nest of a great northern diver on an island some 15 m from the shore. No visits led to successful predation, and on one occasion, an adult diver successfully drove the fox away.
Long-tailed duck *Clangula hyemalis*	No predation of adults observed, but three predated nests were attributed to foxes. Reynolds (1987) discusses behavioural responses to foxes in the study area.
Mallard Anas *platyrhynchos*	No attempted predation of adults observed, but one predated nest attributed to foxes.
Ptarmigan *Lagopus mutus*	As above.
Red-necked phalarope *Phalaropus lobatus*	Successful predation of chicks observed on one occasion, accompanied by vigorous mobbing by adults.
Redpoll *Carduelis flammea*	Predation of adults not observed, but nest predation commonly attributed to foxes and observed on one occasion.
Snow bunting *Plectrophenax nivalis*	Three predation attempts witnessed prior to nesting season, of which one was successful. Some evidence of attempted nest predation suggested by a pair of adults seen mobbing a fox fiercely.
Lapland bunting *Calcarius lapponicus*	Successful predation observed on several occasions of adults roosting or nesting at ground level; egg and nestling predation also often seen or attributed to foxes.

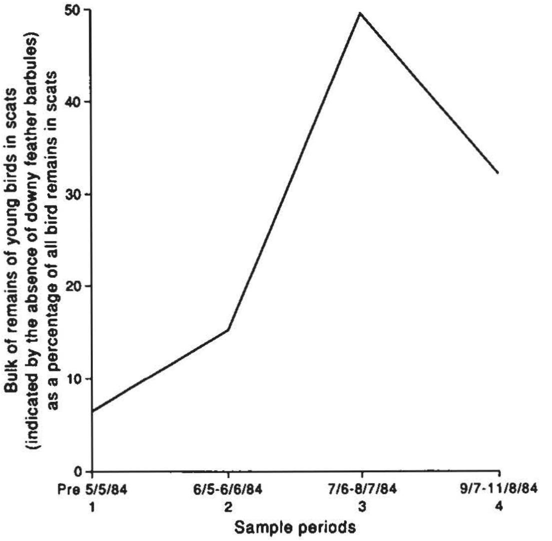


Figure 9. The changing incidence of young birds in arctic fox diet, indicated by the changing incidence in scats of feathers lacking downy barbules, as found on juvenile birds.

ers from ducks and geese were not identified in scats in this study. However, evidence of fox predation upon Anseriformes is presented in Table 4 and Figure 13.

Birds' eggs

The estimated contribution of bird's eggs to the foxes diet (0.2% overall) should be regarded as an underestimate of the importance of this food to the foxes due to the small quantities of undigested remains in scats relative to the original volume.

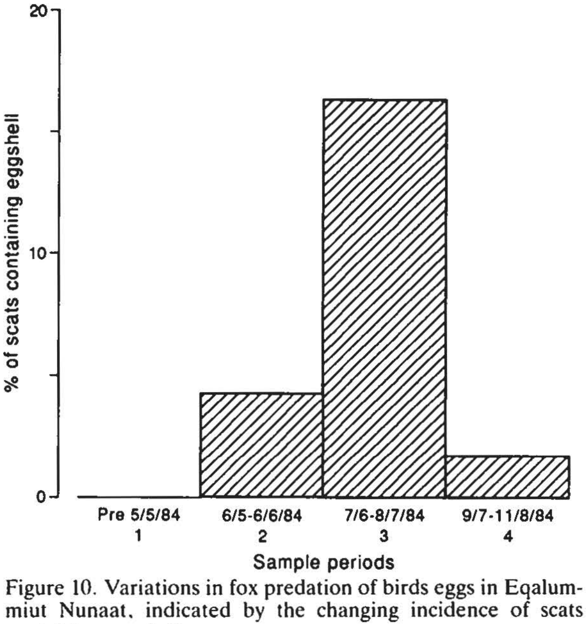


Figure 10. Variations in fox predation of birds eggs in Eqalummiut Nunaat, indicated by the changing incidence of scats containing eggshell.

Eggs were recorded in all except sample period 1 (Figure 10). It is significant that 4.3% of scats in sample 2 contained eggshell, because the period covered by this sample (6th May – 6th June) precedes the discovery of the first clutch of eggs of the bird nesting period. Although it is possible that some earlier clutches were found and predated by foxes, it seems likely that some, if not all, of the egg consumption recorded in sample 2 involved exhumed caches of eggs buried in previous years. This behaviour is described elsewhere in this paper. Support for this comes from the relative estimated sizes of eggs (i.e. "large" or "small" - see Fig. 11) consumed by foxes before and after the onset of egg-laying. Although the sample size is small, Figure 11 suggests that remains of "large" eggs predominated over those of "small" ones in scats collected before the

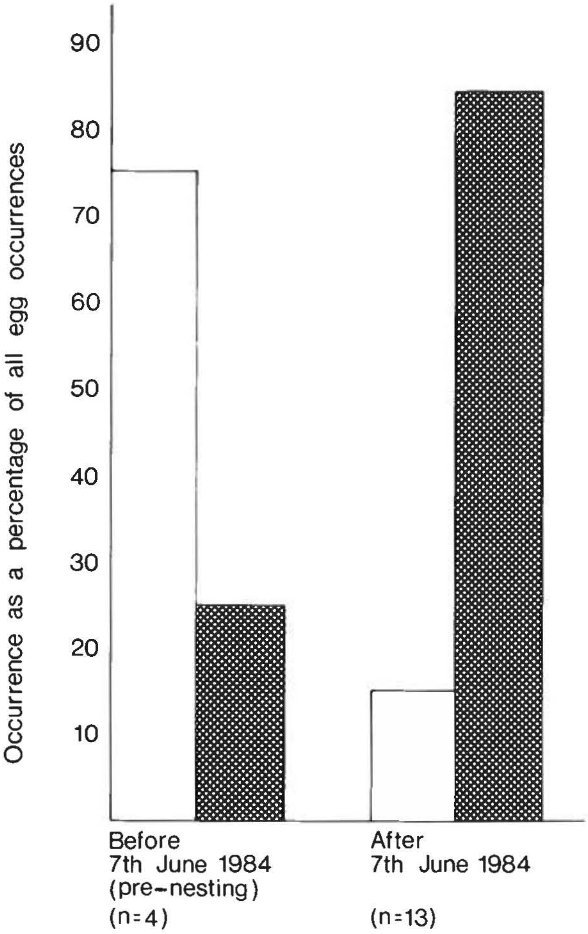


Figure 11. The occurrence in fox scats of "large" (open) and "small" (cross-hatched) eggs in the diet of foxes before and after the onset of egg-laying in the study area. Examples of "large" eggs available on the study area include those of white-fronted geese, ptarmigan and long-tailed ducks; examples of small eggs include those of lapland buntings, redpolls and snow buntings.

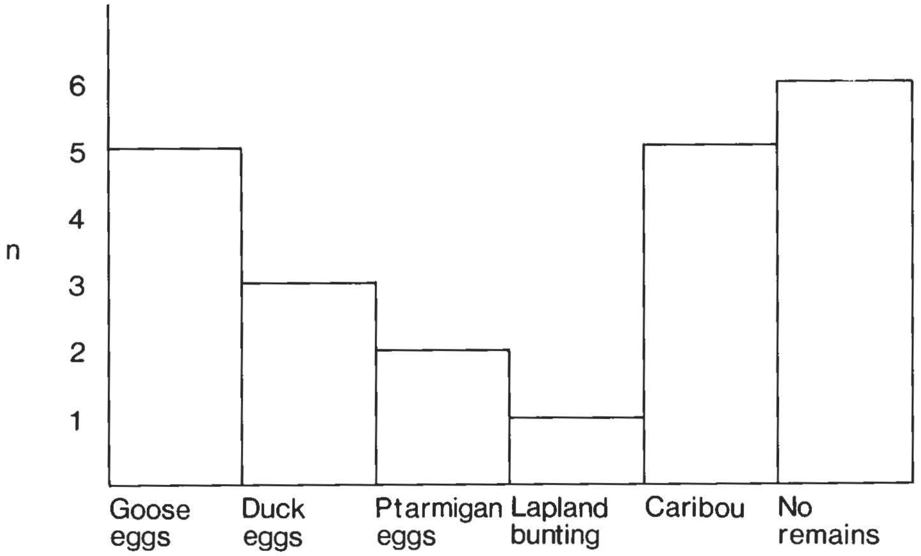


Figure 12. Remains left at 22 unearthed fox caches during early summer 1984 in Eqalummiut Nunaat.

apparent onset of egg-laying, whilst the converse was true later. This may be due to the fact that "large" eggs (such as those laid by ducks, geese or ptarmigan) are more suitable for caching by foxes than "small" eggs by virtue of their greater robustness and energetic cost-effectiveness. All egg remains found at exhumed caches on the study area were from "large" eggs as defined here (Figure 12).

Egg consumption was clearly greatest during the period covered by sample 3 (the main nesting period), when 16.4% of scats contained eggshell (Figure 10). The bulk of this predation was apparently directed towards "small" eggs (Figure 11), probably from the nests of abundant passerines such as Lapland buntings and redpolls.

Arctic char

The bones of arctic char were identified in four scats, all from sample 3. These may have been derived from dead fish released by the melting ice of lakes and streams.

Insects

Of the scats analysed, 58% contained the undigested remains of insects. This type of prey comprised nearly 40% (bulk) of the overall diet of the foxes. Most insect remains were found in samples 2 and 3, when they were by far the most important food eaten by arctic foxes in the study area (Figure 5 and Table 3).

It was not possible to identify accurately all the fragmented insect material recovered from scats. However, analysis of random samples revealed that the most abundant insect prey in the foxes diet were the pupae and larvae of lepidoptera, particularly the moth *Eurois occulta* of the Noctuidae family. These were apparently recovered from the "active layer" of unfrozen soil by foxes scenting them and digging them out. This form of foraging was commonly observed at certain times during the study period (see "foraging behaviour")

In addition to the abundant Lepidoptera remains found in scats, a few bees (probably *Bombus polaris* Curtis) were identified, together with the beetles *Colymbetes dolabratus* Paykull (Dytiscidae) and *Metasyrphus punctifer* Frey (Syrphidae).

Scavenged human food

Evidence of scavenging by foxes was found in one scat from sample 3 which contained a piece of polythene. This coincided with a period when two foxes were in the habit of visiting the researchers' camp and trying to steal food from polythene bags near the tents. As this was the only source of human food in the study area this form of scavenging was clearly not an important source of food, but demonstrates how quickly the foxes adapted to new food supplies.

Dietary information from other sources

Caches of food exhumed by arctic foxes

Identifiable prey remains were found at 16 (73%) of 22 exhumed caches discovered on the study area (Figure 12). The first recently unearthed cache was found on 23rd May 1984, when snow cover was still extensive and the depth of the active layer was limited to a few centimetres. 82% of all freshly unearthed caches were discovered in June following the thaw.

Unearthed caches generally consisted of a neat hole 5-10 cm deep dug in the soil and moss mat. The presence of easily visible remains of exhumed food commonly attracted the observers' attention and led to the discovery of the cache. The range of prey remains shown in Figure 12 may, therefore, be biased towards those, such as eggs, which leave quantities of easily

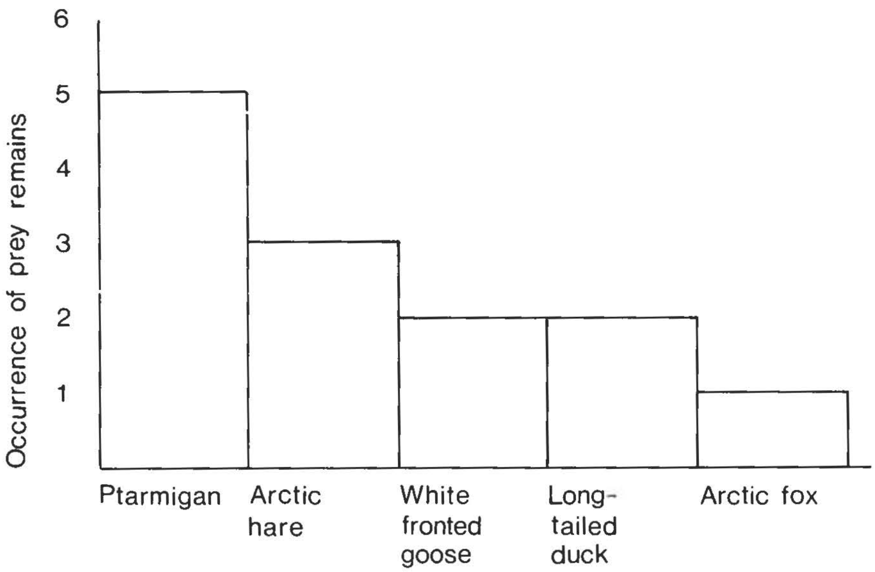


Figure 13. Remains of medium-sized vertebrate prey found at fox resting sites in Eqalummiut Nunaat during 1984.

visible remains after consumption by foxes. The quantity of remains present suggested that only one food item had been buried at each cache.

Eggs were the food type best represented at caches, and 50% of egg remains at caches were identified as those of the Greenland White-fronted goose. Duck eggs at caches were thought to be those of the mallard or long-tailed duck. The condition of fragments of albumen, yolk and membrane present on the remains of freshly-exhumed eggs suggested that they had been buried the previous summer or earlier. Caribou remains found at caches consisted of small pieces of skin and pelage, or small bones such as the carpals and tarsals, often with the hoof sheath attached.

Prey remains

The remains of vertebrate prey were occasionally found at the traditional resting sites used by arctic foxes (Figure 13). Some of these remains were clearly not fresh and may have been a year old or more. However, all are included here as they give some further insight into the foxes' diet. It should be noted that the sample shown in Figure 13 may be biased towards species which leave remains which are durable and easily seen by an observer. The sample excludes prey remains found at caches (see above), together with evidence of kills which could not be attributed to arctic foxes (e.g. clumps of bird feathers in the absence of skeletal material away from a resting site, which could be evidence of raptor predation). The remains of caribou consumed by foxes are considered elsewhere. Figure 13 includes two species, the Greenland white-fronted Goose and the long-tailed duck which are not recorded as predated adults by our other methods of dietary analysis.

Observed interactions with other vertebrates

Detailed observations of foraging arctic foxes produced many records of interactions with other vertebrates, including several predation attempts. These observations, summarised in Table 4, yielded useful additional information on arctic fox feeding ecology as a result of differences in the predator's response to the species encountered on the study area. In turn, potential prey species responded with varying degrees of alarm to foxes. Mobbing of foxes was commonly observed, especially by small passerines. Red-necked phalaropes and a peregrine *Falco peregrinus* were also seen to mob arctic foxes. Other species such as arctic hares and and White-fronted geese appeared to regard foxes as less of a threat, tending to stand alert rather than take flight when a fox was in the vicinity.

Arctic fox behaviour

Detailed observations were made between 5th May and 18th June 1984 of arctic fox behaviour, including foraging, home range use and activity patterns.

Methods

Trapping

In order to collect detailed behavioural information, foxes were caught and fitted with radio transmitters for subsequent tracking. Canadian foot snares were used to catch foxes. This type of trap was developed by the Ontario Ministry of Natural resources as a relatively humane alternative to the traditional leg-hold trap used by fur trappers (Novak 1981).

5 to 10 snares were set between 8th May and 9th June in known foraging areas and near resting areas where foxes were most likely to encounter them. All snares were checked approximately once every 12 hours, usually in the morning and late evening. Problems involving water freezing around the spring mechanism were encountered during May, when the weather conditions caused daily thawing and refreezing of the active layer at the soil surface. This process also led to a loosening of the pegs which anchored the snares to the ground; these had to be checked regularly and hammered in when necessary. Apart from occasional visits to check for signs of disturbance, freezing or peg-loosening, snares were checked by means of binoculars from a distance of at least 50 m to minimise possible adverse effects of human smell upon trapping success. If a snare was sprung abortively, or if it had failed to receive attention from a fox for a period of approximately ten days, it was moved to a fresh location and reset.

Handling of trapped foxes

Rabies is occasionally present in Greenland. As a precaution foxes were only handled by JDSB who had received rabies immunization. However, no evidence of rabies was found during the study.

A snared fox was approached quietly and subdued quickly by dropping a piece of heavy sacking over it. The animal was immobilized by means of an intramuscular injection of Ketamine hydrochloride. Routine measurements were recorded (Table 5, Figure 14), and a collar was fitted bearing a radio transmitter emitting on 173 MHz. The animal was restrained until the effects of the drug had worn off (Figure 15), it was then released at the point of capture. It was later found that foxes could be handled without the use of anaesthesia, so this practice was adopted to minimize handling and recovery time.

Table 5. Biometric and radio-tracking details of two foxes caught and radio-collared in Eqalummiut Nunaat.

Identity	Fox T	Fox R
Sex	female	female
Colour morph	light	dark
Body weight	2,200 g	2,500 g
Head and body length	50 cm	56 cm
Total length	77 cm	79 cm
Pregnancy/lactation	no	no
Capture dates	27.5.84, 9.6.84	28.5.84
Radio-tracking durations	27.5.84 – 8.6.84 9.6.84 – 18.6.84	28.5.84 – 11.6.84
Home range size	13.65 km^2	9.77 km^2

Figure 14. Anaesthetised dark phase female arctic fox (Fox R) being measured prior to being fitted with a radio collar.

Radio-tracking

Radio-collared foxes were located with the aid of portable radio-receivers and hand-held "Yagi" aerials (Figure 16). The transmitters could be detected at a distance of between 1–5 km, depending on the terrain. Once a radio-collared fox was located it was normally possible to maintain visual contact for some time without the need for further radio-tracking. Radio-collared foxes remained unconcerned provided they were not approached closer than approximately 200 m. Observation was aided by the use of 10×40 binoculars. Variations in the pulse of the signal enabled the level of fox activity to be determined without visual observation where necessary, allowing monitoring of activity budgets to continue when the fox was out of view.

The location and behaviour of foxes under observation was recorded at 2 minute intervals on portable tape recorders and subsequently transposed onto maps and recording forms. Two observers operated a shift system to ensure that monitoring coverage was evenly distributed throughout the 24 hour period.

Figure 15. Fox R, a dark phase female recovering from anaesthetic before release.

Observation of non-collared foxes

The presence in the study area of other foxes, which were also easily observed, provided an opportunity to collect additional information upon certain aspects of fox behaviour. For example, detailed observations of fox activity and posture were made at the beginning of the study at 2 minute intervals using Altmans' instantaneous scans (Altman 1974). Variations in coat colour and moulting patterns enabled us to distinguish confidently a number of different foxes. This was facilitated by the use of recording cards bearing fox silhouettes, which were used for making quick sketches of the colour and patterning of foxes observed in the field.

Figure 16. Radio-tracking using a hand held Yagi aerial and portable radio receiver with headphones. Background shows part of study area in mid-June, following main thaw.

Results

Trapping success

Three captures were made of two foxes for a total trapping effort of 135 trap-days. On six occasions traps were sprung but no fox was caught. In addition, traps were disturbed but not sprung on five occasions.

The overall leg-snare trapping success (percentage of captures per trap-day) of 2.2% was considerably greater than the 0.7% achieved by experienced trappers working on a much larger sample of trap nights during tests carried out in Canada (Novak 1981). However, we experienced many more abortively sprung traps: 70% of those sprung failed to result in a capture compared with only 11% in the Canadian study.

The use of this type of trap caused us concern due to the difficulty of retaining the securing peg in the ground, compounded by the effects of freeze-thaw action, and also because of the risk of leg-abrasion from the snare if the fox was not released quickly. In view of this we would in future favour the use of cage traps, particularly as the small size of foxes makes them suitable for this form of trap.

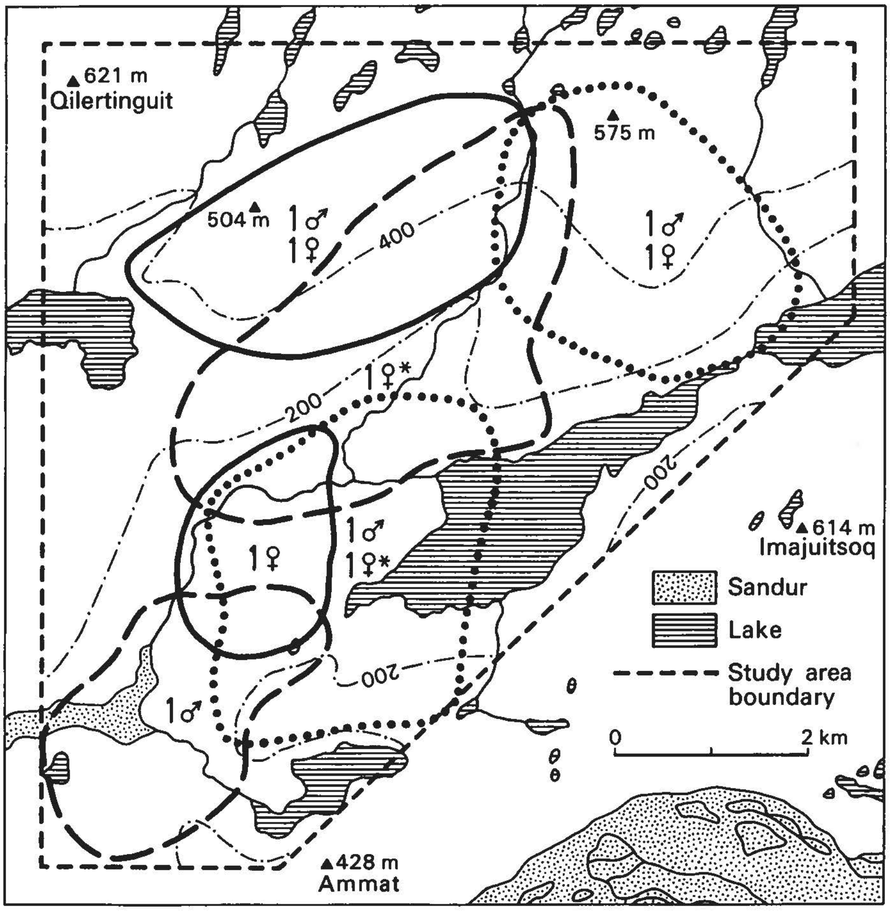


Figure 17. Estimated home ranges occupied by nine foxes during May/June 1984, indicated by regular sightings. The estimated number and sex of foxes occupying a home range is shown in the centre of each range. Animals marked * were radio-collared.

Number of foxes

Within the 44 km^2 study area we identified a minimum of 13 different foxes on the basis of variations in coat colour and moult pattern. Four of these were only seen occasionally, and we presumed that these animals occupied home ranges which lay mainly outside our study area. The remaining nine foxes were seen frequently, and we gained the impression that most of their activity occurred within the study area. If this impression was correct then the population density in our study area approximated to one fox per 5 km^2, with home range size varying between 4–14 km^2.

The frequency of sightings of "known" foxes, together with radio-tracking data from two of them, enabled us to map their home ranges (Figure 17). The sex of the seven foxes which were not caught was inferred on the basis of body size and behaviour. The study area was thought to contain four male and five female foxes; six individuals occupied three home ranges apparently as male/female pairs.

Colour morphs

Dark ("blue") and light ("white") morph foxes appeared to be represented equally on the study area. Of the 13 "known" foxes living within or peripheral to the study area, six were dark and seven were light. It is informative to compare this relatively reliable estimate of the proportions of the two colour morphs with that obtained from random fox sightings made by other expedition members within the same area. Table 6 shows that during May, before the main snow melt, dark morph foxes were sighted three times more often than light morphs; conversely after snow melt in June, light morphs were sighted 2.5 times more often than dark morphs. This perceived difference in the relative proportions of the two morphs in two consecutive months was statistically significant ($x^2=12.54$, $p=<0.001$).

These two divergences from the reliable estimate of 6 dark: 7 light suggests the effects of camouflage upon the visibility of each morph under different conditions; they also emphasise the unreliability of using random fox sightings as a means of estimating the relative occurrence of the two colour morphs. After June it was not possible to identify reliably the two morphs because moulting progressed rapidly, and light and dark morphs became difficult to distinguish in their summer pelage.

Figure 18. Female light phase arctic fox (Fox T) wearing radio-collar. Photograph taken 9th June 1984 when moult was underway, revealing darker summer coat.

Home range use

Two female arctic foxes, one of each colour morph (Figures 15 and 18), were fitted with radio-collars and radio tracked during May and June 1984 (see Table 5 for details of individuals and tracking durations). These two animals were monitored over a period of 23 days between 27th May and 18th June, though tracking of the dark fox (Fox R) ended prematurely when she was found drowned in a meltwater river on 11th June and a postmortem revealed that she had a heavy infection of gut parasites. Previous observations of Fox R's behaviour had indicated that she appeared consistantly more lethargic than Fox T.

Fox T and Fox R occupied separate home ranges which were adjacent and slightly overlapping (see Table 5 for home range sizes). The area of overlap amounted to 0.96 km^2 (4.3% of the two home ranges combined). Figure 19 illustrates the two home ranges estimated by using the minimum area (convex polygon) method (Macdonald *et al.* 1980).

Table 6. Random sightings of the two fox colour morphs made by expedition members,compared with the known occurrence of each morph in the study area. $X^2 = 12.54$ $p < 0.001$

	Dark	Light
Random fox sightings during May (before snow-melt)	30 (75%)	10 (25%)
Random fox sightings during June (after snow-melt)	8 (28.6%)	20 (71.4%)
No. of individuals of each morph known in the study area	6 (46.2%)	7 (53.8%)

Fox T's 13.65 km^2 range occupied a lowland area, with most of her activity occurring at altitudes below 150 m above sea level. Her range spanned a meltwater river flowing between a lake and active sandur valley in the south-west. Fox R's 9.77 km^2 home range occupied the valley of a tributary of the meltwater river immediately to the north of Fox T's range. Fox R occupied a wide altitudinal range, from *Calamagrostis lapponica* grasslands and freshwater marshland at 50–100 m to *Empetrum* moss mat, plateau dwarf heath and fellfield at 500–550 m.

Figure 20 illustrates the extent to which each radio-collared fox used its home range and the area of range overlap. Both foxes tended to concentrate their foraging activity in the area of lowland river valley and marsh west of the lake outflow point. Fox R was not monitored for long enough to reveal in great detail her pattern of home range use. However, she was found to forage in a tributary valley to the north of her main centre of activity, and on four occasions she travelled to the upper slopes (> 400m) of the valley to forage. Outside her main centre of activity, Fox T spent some time foraging in dense *Salix* scrub along the northern shore of a lake, and also in an area of lowland marsh around the western extremity of the lake.

Sleeping sites

Neither of the radio-collared foxes, nor others observed during the study period, appeared to seek underground sleeping or resting sites. Foxes were observed sleeping in *Calamagrostis* grassland (on 6 occasions), in *Salix* scrub (4), on rock ledges (2), under rock overhangs (2), on lake ice (1) and on dried mud (1). One pair of foxes,

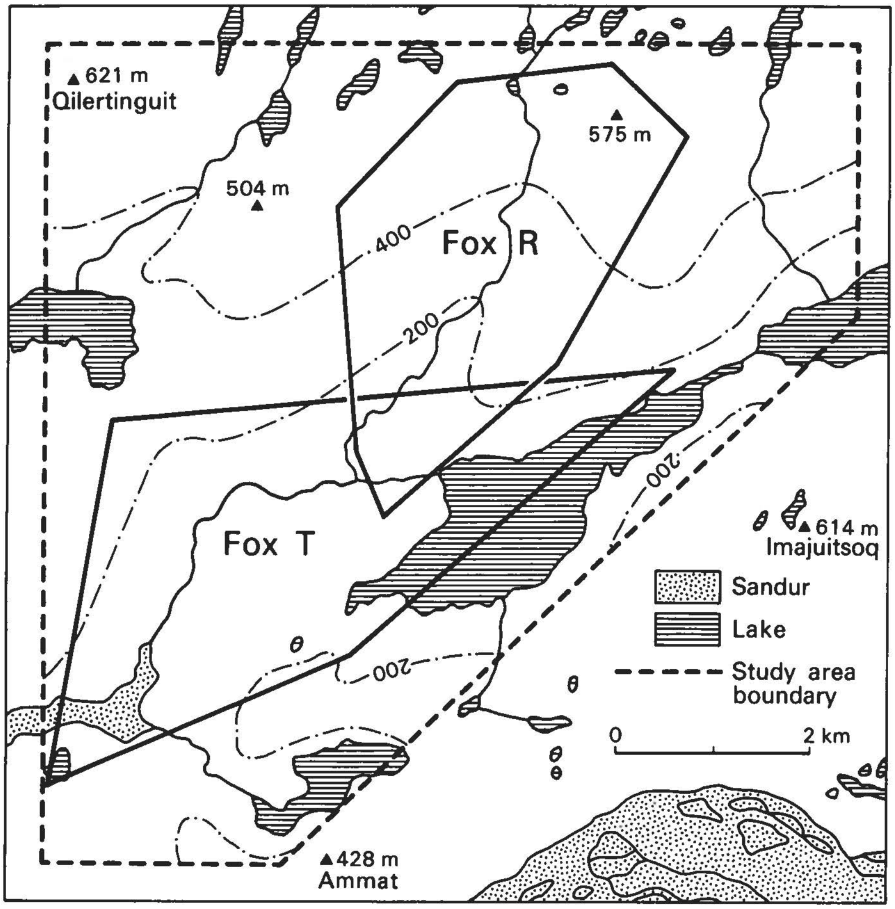
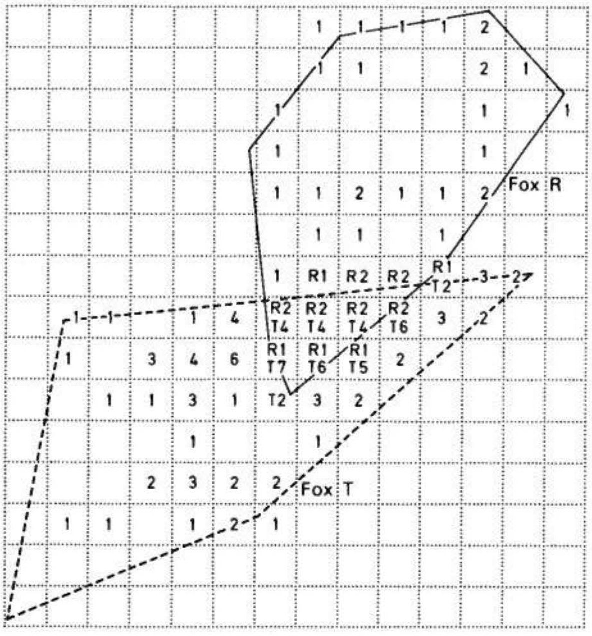


Figure 19. Home ranges of two female foxes indicated by radio-tracking during May and June 1984.



occupying a predominantly high altitude home range, regularly rested beneath or beside a large boulder. The small size of some of the old fox scats at this site suggested that it may have been used as a breeding den in past years. There was no evidence that breeding occurred on the study area during 1984.

Activity patterns

Foxes were recorded as being active (i.e. foraging or travelling) in every hour of the 24 hour study period. In addition to observations of foxes during radio-tracking sessions, records were also made of foxes seen or heard from a goose observation hide in a lowland valley manned continuously between 10th June and 17th July. These records were interpreted as indicators of fox activity. However, this activity was unevenly distributed,

Figure 20. Variations in home range use by the two radio-collared foxes. Figures in each 0.25 km square indicate the number of occasions each fox was recorded foraging in the square. In the area of overlap, figures relating to each fox are identified by the prefix "T" and "R".

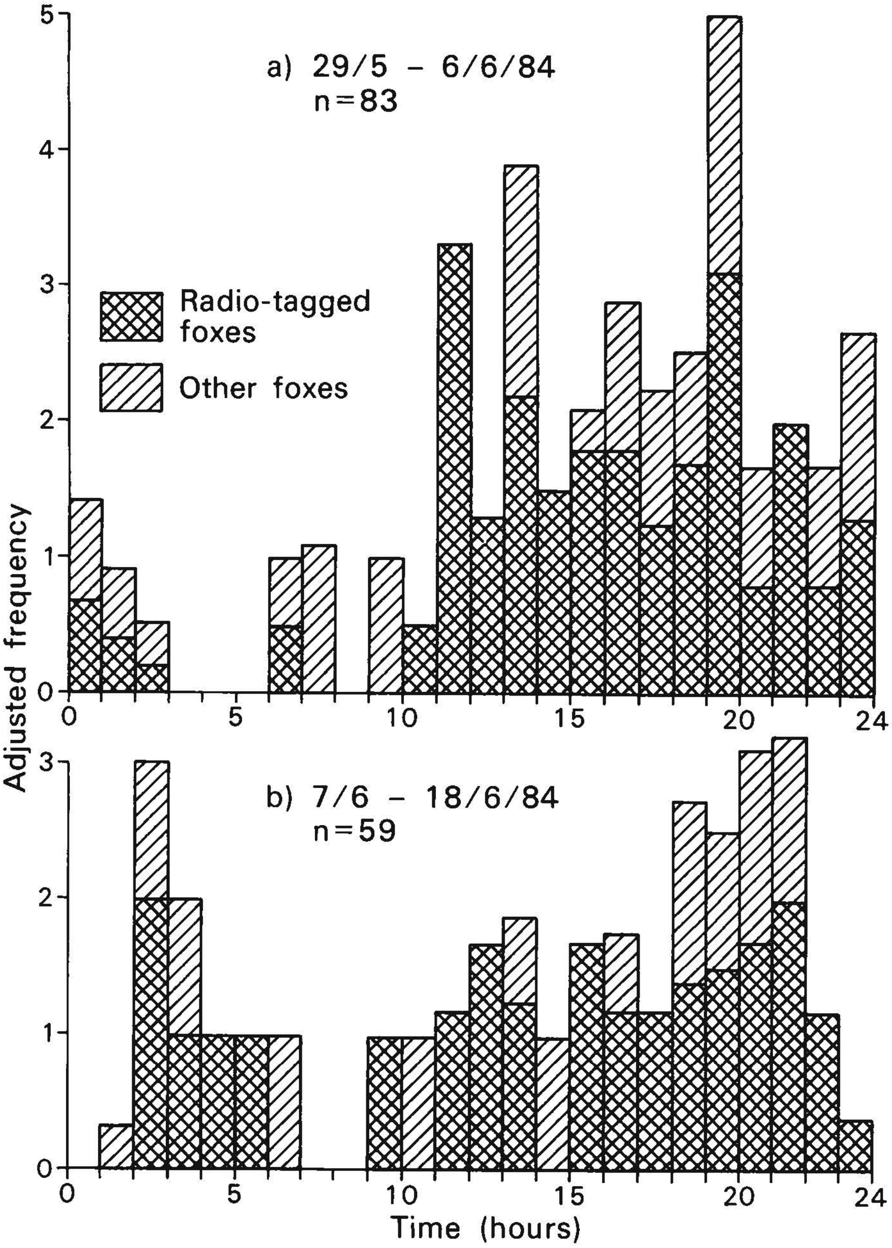


Figure 21. The occurrence of active foxes encountered on the study area a) before the discovery of the first birds nest, and b) during the early/mid nesting period. The data have been adjusted to account for slight variations in observer coverage over 24 hours.

Table 7. Occurrence of active foxes during "night" and "day" over three sampling periods when observer effort was distributed evenly over the 24 hour cycle. Samples A and B were based mainly on observations of radio- collared foxes; sample C was based on the occurrence of foxes seen or heard incidentally during continuous observations of an incubating goose.

	"Night" 20.00h-08.00h	"Day" 08.00h-20.00h		
A) 29th May-6th June (pre-nesting period)	19 (22.9%)	64 (77.1%)	$X^2 = 24.4$	$p<0.001$
B) 7th June-18th June (early-mid nesting)	29 (49.2%)	30 (50.8%)	$X^2 = 0.017$	N.S.
C) 10th June-7th July (mid/late nesting and fledging)	69 (71.9%)	27 (28.1%)	$X^2 = 18.4$	$p<0.001$

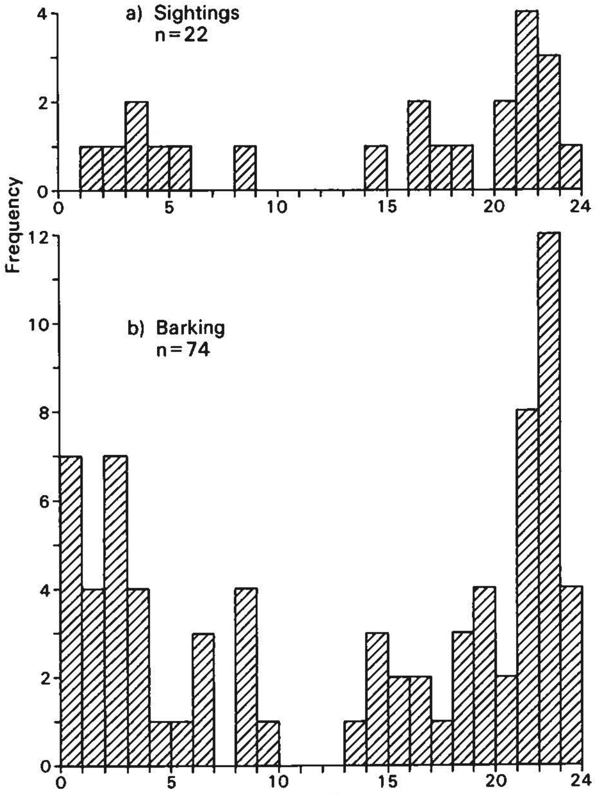


Figure 22. The occurrence of foxes a) seen or b) heard from a hide during continuous observations of an incubating goose between 10th June and 7th July. The hide was situated near the eastern edge of the fox study area.

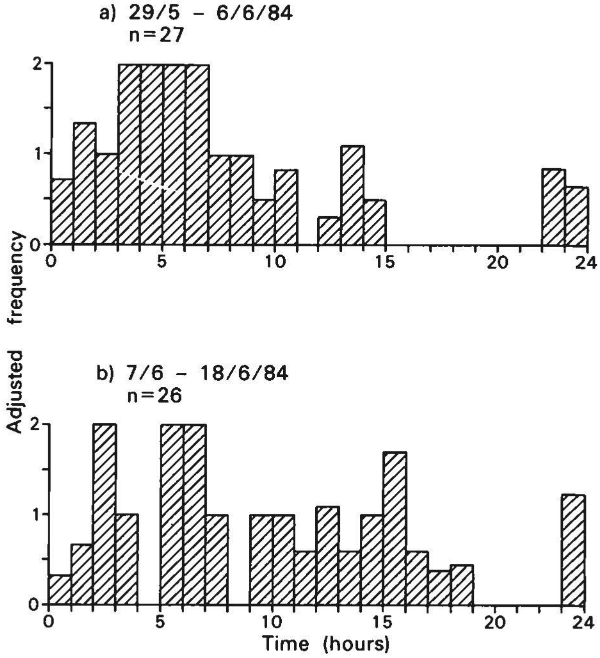


Figure 23. Occurrence of inactive foxes (sleeping or resting) encountered on the study area a) before the discovery of the first birds nest and b) during the early/mid nesting period. The data includes both radio-collared and other foxes and has been adjusted to account for slight variations in observer coverage.

and there was some evidence to suggest that the pattern of this distribution changed with time (see Figures 21, 22, 23 and Table 7). Prior to the passerine nesting season, fox activity tended to be concentrated during "daylight" (0800–2000 hr), when the sun was above the horizon and the active layer on exposed ground thawed slightly. During this period, most encounters with sleeping or resting foxes occurred at "night" (Figure 23). However, once passerine nesting had begun, active foxes were encountered as frequently during the "night" as during the "day". Towards the end of the passerine nesting and fledging period (10th June – 7th July) records of foxes seen and heard from a hide suggest that fox activity was concentrated during the "night" (Figure 22). These apparent changes in the distribution of fox activity may have been influenced by a number of factors, such as changing temperature and light regimes. However, the dietary evidence (Table 5) of a shift in fox predation from soil-inhabiting insects towards birds in the latter part of the study suggests that prey availability may have been an important influence. The insects were mainly available to foxes during "daylight" hours when the soil surface was thawed; nestling and fledgling birds, however, were available to foxes during both "day" and "night". Indeed the tendancy of both adult and juvenile passerines to roost at ground level at "night" may make them especially vulnerable to fox predation at this time.

The influence of caribou carrion on fox behaviour.

At an early stage in our study it became clear that a large number of caribou had died during the preceding winter (1983/84), and that the carcasses of these animals were an important food source for the foxes (Table 3). In order to quantify the distribution and density of this food resource, during June 1984 we undertook a systematic search of an area of 32 km^2 which encompassed the bulk of the home ranges of the two radio-collared foxes. The results of this search are illustrated in Figure 24.

Within the 32 km^2 area of search, we counted 117 carcasses of caribou which had clearly died during the preceding winter (as indicated by the presence of flesh, abundant fur, and the absence of vegetation growing over skeletal remains). This represented a mean density of 3.7 carcasses per km^2. However, carcass density was 3.8 times greater in those parts predominantly below 150 m above sea level (6.5 carcasses per km^2) than in the remaining higher altitude areas to the North (1.7 carcasses per km^2; Figure 24).

Fox T, occupying a larger home range than Fox R in a

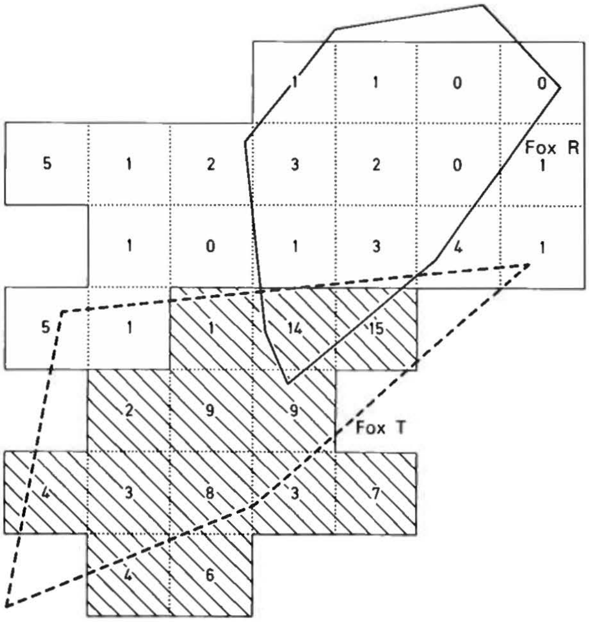


Figure 24. Distribution of carcasses of caribou which had died during the winter of 1983/84. The number of carcasses found within each 1 km square is indicated. Squares containing land predominantly below 150 m above sea level are shaded. The home ranges of the two radio-collared foxes are also shown.

predominantly lowland area, had access to more caribou carcasses. Fox T's home range was found to contain 76 carcasses at a density of 5.6 per km^2, while Fox R's home range contained 39 at 4.0 per km^2. However, Fox T was known to share her home range with at least one other fox, while Fox R was apparently solitary. It is significant that the limited area of overlap between the two radio-collared foxes home ranges occurred in the area where caribou carcass density was found to be highest (Figure 24).

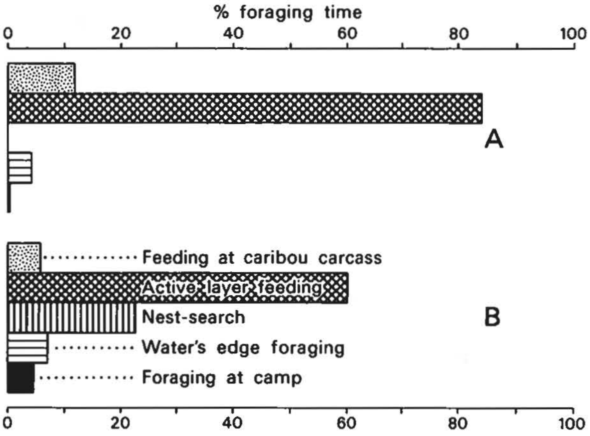


Figure 25. The proportion of fox foraging time spent in five foraging categories, showing (A) the period prior to the onset of passerine nesting (29th May-6th June; 1438 minutes observation) and (B) the period during passerine nesting (7th-18th June; 951 minutes observation). Data from 7 foxes, including two radio-collared individuals.

Foraging behaviour

During our observations of both radio-collared and noncollared foxes, five principal types of foraging activity were identified (Figure 25).

I) Carcass feeding. Foxes visited caribou carcasses to chew at skeletal material and the frozen flesh attached to it; often several carcasses were visted in succession by a fox during one foraging bout. By the end of May, when detailed observations on all foraging activities were initiated, most available flesh had apperantly been removed from carcasses by foxes. Figure 25 shows that foxes spent relatively little of their foraging time at caribou carcasses thereafter. Dietary information suggests that carcass feeding was of much greater importance earlier in the season (Figures 5 and 7).

II) Active layer feeding. Foxes were observed to spend prolonged periods in discrete areas digging and scratching in the moss mat and shallow (1–2 cm deep) thawed surface layer of areas of snow free ground. This form of foraging occupied more of the foxes' time than all others combined both before and during the passerine nesting season (Figure 25). Active layer feeding was clearly only possible at those times and in those places where there was a sufficient depth of unfrozen soil or vegetation to enable foxes to dig up items of food. During early May, when snow cover was extensive and air temperatures were permanently below freezing point, detailed observations using Altman scans were made of foxes during bouts of active layer feeding on a south facing hillside above our base camp. Most data were collected from a pair of foxes occupying a den beneath a large boulder.

One or both foxes were normally visible sleeping beside this boulder before and after foraging bouts. They were never seen to commence active layer feeding before noon (mean start time 14.59h +/− 1.07h n = 6); foraging bouts lasted on average 6.06 hours (1.35h n = 4) and tended to end as frost began to harden the soil surface in the snow free patches (mean 21.03h +/− 0.31 h n = 5). During foraging bouts over the 7 days of observation, foxes spent 69.5% of their time,in patches of snow free ground. These comprised an estimated 10% of the hillside over which they foraged. The foxes spent more time standing, sniffing and digging when they were in snow-free patches than when they were on snow (Figure 26). When on snow they spent significantly more time moving (walking or trotting) with head up ($X^2 = 355.4$:$p<0.001$). This was probably related to the greater availability of invertebrate prey in the limited areas of snowfree ground.

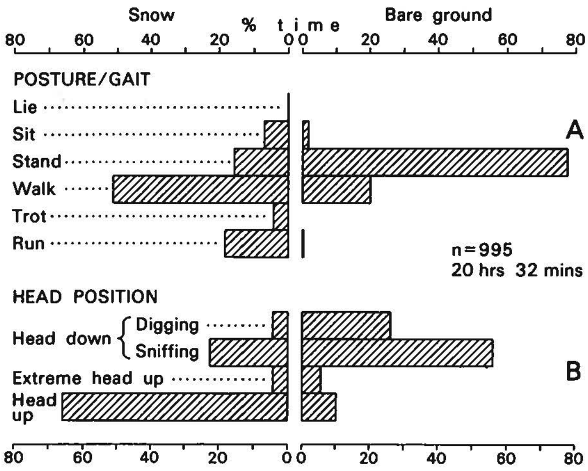


Figure 26. The activity budget of foxes during "active layer feeding" between 5th-11th May. Observations were made over 20 hours 32 minutes on two or more foxes foraging on a south facing hillside with 90% snow cover. Data are presented to show the amount of fox foraging time occupied by various postures or gaits (A) and head positions (B), when the animals were on snow-covered or snow-free ground.

Close observation of Fox R during active layer feeding in moss/dwarf shrub habitat at 450 m above sea level, revealed a mean prey capture rate of 4.5 prey items per 5 minutes foraging (n = 4 range 4–6). Prey items were clearly small, and analysis of a fresh dropping produced by Fox R during active layer feeding revealed the remains of large numbers of lepidoptera larvae and pupae. As indicated elsewhere in this paper, such invertebrate prey was found to make up a very significant proportion of the diet of foxes in our study area.

III) Nest search. After the onset of egg laying by passerines in early June, foraging foxes were observed to search, apparently deliberately, for nests. Foxes walked or trotted in a "zig-zag" fashion over areas of short vegetation on lower ground, often pausing to sniff the air. This behaviour was distinct from that described in II) above, in that foxes moved more rapidly, over a wider area, without pausing for more than a few seconds. On several occasions we observed this strategy resulting in the successful predation of a clutch of eggs or nestlings of Lapland buntings; on one occasion Fox T was seen carrying a fresh Greenland white-fronted goose egg which had been recently taken from a nest.

In areas of taller vegetation, such as *Salix* scrub, foxes were seen to walk slowly with the head raised, pausing frequently to listen and sniff. Having located a nest some 0.5–1.0 m above ground level by this means, foxes were seen to spring into the air, landing on or near the nest. Nests of redpolls, for example, were predated in this manner.

IV) Water's edge foraging. On occasions, foxes were seen to concentrate their foraging activity along the margins of lakes and meltwater streams. Although it was not possible to identify the prey taken during this activity, it is likely that foxes were scavenging for remains of arctic char and three-spined stickleback, as well as searching for the nests of waterbirds such as long-tailed duck, mallard and red-necked phalarope.

V) Foraging at camp. During the course of the study, two foxes developed the habit of visiting camps established by the expedition and foraging for food scraps. This behaviour comprised 4.5% of observed fox foraging time during the latter half of the study. However, it is felt that this figure may have been exaggerated by the greater likelihood of this activity being observed.

Discussion

Environments with much seasonal variability in the availability of food are believed to exert selective pressures on resident species, favouring those with broad ecological niches (e.g. Levins 1968). The success of such "generalist" species, inhabiting markedly seasonal environments, is likely to depend on an ability to respond promptly to sharp changes in the relative availability of different prey sources. The results of this study indicate that the arctic fox in west Greenland behaves as a generalist predator, displaying a considerable degree of opportunism in its responses to changing prey availability.

Composition of the foxes' diet showed marked variations with time. For example, prior to the onset of snow melt, caribou carrion was the main food. As this finite food source was depleted, and as areas of bare ground were revealed by snow melt, insects from the soil became the dominant prey. Insects were finally superseded in the diet by birds during the nesting and fledging periods. Although these three principal prey types were available and consumed by foxes in all of the four periods sampled, attention was shifted to concentrate on that most available at the time. Furthermore, foxes apparently responded to diurnal changes in prey availability, for example by concentrating their "active layer feeding" at times when the sun's warmth had softened the normally frozen soil surface. These conclusions concur with those of a more detailed study of arctic fox ecology carried out by Hersteinsson (1984) in Iceland.

The numbers of caribou in west Greenland have, in the past, undergone long-term fluctuations (Vibe 1967, Meldgaard 1986). At the time of our study (1984) numbers in the Sisimiut area of west Greenland, which includes the study area, had reached a minimum following a population decline which started in the late 1970s (Thing 1984, Meldgaard 1986). The causes of this fluctuation in caribou numbers in west Greenland have been the subject of much debate. One plausible explanation for the periodic crash in caribou numbers is the overexploitation of winter forage (Roby and Thing 1985). Of added significance to arctic foxes in our study area is a change in the caribou's migratory behaviour associated with the population crash. Meldgaard (1986) observed a decrease in the seasonal long migrations between the coast and inland areas, with caribou becoming more stationary and wintering in inland areas such as Eqalummiut Nunaat. As a result of this change, winter mortality among caribou provided a major food resource to arctic foxes in the study area.

The unusually deep, complete and long lasting snow cover in Eqalummiut Nunaat in the winter of 1983/84 is thought to have contributed significantly to the mortality of caribou already in poor condition following the population crash (Thing 1984, Roby and Thing 1985). The abundance of caribou carrion at the beginning of our study should therefore be regarded as a temporary and perhaps unusual phenomenon. It coincided with a period prior to snow melt when other foods were generally unavailable to foxes; migrant birds had not arrived and potential insect prey were in frozen soil beneath deep snow.

Given the absence of alternative prey it is likely that the unusual abundance of caribou carrion at such a critical time enabled more foxes to survive on the study area than would have been the case in more typical winters. This may provide an explanation for the greater density of foxes resident on the study area compared with observations made in 1979 by the same study group. In 1979 no major caribou die-off had occurred during the previous winter and in a search of a c.50 km^2 area only 2 carcasses were found of caribou that had died in the preceding winter or more recently (Hardy and Stroud 1981). Six foxes were thought to be resident on the same study area which supported 9 foxes in 1984 (Fox and Stroud, 1981). Similar conclusions were reached in Finland where the abundance of reindeer carcasses following the severe 1986/87 winter was thought to be at least partly responsible for the presence of unusually large numbers of arctic foxes in summer 1987 (Kaikusalo 1988).

There have been few estimates of home range size of foxes in west Greenland prior to this study. Longstaff (1932) estimated that one pair near Godthaab Fjord covered 20 km^2, while Fox and Stroud (1981) noted that one distinctive individual was observed over an area of at least 30 km^2. In the present study home ranges were smaller, (4–14 km^2), and more comparable to those recorded by Hersteinsson and MacDonald (1982) for arctic foxes inhabiting relatively productive coastal habitat in Iceland.

It is remarkable that there was no evidence of successful breeding by foxes in the study area during 1984. During 1979 when foxes were scarcer, young cubs were observed on several occasions in the same area (Fox and Stroud pers.comm.). Although caribou carrion was temporarily abundant in early 1984, there is evidence to suggest that fox prey was significantly less abundant in the spring and summer of 1984 than in 1979. Fox *et al.* (1987) noted that Lapland buntings were approximately 3–5 times less abundant in their favoured breeding habitat in 1984 than in 1979. This considerable difference in the density of an important avian prey species may have been influenced by similar variations in the abundance of its invertebrate food. Pitfall trapping (Fox *et.al.* 1987) suggested that terrestrial insects and arachnids may have been scarcer in 1984 relative to 1979. Of particular significance to both foxes and insectivorous birds was the scarcity in 1984 of larvae of the moth *Eurois occulta;* in 1979 these had been present in enormous numbers (Fox *et al.* 1987). These observations may offer some explanation for the absence of successful fox breeding in 1984, particularly if an element of severe prey scarcity occurred at a critical stage in the process of foetal development. Such conditions may have occurred during May 1984, when caribou carrion became depleted, insect prey were apparently scarce, and migratory birds had not begun nesting. Thus an abundance of carrion enables a greater number of foxes to survive the winter, but lack of food in the early summer could mean that breeding fails.

Piantanida (pers.comm.) noticed that insects also occurred in the summer diet of foxes in the area of NE Greenland where lemmings occur; in one sample of droppings collected from a den away from the coast insects amounted to 33.9% of prey occurrences. However, the significance of invertebrate prey was not recognised by Braestrup (1941) in his review of the arctic fox in Greenland. He reported that during periods of food shortage foxes in West Greenland were thought to survive by exhuming prey cached during times of plenty. Although foxes in our study exhumed cached prey, it is interesting to speculate whether the importance of this food source has been exaggerated in the past by observers misinterpreting the "active layer feeding" (involving digging for insects) which occupied the majority of fox foraging time in this study.

The great importance of soil-inhabiting insects to arctic foxes in our study is comparable to the exploitation of earthworms *Lumbricus terrestris* by the closely related red fox *Vulpes vulpes* (Macdonald 1980). Both predators possess the high degree of adaptability necessary for the exploitation of such diverse prey as lagomorphs, which are large and fast moving, and terrestrial invertebrates which are small and immobile by comparison.

Young birds were an important food source during the latter period of the study (9th July-11th August 1984). Larson (1960) has speculated that fox predation on breeding birds is much heavier in non-lemming parts of the arctic than in lemming areas, and that this pressure has an influence on the distribution of certain breeding bird species. However, Larson's (1960) hypothesis is based on the assumption that arctic foxes behave as specialists, preying almost exclusively on lemmings where they occur, and specialising on the eggs and young of birds in non-lemming areas. This was evidently not the case in our study, where foxes behaved as opportunists and only preyed heavily on birds when they were especially abundant. Similarly in Piantanida's (pers. comm.) study in the lemming area of NE Greenland, foxes preyed in an opportunistic manner, such that both birds and lemmings contributed significantly to the diet, although the latter tended to predominate.

Given the apparent relationship between the availability of caribou carrion in winter/spring and numbers of arctic foxes present in the following summer, one may speculate that fox predation upon ground nesting birds is heaviest following those winters when caribou die in large numbers. Data available from two contrasting years in Eqalummiut Nunaat tend to support this hypothesis: Fox *et al.* (1987) noted that losses of Lapland bunting nests due to predation (by both arctic foxes and ravens) were heavier in 1984 than in 1979, when no caribou die-off was observed; furthermore fox predation of white-fronted goose nests was considerably heavier in 1984 (83% of known nests were predated) than in 1979 when 43% of known nests were predated (Fox and Stroud, 1988).

Increased predation by arctic foxes on Brent geese *Branta bernicla bernicla* has been observed following a population crash of lemmings, and the consequent influence of lemming cycles on Brent goose breeding success has been the subject of much discussion (Summers 1986, Owen 1987, Dhondt 1987). Whilst the effects of the long caribou cycle are difficult to compare with those of a 3 year lemming cycle, similarities can be drawn between the two examples in the way foxes readily switch major prey items depending on availability.

Fox predation on white-fronted geese

The significance of egg predation by foxes is reflected in the behaviour of incubating white-fronted geese, which appear most vigilant at times of peak arctic fox activity (Stroud, 1982). Our observations suggest that fox predation is only successful when both adult geese are absent from the nest. The nests of geese which need to leave the nest to feed frequently during incubation are consequently particularly vulnerable, thus timing of these departures with relation to inactive fox periods can reduce this risk. Predation of goslings and adult geese is apparently uncommon in Eqalummiut Nunaat, although Fowles (1981) recorded nine unsuccessful attacks by foxes on adults and family groups, and a fox-predated goose was also found on an old nest.

The influence of fox predation on the nesting behaviour and strategy of Greenland white-fronted geese remains unclear, since the highly dispersed, solitary nesting habit of this species has both advantages and disadvantages in terms of predator avoidance, when compared with the colonial nesting habit shown by other arctic nesting geese such as the lesser snow goose *Anser caerulescens* (Fox and Stroud 1988). However, it is clear that the arctic fox is a major predator of the eggs of white-fronted geese in West Greenland. Indeed it is felt that this may be one factor responsible for the low productivity of the Greenland white-fronted goose, with only a relatively small proportion of pairs breeding successfully in any one year (Fox and Stroud, 1988).

Conclusions

This study shows that the arctic fox in non-coastal West Greenland feeds on a broad spectrum of prey types, and responded in an opportunist manner to relative changes in prey availability. The unusual abundance of caribou carrion was thought to have aided the survival of foxes over the winter, but the relative scarcity of soil-surface insects and ground-nesting birds in 1984 may have inhibited sucessful breeding on the study area.

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