THE HUNTING ECOLOGY OF ARCTIC FOXES (Alopex lagopus) NEAR CAPE CHURCHILL, MANITOBA

BY

JAMES BAHR

A Thesis Submitted to the Faculty of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

Department of Zoology

University of Manitoba

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Abstract: Several aspects of arctic fox hunting ecology were studied during the summers of 1985 and 1986. Pup development was observed at one den during the summer of 1985.

Pup development was observed on an ad libitum basis. The pups' rapid behavioural maturation closely paralleled their rapid physical growth. As the pups matured, their responses to stimuli, their repertoire of behaviours and vocalizations, and their activity patterns changed. The pups expanded their repertoire of physical maneuvers as their strength and coordination increased. Physical and behavioural developments led to a maturation of predatory behaviours and skills of self preservation.

The hunting ecology and food habits of adult arctic foxes were studied by following male foxes on hunts. Foxes hunted along similar routes each day but did not hunt in the same area twice consecutively. Foxes covered the greatest proportion of their distance and made the greatest proportion of their kills in the habitat that probably harboured the highest prey densities. They used their entire home ranges in June and July even when most Canada geese (<u>Branta</u> <u>canadensis</u>) and snow geese (<u>Chen</u> <u>caerulescens</u>) were concentrated in specific areas after late June.

The foxes travelled at an average rate of 5.3 km/h and could cover 25 km or more during a day of hunting. When lemmings (<u>Dicrostonyx</u> <u>groenlandicus</u>) were abundant during 1985, the foxes averaged more attacks, kills and meals per time and per distance than in 1986 when lemmings were less abundant. Overall, the foxes were successful in 87% of capture attempts for lemmings, in 64% of attempts for defended goose nests and in all attempts on shorebird, duck, passerine and ptarmigan nests.

In 1985, lemmings accounted for the majority of the adult foxes' diet before goose hatch. Passerine clutches made up most of the remainder and the foxes rarely ate cached food during hunts. In 1986, shorebird eggs and eggs from caches accounted for the majority of the foxes' diet. After goose hatch in both years, goslings and adult geese became important food items but the foxes did not abandon the food sources they utilized before hatch.

Acknowledgements

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INTRODUCTION

Arctic foxes (<u>Alopex</u> <u>lagopus</u>) are opportunistic predators and scavengers that will utilize any food source (Garrott and Eberhardt 1987). During the summer, their food habits reflect the availability of the prey species within their home ranges (Chesemore 1968, Fine 1980, Hersteinsson 1984) and their activity cycles and patterns of habitat use may be influenced by the activity patterns and locations of prey (Speller 1972, West and Rudd 1983).

Along the west coast of Hudson Bay near Cape Churchill, Manitoba, numerous sandy beach ridges provide abundant den habitat for arctic foxes. The adjoining peat lowlands strewn with lakes and ponds harbour a variety of prey: lemmings (<u>Dicrostonyx</u> <u>groenlandicus</u>), Canada geese (<u>Branta</u> <u>canadensis</u>), willow ptarmigan (<u>Lagopus</u> <u>lagopus</u>) and several species of shorebirds, eg. dunlin (<u>Calidris</u> <u>alpina</u>) and semipalmated sandpiper (<u>Calidris</u> <u>pusilla</u>), ducks, eg. oldsquaw (<u>Clangula</u> <u>hyemalis</u>) and ground-nesting passerines, eg. Lapland longspur (<u>Calcarius</u> <u>lapponicus</u>).

Though lemming populations fluctuate between years, the variety of avian species contributes to a relatively stable supply of avian prey from year to year. Within years, the goose populations and distributions within the study area change from a scattered population of nesting Canada geese (<u>Branta</u> <u>canadensis</u>)(D. Rusch pers. comm.) before hatch to a more concentrated and larger population of both Canada geese and snow geese (<u>Chen</u> <u>caerulescens</u>) after hatch. As the Canada geese and goslings move to gosling-rearing areas along the sea coast, they are joined by several thousand snow geese and goslings from La Perouse Bay, about 8 km WNW of the study area.

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The density of nesting Canada geese in the study area has been declining through the last two decades. Hypotheses concerning the effects of researcher disturbance and competition with increasing numbers of snow geese in the established brood-rearing areas are under consideration. Also, the impact of arctic foxes on the Canada goose population is unknown.

The objectives of this project were to:

1) examine the arctic foxes' hunting ecology and food habits.

2) estimate the foxes' impact on the local Canada goose population.

3) examine goose defenses to fox predation.

4) observe the growth and development of the fox pups.

THE STUDY AREA

Location

The study area is near Cape Churchill, Manitoba along the west coast of Hudson Bay, from 58°35'50" to 58°43'55" North Latitude and from 93°8'12" to 93°15'36" West Longitude. The UTM grid references for the four corners of the study area are 850950, 850100, 920950 and 920100. These boundaries encompass an area of about 105 sq.km of which roughly 19% are shallow lakes and ponds. There are 15 known arctic fox dens and one known red fox den in the study area (Fig. 1).

Geology

Precambrian age granite and gneiss of the Canadian Shield surround Hudson Bay. Along the southwestern coast of the Bay, including Cape Churchill, these Precambrian rocks are overlain by undeformed lower Palaeozoic age limestone and siltstone sediments of marine origin (Whitmore and Liberty 1968).

During glaciation in the Pleistocene, the Laurentide ice sheet approximately centered on Hudson Bay and depressed the region under its weight. During deglaciation, Atlantic water penetrated into the Hudson Bay area and formed the Tyrrell Sea. Isostatic rebound of the land upon reduction of the ice load caused the Tyrrell Sea to recede, exposed a border of postglacial marine sediments 50-150 km wide, and formed countless beach ridges and strand lines around present day Hudson Bay (Lee 1968, Innes et al 1968).

Physiography

The study area contains many north-south oriented sand or gravel beach ridges separated by peaty lowerlying areas strewn with shallow lakes and ponds.

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Figure 1. The study area near Cape Churchill. Camp (Nestor 1) was about 250 m northwest of Den B. Dens A,B,D and F were the object of study in 1985 while dens A,C,D and E were the object of study in 1986. The main brood-rearing areas were at Bear Bay and Baskett Bay.

STUDY AREA

MANITOBA

N

BASKETT BAY

E

A

D

B

C

BEAR BAY

HUDSON BAY

● FOX DEN

BEACH RIDGE

LAKE

0   1   2
KILOMETERS

4
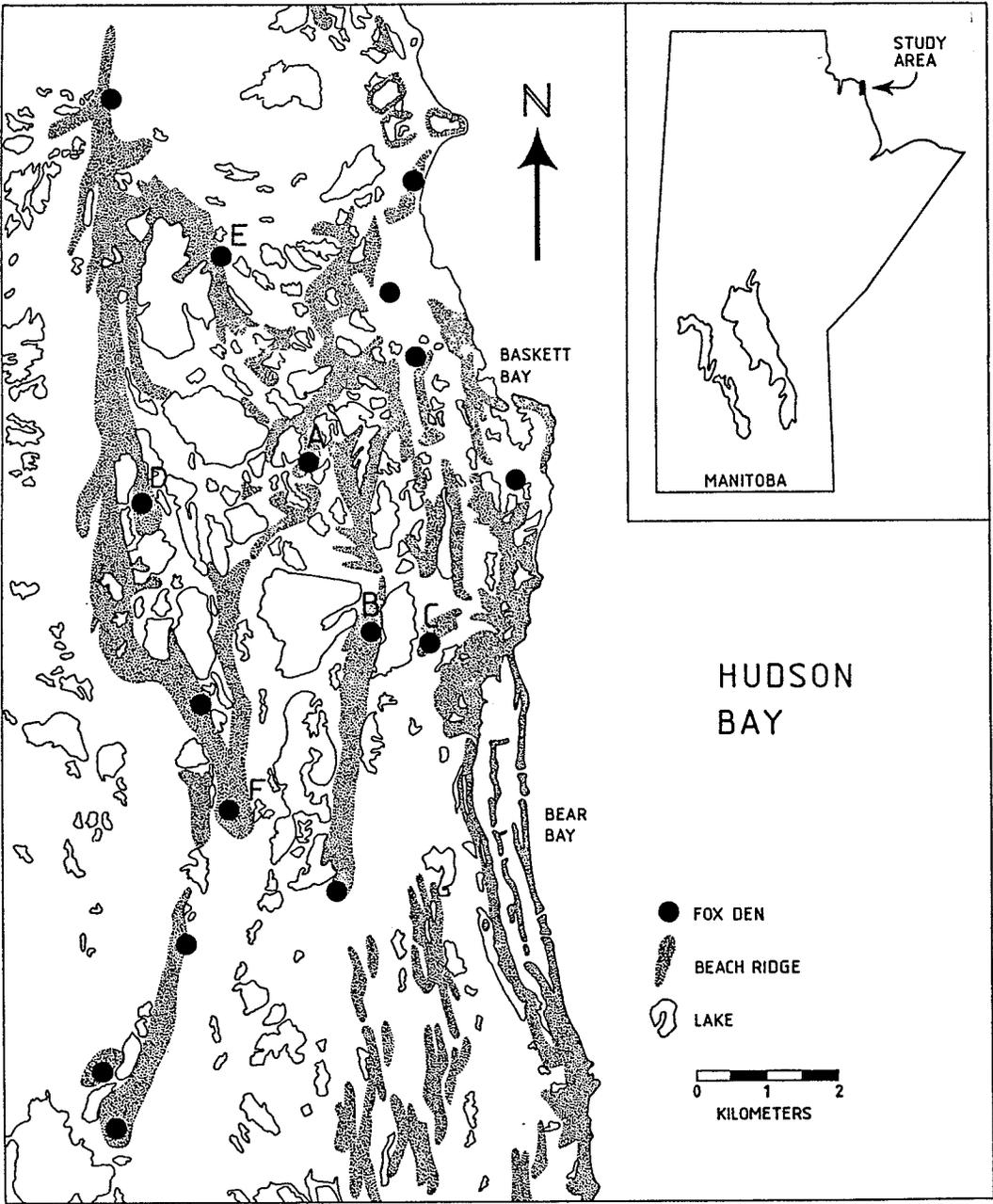
Drainage patterns are immature and drainage is poor. The permafrost is continuous and it lies from 30-50 cm below the surface in the low, wet tundra (Ritchie 1960). The permafrost lies farther below the surface under beach ridges, along rivers and in tidal areas along the coast (Johnson 1987).

About 10% of the study area is more than 15 m above sea level, while 60% is between 7.5 and 15 m, and 30% is below 7.5 m in elevation. The area of greatest elevation occurs as a continuous region from the west-central to the northwestern portions of the study area. The area of lowest elevation occurs as a strip along the Hudson Bay coast.

The eastern border of the study area is the shore of Hudson Bay, which consists of sand or gravel beaches with some scattered boulders, and extensive mud flats at low tide. The western border of the study area lies just inland of the western limit of the beach ridges. The physiographic features of the study area continue beyond the northern and southern borders of the area.

Permanent lakes are often surrounded by peat pressure ridges formed by the outward expansion of ice as the lake freezes in autumn. Lakeshores are irregular and they often exhibit several points as well as islands. A few raised peat polygons occur on the wet tundra.

Climate

Hudson Bay has a strong climatic influence on the surrounding coastline. The cooling influence of the Bay delays the onset of spring and produces cool summer temperatures. Autumn temperatures are moderated though the influence is more evident east of the Bay due to the prevailing northwest winds during that season. Winters along the coast are generally colder than those in other areas at the same latitude. However, temperature extremes are infrequent compared to inland areas due

to heat transfer from the water to the air at ice leads and through the ice on the Bay (Thompson 1968, Savile 1968).

The Environment Canada weather station at the Churchill airport, about 50 km west of the study area, reports the following climate data:

The mean annual temperature is $-7.2^{\circ}C$. July is the warmest month (mean = $11.8^{\circ}C$) and January is the coldest (mean = $-27.3^{\circ}C$). The vegetative season extends from about the last week in June to mid-August, although frost can occur in any month (K. Johnson, pers. comm.).

The mean annual precipitation is 40.6 cm. Most precipitation falls between July and September while the least falls between January and March. The mean annual rainfall is 23.3 cm with the most falling in August (mean = 6 cm). Fog occurs on average 7 days per month from May to August. The mean annual snowfall is 185.3 cm with the most falling in November (mean = 40 cm). The greatest cover thickness occurs in March (mean = 47 cm). The average duration of persistent snowcover is 211 days and extends from late October to late May.

Windspeed is fairly constant throughout the year but the average maximum occurs in November (mean = 25.6 km/h) and the average minimum occurs in July (mean = 19.3 km/h). The prevailing winds are northerly during the summer, westerly during the winter and northwesterly during the spring and autumn.

Human Habitation

The prehistoric presence of aboriginal peoples along the Hudson Bay coast from Cape Churchill to Cape Tatnam has not been verified, probably due only to a lack of investigation (Trudeau 1968). Taylor (1968) speculates that Indian hunters were transient in this area. A Pre-Dorset archaeological site near Shamattawa, and several Pre-Dorset, Dorset and Thule sites north and west of Churchill (Riewe et al

1989) suggest that Eskimo peoples also travelled this stretch of coastline. Nowadays, Inuit from Eskimo Point (Riewe et al 1989), Swampy Cree (Trudeau 1968) and citizens of Churchill visit this area to trap and to hunt.

Between 1944 and 1965 the Canadian and U.S. Armies conducted field exercises and equipment trials on Cape Churchill (Johnson 1987, M. Gillespie pers. comm.). Their vehicle tracks and refuse can still be seen on the beach ridges of the study area.

In the late 1960's, the Manitoba Dept. of Natural Resources established a permanent camp (UTM grid reference 890023) in the study area and began long-term research on Canada geese. The Canadian Wildlife Service also bases polar bear research from this camp. The camp (Nestor 1) is active from early June to early August or September, with up to ten people present at any time.

In 1972, Queen's University built a camp (Nestor 2) at La Perouse Bay for long-term snow goose research. This camp is active from late April to mid-August and holds up to 22 people.

During summer and autumn, numerous tourists visit Churchill and the Cape Churchill area to observe the local wildlife, especially birds and polar bears.

Vegetation

Didiuk (1979), Johnson (1987) and Ritchie (1960) describe the habitats and vegetation of Cape Churchill. In the study area, the three physiographic regions (Fig.2) and some of their flora are:

1) Coastal Flats

This area consists of coastal saline sedge and grass meadows that grade into tidally flooded mud, sand and boulders. In the study area, coastal beach ridges separate the meadows. To the south, however, the meadows form an almost continuous strip (average width = 0.5 km) along the coast to the mouth of the Broad River. The

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Figure 2. The physiographic regions of the study area. The solid lines indicate
the boundaries of the three regions (after Didiuk 1979).

INTERIOR
SEDGE
MEADOW

BEACH
RIDGE

COASTAL
FLATS

N

BASKETT
BAY

HUDSON
BAY

BEAR
BAY

Beach Ridge

Lake

Camp

0   1   2
    Kilometers
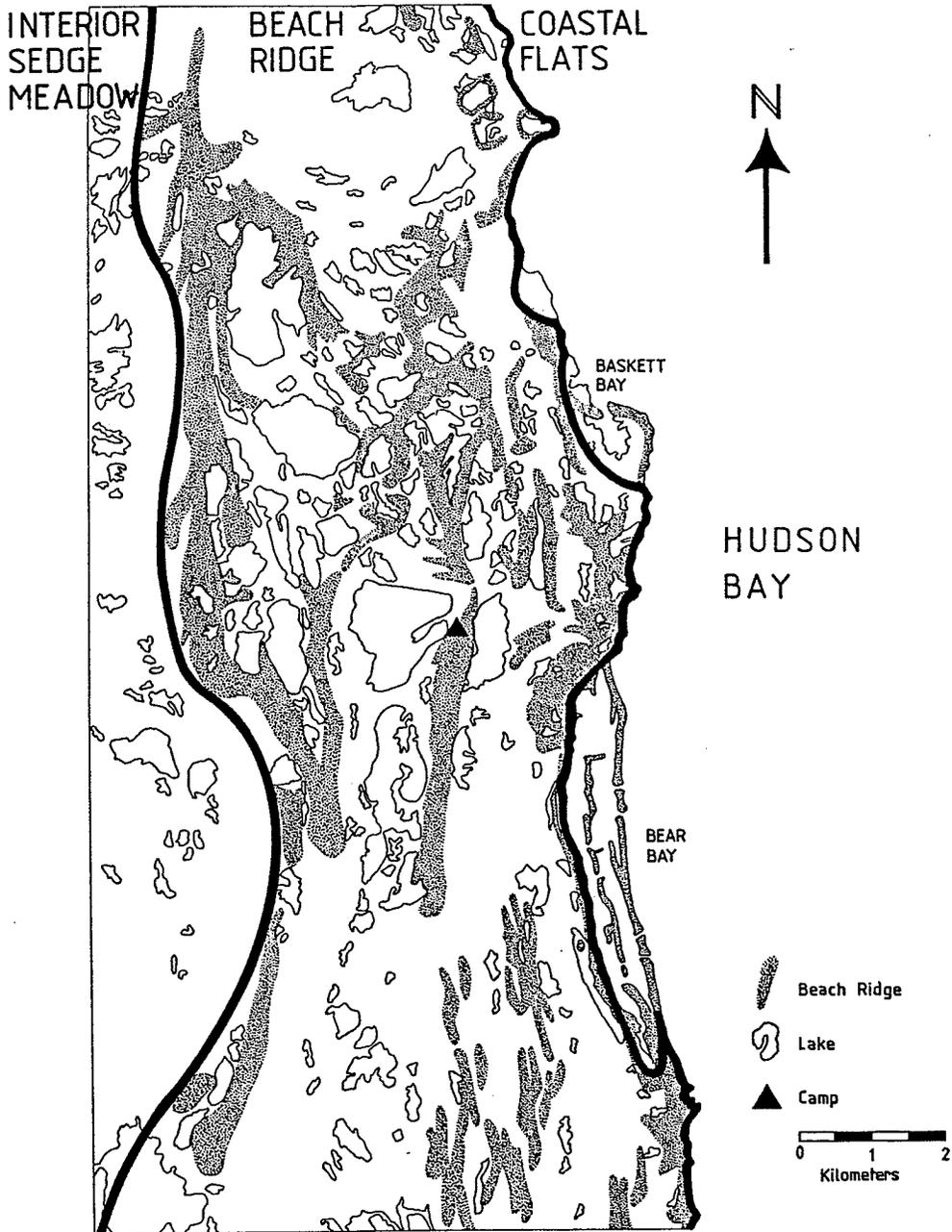
soil in the meadows consists of a thin organic layer overlying marine alluvium (Didiuk 1979). Some typical plants of the saline meadows are (Johnson 1987, Didiuk 1979):

> Triglochin maritima
>
> Calamagrostis deschampsoides
>
> Dupontia fisheri
>
> Puccinellia phryganodes
>
> Carex subspathecea
>
> Ranunculus cymbalaria

2) Beach Ridge Area

This area is a mosaic of beach ridges, peat lowlands and lakes. A variety of plant communities exist and intergrade according largely to the moisture regime (Johnson 1987). The two major habitats in this area are:

a) Beach Ridges: These ridges are relic sand and gravel beaches left high and dry as isostatic rebound of the land (about 1 m/century) causes the Hudson Bay shoreline to recede (Johnson 1987, Lee 1968). The ridges have a xeric to well-drained moisture regime and have a deeper permafrost table than the adjoining peat lowlands (Johnson 1987). The vegetation on the ridges is a low-growing lichen-heath community. Typical plant species are (Johnson 1987):

> Polygonum viviparum
>
> Saxifraga oppositifolia
>
> Dryas integrifolia
>
> Hedysarum mackenzii
>
> Shepherdia canadensis
>
> Arctostaphylos alpina

Rhododendron lapponicum

Achillea nigrescens

Beach ridges along the coast have been exposed more recently than ridges farther inland and thus support a community of colonizing plants such as:

Trisetum spicatum

Elymus arenarius

Festuca brachyphylla

Potentilla pulchella

Potentilla multifida

Epilobium angustifolium

Androsace septentrionalis

Castilleja raupii

Matricaria ambigua

b) Peat Lowlands: In the low-lying areas surrounding the beach ridges, the marine alluvium is covered with a layer of peat (depth<1 m). A high permafrost table and poor drainage cause the formation of treeless bogs strewn with lakes, ponds and areas of standing water. Distinct plant communities exist but they intergrade to form many intermediate types (Ritchie 1960, Speller 1972, Johnson 1987). Typical plant species in the peat lowlands are (Ritchie 1960, Johnson 1987):

Sphagnum sp.

Carex aquatilis

Carex gynocrates

Carex rariflora

Saxifraga hirculus

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Rubus chamaemorus

Andromeda polifolia

Kalmia polifolia

Ledum decumbens

Pedicularis sudetica

Pedicularis flammea

Bartsia alpina

Pinguicula vulgaris

Low, narrow peat ridges occur along the edges of many lakes and ponds in the peat lowlands. These ridges are better drained than the surrounding area. Some typical plant species found on the pressure ridges are (Johnson 1987):

Salix myrtillifolia

Salix lanata

Myrica gale

Betula glandulosa

Anemone richardsonii

Pyrola grandiflora

3) Interior Sedge Meadow

This area is a peat lowland to the west of the Beach Ridge Area. The Interior Sedge Meadow contains both lake systems and extensive peat bogs devoid of water bodies. There are few upland features (Didiuk 1979). In the study area, the plant species of the Interior Sedge Meadow are the same as those found in the peat lowlands, but farther inland, stunted Picea mariana occur (Ritchie 1960, Didiuk 1979).

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Methods and Materials

My original plan for data collection on this study was to observe hunting foxes from a stationary vantage point as Speller (1972) had done but the topography and vegetation of the study area allowed for only brief observations of foxes followed by long periods of scanning. I soon learned that I could follow male foxes on hunts and gather the desired data with no apparent disturbance to the foxes; therefore, I abandoned the original plan early in the 1985 field season.

I followed foxes on hunts during the summers of 1985 and 1986. In both years, data were gathered on the adult males of two dens. In 1986, I attempted to gather data on the male of a third den but that fox proved unsuitable after several unsuccessful attempts at habituation. Female foxes were not followed on hunts since they were always disturbed by my presence.

Hunts began when the fox left the den or when I contacted a fox in the field. Hunts ended when the fox returned to the den, took a nap or when I lost contact with the fox. During hunts I trailed from 70-120 m behind the fox though in 1986 I often exceeded these distances as I tried to take advantage of topographic features to minimize my disturbance of geese. Observations were made with the naked eye or with a 20X spotting scope mounted on a home-made rifle stock. During 1985, observations were concentrated on type of prey, capture success rate and the fate of captured items. In 1986 the same data were gathered with the addition of hunting routes and the time and distance between capture attempts. All observations were recorded in a note book in 1985 and on data sheets and 1:50,000 maps in 1986.

This method was not without drawbacks. The only reliable way to make contact with a fox was to wait at a den until the fox arrived then follow the fox as it

departed. Also, the frequency of lost contacts was high (66% overall). These constraints resulted in an inefficient use of field time that could have been eliminated with the use of mobile radio telemetry equipment. There were no funds for such equipment. In its absence, the method used was the only one feasible.

Besides following foxes on hunts in 1986, I observed a goose brood-rearing area from an observation tower in an attempt to gather data on the foxes' attack success rate on geese and goslings. The geese were extremely wary and mobile after hatch and such data were difficult to obtain on hunts since my presence was alarming to the geese. However, the few days spent in the tower were not productive so the procedure was abandonded.

Results and Discussion

Table 1 and Figure 3 summarize the basic hunt observation data. In 1985 I stopped gathering hunt data after 1 July in part so that I could observe the pups' diet but also because my presence on hunts after goose hatch in late June would be disruptive to the foxes' efforts to capture geese. In 1986, hunt data after goose hatch were considered necessary so I observed hunts in July.

During June of 1985 the male foxes returned to their dens reliably during the day so I was able to observe many hunts during that month. In 1986, however, the male foxes were much less regular in their visits to their dens. There were many days when they did not return to the den at all during the daylight hours. The reasons for this were unclear. They may be related to a nocturnal activity pattern observed by Speller (1972) and Burgess (1984) where the adult fox rests somewhere other than the den (Burgess 1984). Garrott et al (1984) stated that adult foxes seldom visited the den during midday. The reasons may also be related to the bringing of food to the den. Macpherson (1969) and MacFarlane (1908) saw that arctic foxes cached large

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Table 1. A summary of observation time and distance covered for hunts near Cape Churchill in 1985 and 1986.

	1985	1986
Observation period	5 June - 1 July	9 June - 24 July
Number of hunts observed	22	16
Average duration of hunts (min.)	77	67
Range of hunt duration (min.)	15-220	15-180
Total time of hunt observations (min.)	1690	1070
Average distance of hunts (m)		.5500
Range of hunt distance (m)		1000-11,100
Total distance of hunt observations (m)		88,050

Figure 3. Basic hunt observation data for hunts observed near Cape Churchill in 1985 and 1986. Distance data were not recorded in 1985.
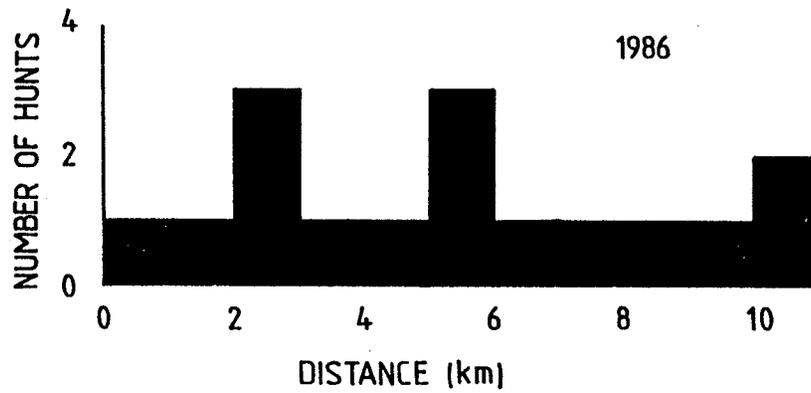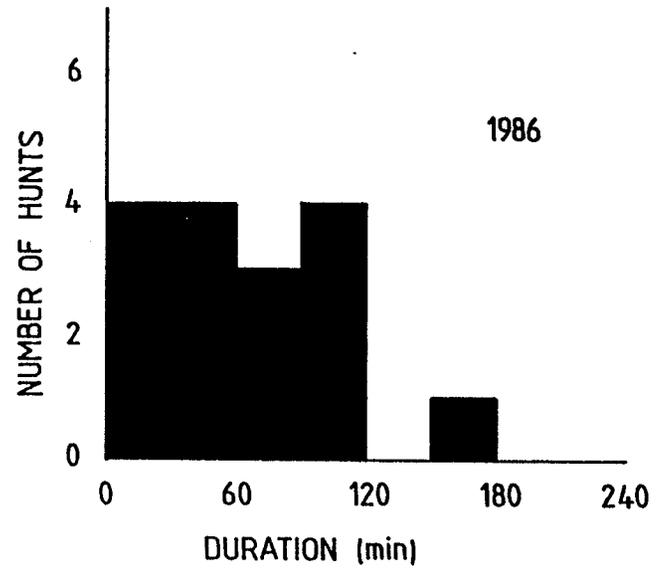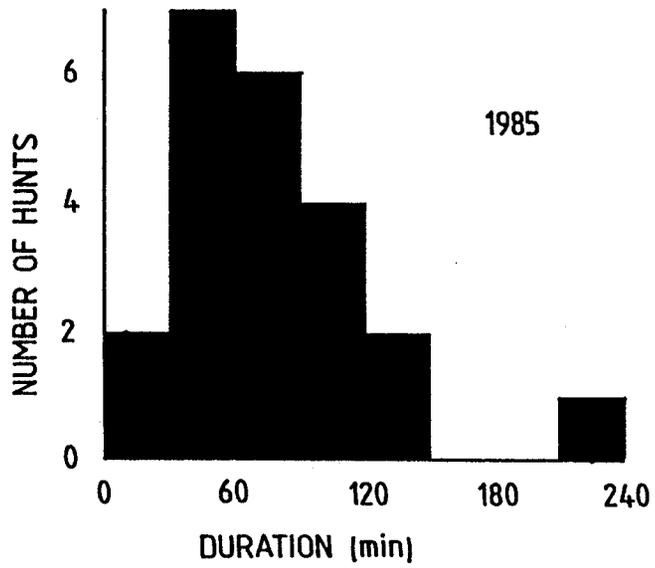
numbers of lemmings in their dens. Because eggs in both years of this study were either cached near the capture point or were eaten on the spot, perhaps the scarcity of lemmings in 1986 resulted in fewer visits to the den because the foxes caught fewer lemmings to cache there. When food supplies were quite limited, adult foxes visited their dens relatively infrequently (Underwood 1975).

In any case, the low number of recorded hunts in 1986 was due mainly to the lower number of fox visits to their dens during the daylight hours, to several days of inclement weather and to time spent in the observation tower and with the third male fox that would not habituate to my presence.

Twenty seven of the total 38 hunts were not observed in their entirety. Therefore, the hunt duration and distance data in Table 1 and Figure 3 do not reflect true averages, ranges or distributions of entire hunts. During hunts, the fine details of a fox's zig-zagging path could not be recorded accurately since the width of the pencil line on the map corresponded to a 25-40 m wide band in the field. Therefore, the distance figures in Table 1 are minimums though they are probably within 15% of the true values. Because I was dependent on the foxes, I simply accumulated observation time as the opportunity arose. No conclusions can be drawn concerning the foxes' kill success during different periods of the day; however, the foxes caught prey at any time during the daylight hours. Avian prey were attacked as they were encountered and failures were specific to the events of the attack. Speller (1972) attributes the arctic foxes' nocturnal activity pattern to the lack of lemming activity during the middle of the day. In this study, lemming activity or the lack thereof probably had little effect on kill success since the foxes rarely failed to dig lemmings from their burrows.

<u>Hunt Duration and Distance</u>

Eleven of the 38 hunts were observed in their entirety (Table 2). Fewer entire hunts were recorded in 1986 than in 1985 due to my efforts to select routes and use topographic features to minimize my disturbance of geese. These efforts resulted in a high rate of lost contact in that year (81%).

No conclusions can be drawn concerning hunt duration or distance covered during hunts. However, entire hunts ranged from 15 min. where the fox left the den upon sighting a flock of geese, killed two goslings from that flock then returned to the den with one of the goslings, to 220 min. where the fox made many investigations and kills in several lowland areas then took a nap beneath some willows. On one hunt in 1986 the fox was still on the outward phase of the hunt after 180 min. when contact was lost. The distance covered during the entire hunts in 1986 ranged from 2300 m where the outward phase of the hunt ended with the retrieval of a cached gosling, to 4250 m where the fox made a loop through a lake-strewn lowland adjacent to its den. The 220 min. hunt (above) was observed in 1985 and was estimated to have covered 18 km. On the above mentioned 180 min. hunt, the fox covered over 11 km and was 5 km away from its den when contact was lost. All 16 hunts observed in 1986 extended beyond a 1000 m radius of the den.

Between 19 and 28 June in 1985 I observed five brief hunts from two to nine minutes in duration. At a den adjacent to a large lowland area, the male fox hunted in that lowland and stayed within 200 m of the den. At another den on a wide beach ridge beside a large lake, the male proceeded directly to a lowland area about 300 m away and stayed within 500 m of the den. During these hunts the male caught only one lemming, returned to the den immediately upon capturing the lemming and either gave it to the female (in one instance) or put it in a den entrance. Once when the lemming was put in an entrance, the female emerged immediately with a

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Table 2. A summary of observation time and distance covered for entire hunts near Cape Churchill in 1985 and 1986.

	1985	1986
Number of hunts observed	8	3
Average duration of hunts (min.)	90 (S=65)	33 (S=26)
Range of hunt duration (min.)	35-220	15-62
Total time of hunt observations (min.)	716	98
Average distance of hunts (m)		3000 (S=1050
Range of hunt distance (m)		2300-4250
Total distance of hunt observations (m)		9050

lemming and ate it. In the other three cases the male had returned with several lemmings (4-6) immediately before the brief hunt and of these, the female in one instance took those lemmings and ate them. The female did not emerge from the den in the other two instances. The purpose of these brief hunts was probably to bring food to the female and perhaps to supplement food brought for her to the den immediately beforehand.

Speller (1972) found that most hunts by male foxes were under 80 min. in duration but could be longer than 180 min. He also found that male foxes made the most hunts either within a 200 m radius of the den or beyond a 600 m radius of the den. In the present study, the lack of hunts completely within a 1000 m radius of the den was due to the distribution of productive hunting grounds within the foxes' home ranges.

Movements and Foraging Patterns

Speller (1972) defines several hunting intensities and he saw that arctic foxes hunted at various intensities according to prey densities in the immediate surroundings. The foxes hunted at low to moderate intensities until they found places where lemmings were abundant, then they hunted very intensely within a small area. Foxes foraged along fairly specific routes "as they travelled towards areas where hunting had been successful in the past or to places where they might expect successful hunting" (Speller 1972). They typically backtracked as they returned to the den so as to retrieve lemmings that they had killed and cached during the outward phase of the hunt (Speller 1972).

Fine (1980) saw that while arctic foxes foraged, they held their heads low and they zig-zagged as they loped at moderate speeds. Foxes held their heads upraised as they "seemed to move with purpose towards a definite goal...An adult carrying

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food back to its den, quickly and directly, typified this movement pattern" (Fine 1980).

In the present study, foxes travelled at an overall average rate of 5.3 km/h (range = 2.8-10 km/h) during hunts in 1986. These figures were calculated from the total distance covered during hunts as traced on maps while I followed the foxes, and they include the time spent on attacks and investigations. The foxes' actual lope speed was estimated to range from 7-11 km/h. These figures are close to the mean lope speed of 7.6 km/h (S = 2.3 km/h) observed by Hersteinsson (1984).

The foxes loped as they foraged, and their lope speed seemed to vary with hunting intensity. They slowed to a trot or a walk as they passed through standing water, investigated something, foraged through bushes and sometimes as they searched for a spot to cache a captured item. As they walked through standing water more than a few centimeters deep, the foxes took care to lift their feet clear of the water on each step, and they sometimes took the opportunity to drink. The foxes increased their lope speed as they were returning to the den with food, as they crossed wide beach ridges, moved toward a distant flock of geese - in short, as they travelled directly and purposefully toward a goal. In such cases, they travelled with their head upraised to various degrees.

Adult foxes galloped as they charged a flock of geese, ran away from geese defending their nests, ran away from fearful stimuli, eg. caribou, or as they were engaged in agonistic chases with other foxes. Their speed could not be estimated in such cases but in a subjective evaluation, it was faster than seemed possible for an animal of the foxes' stature and is best described thus: the foxes "did not appear to be running, so much as flying low" (Mowat 1973).

On a few occasions, I saw a fox gallop away from something, eg. a group of caribou, then press himself flat on the ground on the opposite side of a hill or

ridge. From that position, the fox watched the stimulus by peeking over the crest of the hill (Fig. 4). On such occasions, the fox seemed only mildly alarmed. When a fox was more alarmed, he ran or loped away with a stiff back and with his legs extended stiffly, but his gait was very springy. As he loped away from the stimulus, he turned slightly to one side then to the other as he looked back over his shoulders. The turns did not result in a zig-zagging course. Rather, the fox yawed to the left then to the right as he moved away along a fairly straight line. If the stimulus did not move, then the fox sometimes stopped broadside and watched it for a while, then loped away. If the stimulus moved, the fox again moved away in the stiff-legged lope, then perhaps stopped again to watch from farther away. Finally, the fox would lope away and go about his business.

During one agonistic chase between two foxes, the chasee watched the chaser approach from a distance. The chasee then made two or three spy-hops as he accelerated and galloped away (Fig. 5). The spy-hops did not seem to be as much hops as they were skips, though the fox reared up on his hind legs.

In lowland areas, the foxes loped in narrow to wide and often irregular sweeps across their general direction of travel. In hummocky areas, their sweeps tended to be narrower and their turns more frequent as they weaved their way between the hummocks. On occasion the foxes stopped sweeping, loped forward for several meters in the general direction of the hunt then began to sweep again. This may actually have been part of the zig-zagging, but it may also have been in response to a patch of vegetation associated with an absence of prey or simply that the fox saw something up ahead that he wished to investigate. The foxes tended to make wider sweeps in areas with fewer hummocks. On wide peninsulas or in small lowland areas boxed in by lakes, the foxes' path sometimes seemed erratic as they foraged back and forth, around and about the area.

Figure 4. A fox lies flat on the ground to conceal himself while he watches

something on the opposite side of the hill. The fox's ears are flattened

laterally.

22
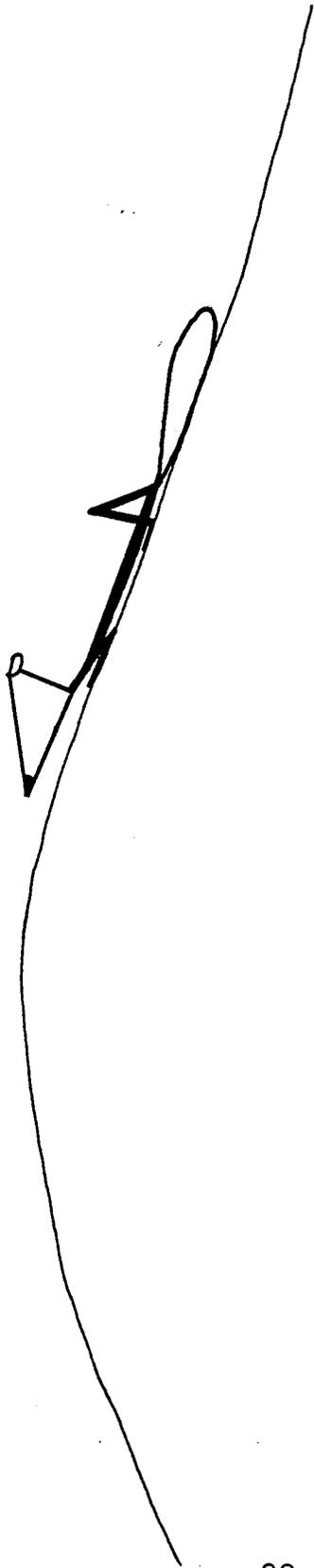
Figure 5. A maneuver that arctic foxes use to watch a pursuer: the spy-hop. The sequence runs from right to left. In (iii) and (iv) the fox is looking back over his shoulder to watch a pursuer.

v   iv   iii   ii   i
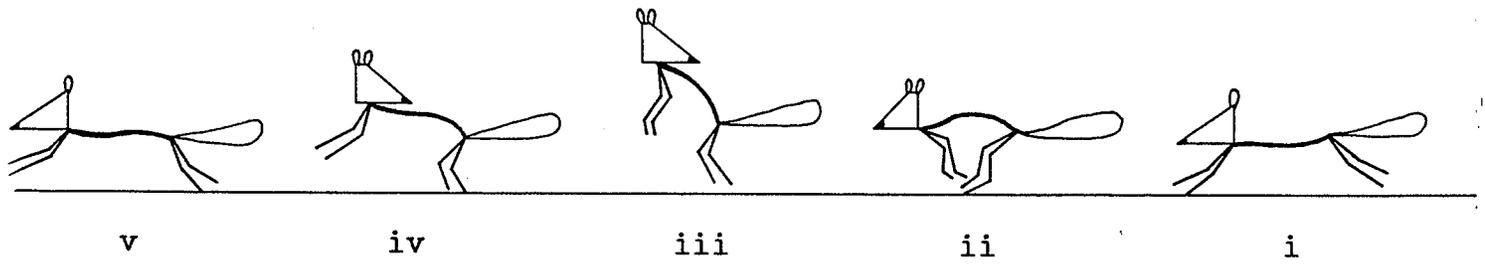
The foxes foraged with their noses held close to the ground but they scanned the area ahead of them constantly, and they often raised their heads momentarily to look around and to sniff the wind. Investigations ranged from a quick head turn and simultaneous sniff where the fox did not even break stride, though he may have slowed down slightly, to sudden stops where the fox investigated a spot for several seconds before he moved on. As he loped along, the fox sometimes wheeled suddenly and followed a seemingly airborne scent trail to a moss hummock a few steps upwind. In some cases, the source of the scent seemed more distant; the fox did not wheel so suddenly, and he stood for a moment with his nose upraised into the wind. In such cases, he sometimes took a step or two upwind with his nose upraised before he lowered his head again and continued on. When a fox captured a prey item, he usually cached it then left the vicinity as he continued to forage. In one incident in 1985, however, a fox caught and cached a lemming, then foraged for a short time around the capture sight and caught a few more lemmings before he moved off.

In willow patches or on wooded shorelines, the foxes walked or trotted as they weaved their way through the brush, and they narrowed their eyes, laid back their ears and led with their noses as they moved through thick tangles of branches. Foxes swam readily across narrows in lakes when the gap was too wide to jump across (about 3-4 m), and they did not hesitate to swim out to islands in lakes in order to forage there. The islands, however, were usually close to shore (about 5-15 m). The foxes shook their whole bodies upon exiting the water, and they seemed to dry out quickly as they continued to forage.

When foxes jumped across narrow gaps, eg. a narrow stream, the jump seemed to be little more than a horizontal pounce taken in stride. The front feet landed simultaneously and separate from the hind feet, which also landed together. As the gaps became wider, the foxes coiled on their haunches and the pounce graded into a

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leap where the hind feet landed sooner after the front feet. On extremely wide

gaps, the foxes hesitated, coiled on their haunches and even curved their backs in

preparation for the take-off. Before the take-off, the foxes often made one to

three false starts, as though they were trying to jump but that their feet were

stuck to the ground. The actual take-off, or uncoiling of the haunches and back,

occurred in an instant, and through most of the flight, the fox appeared to be in

landing position. The front feet landed first but were followed instantly by the

hind feet (Fig. 6). No matter how wide the gap, the foxes always landed within

about 15 cm of the water's edge.

As foxes crossed beach ridges in moving from one lowland area to another, they

typically kept their heads low as they started up one side of the ridge. However,

they soon raised their heads and they scanned the lowland ahead of them as they

crested the ridge. They lowered their heads again to forage as they neared the

bottom of the ridge and entered the new lowland.

During the course of a hunt, the foxes travelled in a loop that began and ended

at the den. The outward ie. foraging phase of the hunt made up most of the loop but

this phase could end at any time as the fox retrieved an old cache or retained a

fresh kill, then retrieved caches from previous hunts as he loped quickly and

steadily back to the den. During this inward phase, the fox typically collected

only cached items. On two occasions, however, the fox stopped, killed a lemming and

included it in the mouthful of lemmings he was carrying.

Within 100-300 m of the den, the foxes followed fairly specific routes that led

them, for example along a beach ridge or between two lakes. Beyond those radii, the

foxes entered lowland areas through which their paths were less specific but were

often similar. Figure 7 shows the initial paths that foxes followed from their

dens in 1985, and the lowland areas to which they led. The fox from den B was not

25

Figure 6. Two ways that arctic foxes jump across gaps. A) a jump across a narrow gap is similar to a pounce. B) a jump across a wide gap is similar to a leap. See text for full descriptions.

A

B
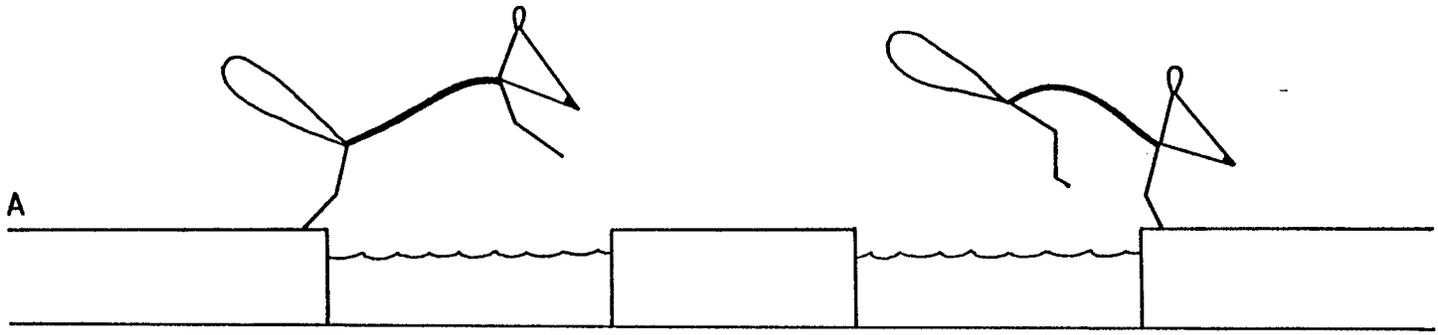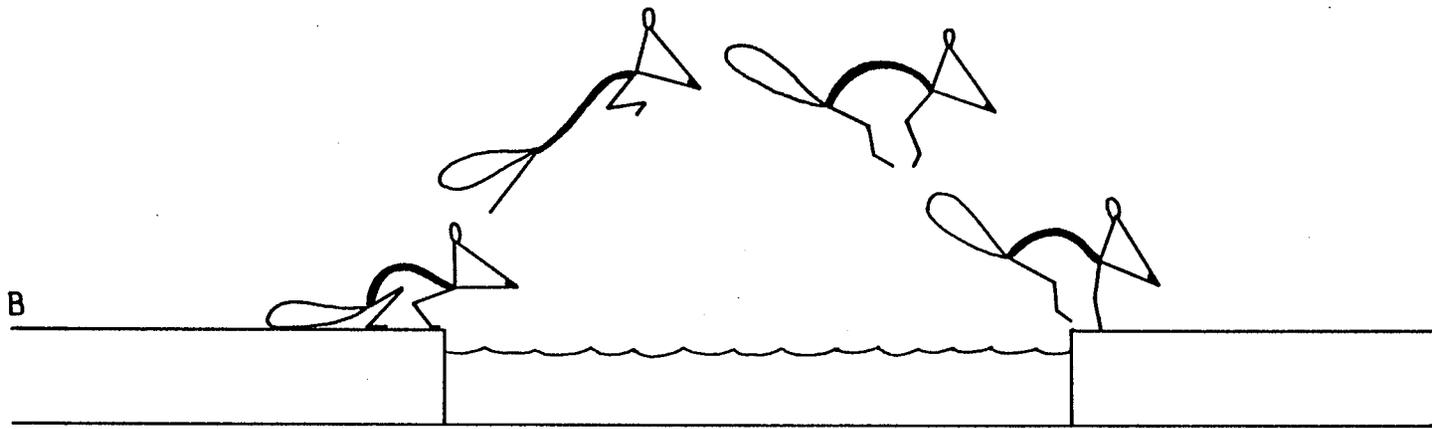
Figure 7. Lowland areas where foxes hunted in 1985. The fox from den A hunted in lowlands #1-5 while the fox from den B hunted in lowlands #1-3. The broken arrow leading from den B to lowland #6 indicates that the fox from den B probably hunted in that lowland area.

BASKETT
BAY

HUDSON
BAY

BEAR
BAY

● FOX DEN

BEACH RIDGE

LAKE

0   1   2
KILOMETERS
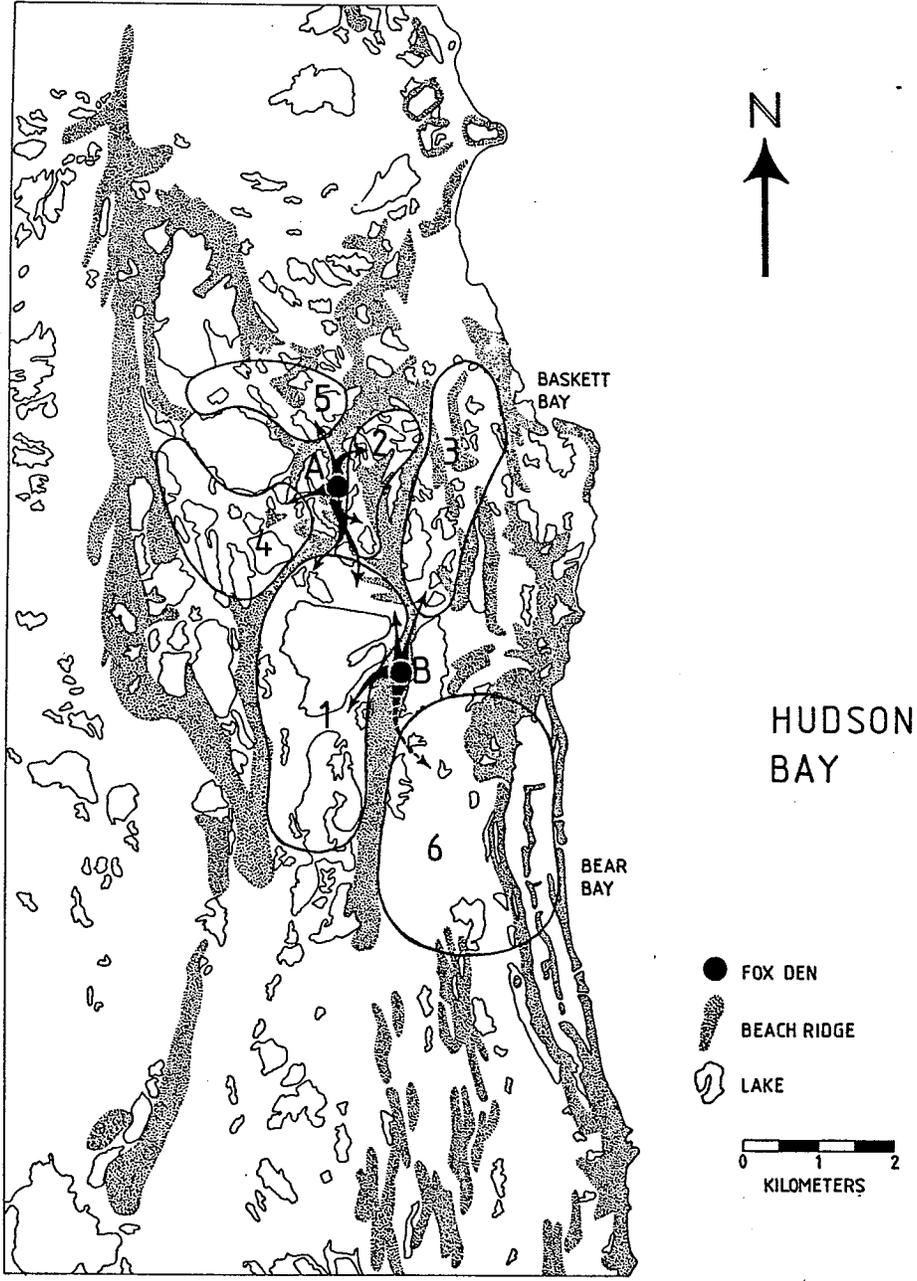
observed in area number six but fox tracks along the beach ridge led to that area from the den. Hunting routes were mapped in 1986 and Figures 8 and 9 show the actual ground that foxes covered during hunts in that year. Though only 16 hunts were observed for both foxes, the variability in the observed routes lead me to suspect that the lowland areas were explored more extensively than the blackened areas in Figures 8 and 9 would indicate.

Lowland areas were more or less delineated by beach ridges. During a hunt, a fox may stay within one lowland area or he may pass through several such areas by crossing over beach ridges. The foxes need not explore one area entirely before moving to another. Foxes may go on several hunts per day, but on consecutive hunts they typically loop through a part of their home range other than the part they had just traversed. The total distance covered during a day of hunting was not determined, but a fox covered an estimated 25-30 km during 5.67 hours of hunting on one day in 1985.

Habitat Use

Morse (1980) reviewed the principles of habitat selection. There is little doubt that animals actively select habitats, but the bases for selection remain open questions. An animal's preferences for certain habitats appear to have an innate component but these preferences are subject to modification through learning, and the relative importance of these factors is unknown. "Evidence...suggests that innate factors may sometimes provide the coarse tuning and learned factors the fine tuning for habitat selection" (Morse 1980).

According to Morse (1980), selection is often assumed to employ cues that can be ascertained quickly. However, little is known about the cues themselves; their properties, the number of cues employed and the ways they are combined to reach a

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Figure 8. The actual ground covered by the fox from den A during hunts in 1986.

The areas enclosed by the dotted lines are suspected hunting areas.

Refer to Figure 1 for the location of den A.

N

BASKETT
BAY

HUDSON
BAY

BEAR
BAY

BEACH RIDGE

LAKE

0   1   2
KILOMETERS
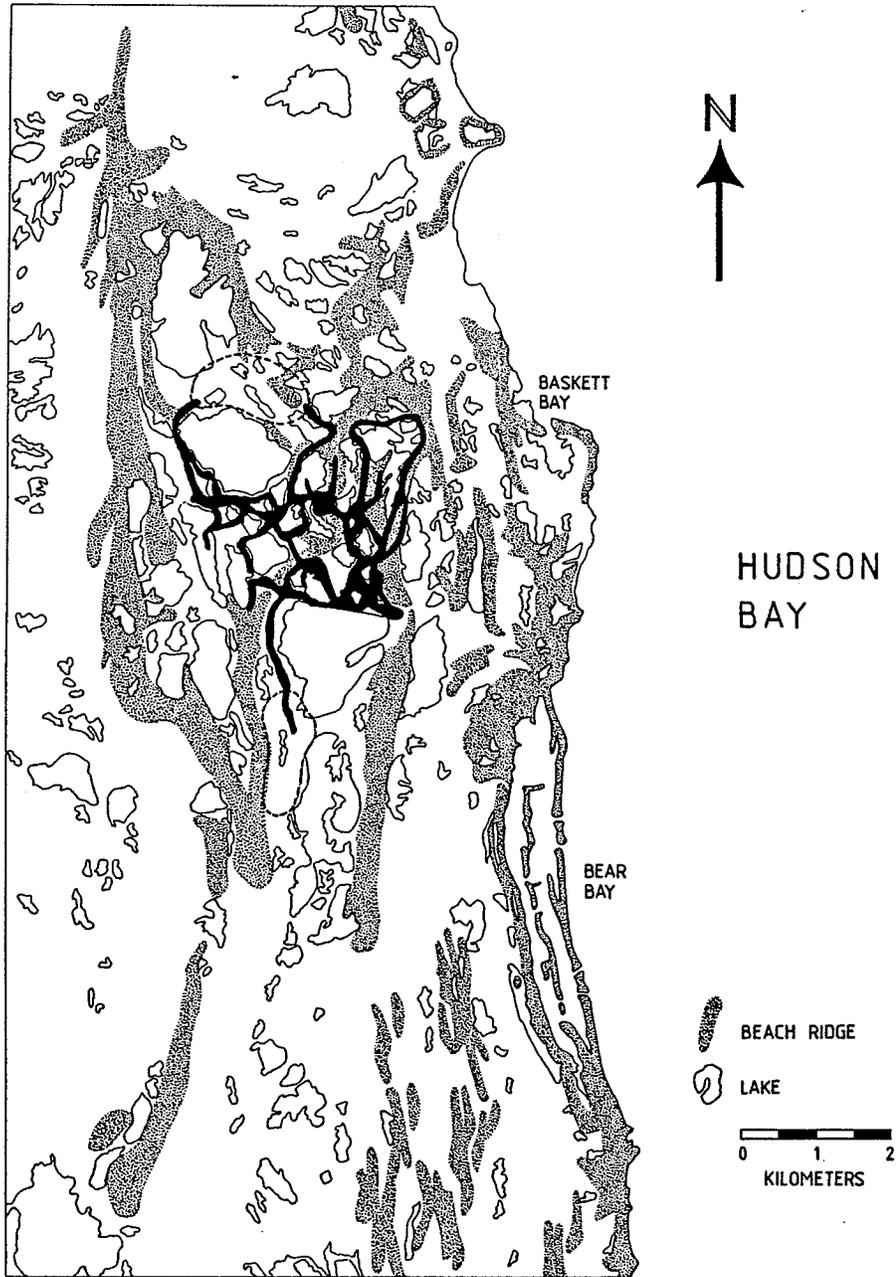
Figure 9. The actual ground covered by the fox from den C during hunts in 1986.

The areas enclosed by the dotted lines are suspected hunting areas.

Refer to Figure 1 for the location of den C.

N

BASKETT
BAY

HUDSON
BAY

BEAR
BAY

BEACH RIDGE

LAKE

0   1   2
    KILOMETERS
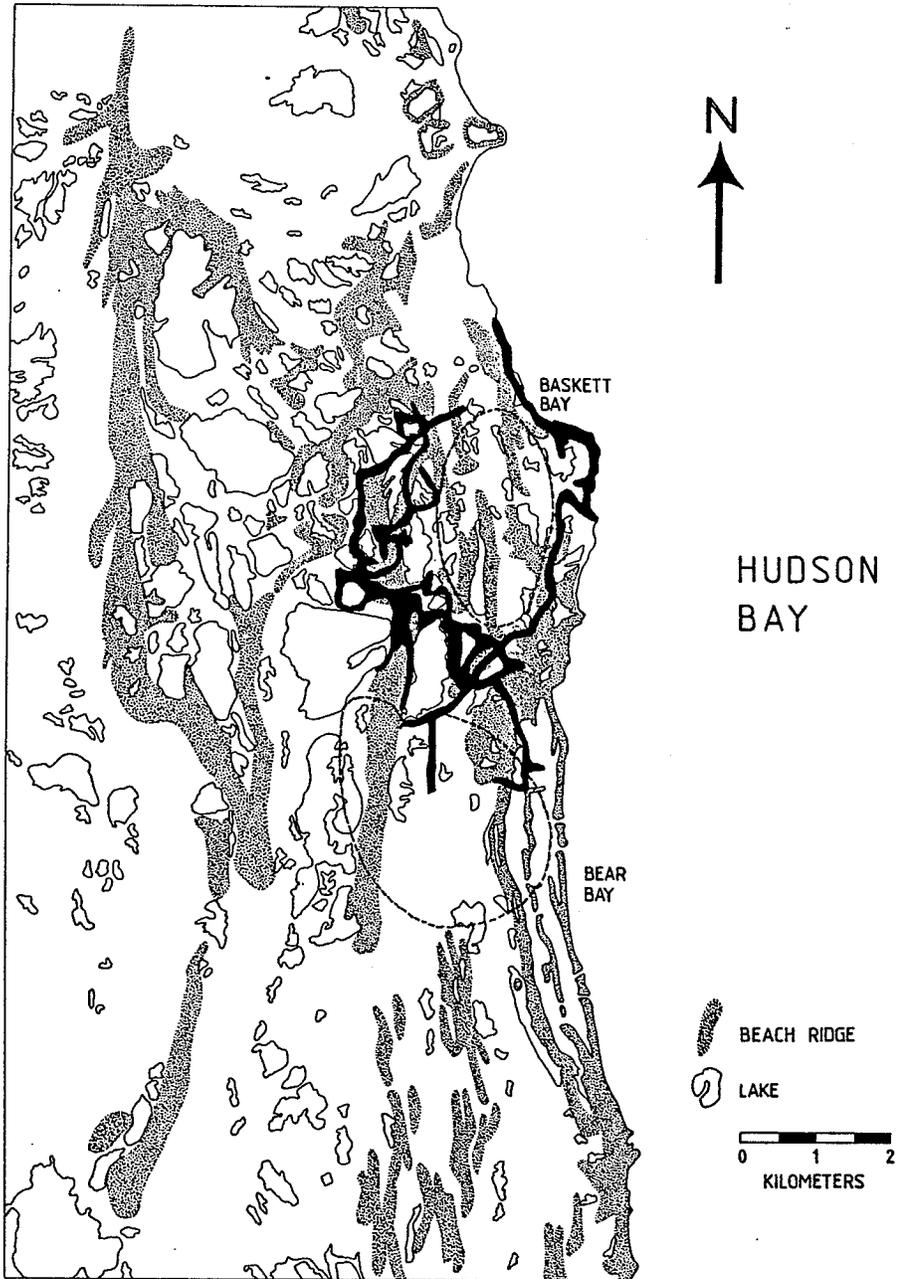
selection decision. In some cases, the food supply may be the most important factor in the selection process. If food supplies fluctuate, however, then animals may be unable to respond to food alone, and other factors then become important, eg. the vegetation cover and its effects on an animal's ability to move about and to forage. In the end, the habitat chosen may not be ideal, but it provides a balance of factors. "In a broad sense the selective basis for habitat selection is apparent; it will result in improved reproductive success" (Morse 1980).

Burgess (1984) found that arctic foxes used some habitats in greater or lesser proportions than would be expected from the availability of those habitats. Speller (1972) saw arctic foxes hunt along routes that passed through or led to productive hunting grounds. Foxes in some coastal areas seemed to limit their foraging to productive beach areas (West and Rudd 1983). These findings indicate that arctic foxes sometimes select habitats rather than just move about at random.

Three habitats were delineated in the present study area: beach ridge, peat lowland and lakeshore. Table 3 shows the foxes' habitat use in 1986, and the proportion of captures in each habitat in both years. The foxes' patterns of movement were essentially the same in both years of this study, so the 1986 values for habitat use in Table 3 provide a reasonable estimate of the foxes' habitat use in 1985.

a) the Peat Lowlands

The peat lowlands contained a variety of plant communities that ranged from sedge marsh in areas of standing water, to heath-sedge-hummock in more mesic locations with a peat substrate. Speller (1972) describes several lowland plant communities while Johnson (1987) lists the plant species common to peat lowlands in the Churchill region. All available prey types in the lowlands were generally associated with peat hummocks or other features of microrelief. Lemmings burrowed

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Table 3. The proportion of the total distance covered by arctic foxes in three habitats near Cape Churchill in 1986, and the proportion of the total number of kills in each habitat during hunts in 1985 and 1986.

| | Proportion of total distance covered (1986) | Proportion of total #kills | |
		1985	1986
Beach Ridge	22%	1%	—
Peat Lowland	71%	96%	80%
Shoreline	7%	3%	20%

into hummocks while several types of birds nested on top of hummocks. A partial list of avian prey species in the lowlands includes: dunlin (Calidris alpina), semipalmated sandpiper (Calidris pusilla), least sandpiper (Calidris minutilla), northern phalarope (Lobipes lobatus), lapland longspur (Calcarius lapponicus), Canada goose (Branta canadensis) and willow ptarmigan (Lagopus lagopus).

Foxes foraged in almost all parts of the lowland areas but they appeared to favour areas of moss hummocks. Willow patches were investigated when they were encountered but foxes sometimes passed by willow patches along their paths. Foxes did not forage in sedge marshes but they passed through patches of this habitat on occasion.

Foxes caught all prey types except duck eggs in the lowlands. The proportion of captures in the lowlands was greater in 1985 than in 1986 due to the abundance of lemmings in the former year. In 1985, lemmings were the most frequently caught prey item, and all lemmings but one were caught in the lowlands.

b) Shorelines

A variety of shoreline types existed in the study area. They ranged from those that were level with the adjacent peat vegetation and were devoid of willows, to those that were well over one meter high and had a dense willow cover. The former were simply places where the peat layer of the lowlands ended abruptly, while the latter were the peat pressure ridges.

Lemmings dug burrows in peat pressure ridges, especially amongst the roots of willows. Oldsquaws (Clangula hyemalis) sometimes nested on elevated shorelines. Common eiders (Somateria mollissima) nested almost exclusively on islands in lakes, but one eider nest was found on a lakeshore. Canada geese nested on shorelines but that was not a preferred habitat for them because snow retention in willows and ice on lakes in spring create cold microclimates that are unfavourable for early nesting

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(D. Rusch pers. comm.). I suspect that some species of shorebirds nested on some shorelines, but the foxes did not find any shorebird nests in that habitat. However, some shorebird nests were found on moss hummocks adjacent to a lakeshore.

The foxes' use of shorelines ranged from brief investigations or quick attacks on a single prey item, to more prolonged investigations where the fox either investigated a limited section of shoreline more intensively or foraged for a longer distance along the lakeshore. The foxes rarely foraged on shorelines devoid of willows. If they did so, then it was for brief investigations only. One notable exception occurred in 1985, where a fox foraged extensively along a shoreline that was so extremely convoluted and dissected, with many slender peninsulas and small islands close to shore, that the fox could forage on one convolution, peninsula or island, then leap to the next and continue on. For the most part, however, foxes foraged on brush-covered shorelines. Foxes captured duck eggs, goose eggs and goslings in this habitat.

c) Beach Ridges

The vegetation on beach ridges was generally a lichen-heath plant community at the summits and a heath-sedge community on the sides of the ridges. Many ridges had a large proportion of bare ground, ie. sand or gravel, at the summit with patches of Dryas integrifolia dispersed at various densities. Lemmings dug burrows in beach ridges, especially under rocks or patches of Dryas. Oldsquaws, lesser golden plovers (Pluvialis dominica), stilt sandpipers (Micropalama himantopus) and horned larks (Eremophila alpestris) nested in the vegetation on beach ridges (D. Rusch pers. comm.).

Beach ridges were not hunting grounds. They were used only for direct travel when the fox left or returned to the den, or when he moved from one lowland area to another.

In the two summers of this study, only one lemming was captured and one passerine nest was preyed on in this habitat. The lemming was detected as the fox was returning to the den with food. The fox stopped, dug the lemming from its burrow and brought it to the den along with the food he was already carrying. The passerine nest was in the vegetation on the side of a ridge. The fox encountered the nest fortuitously as he crossed the beach ridge on his way to a lowland on the other side.

Data from the goose research in the study area (D. Rusch pers. comm.) show that most geese nest in the lowlands, while the small mammal trapping plot and observations of lemming burrows indicated that most lemmings also lived in that habitat. The densities of ducks, passerines and shorebirds in their respective habitats were unknown. Altogether though, I suspect that the majority of prey lived in lowland areas.

Speller (1972) saw that arctic foxes spent the most of their hunting time in moist hummocky habitats, and that drier habitats, ie. lichen-heath and heath-sedge, and lakeshores were not used extensively. Lemming (Dicrostonyx groenlandicus) burrows in drier habitats were typically long, twisted and dug deep into the substrate. Foxes did not attempt to dig lemmings out of such burrows probably because "the digging would be long and tedious and easier rewards are gained from digging out the soft peaty burrows" of lemmings in moist hummocky areas (Speller 1972). This suggestion was borne out by observations in the present study. The one lemming caught on a beach ridge required the fox to dig a hole up to his flanks, whereas burrows in moss hummocks rarely required the fox to dig deeper than his own head.

Speller (1972) observed that foxes foraged along vegetated shorelines for the nests of ducks, geese, shorebirds and loons, but that foxes did not use that

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habitat extensively. With the profusion of lakes and ponds in the present study area, the shorelines seemed to be underutilized with regard to the distance covered in that habitat. Foxes typically used a circling attack when they attempted to capture goose eggs (see Capture Attempts for Geese). However, this method could not be used when the goose nest was on a shoreline or peninsula, and geese nesting there seemed able to defend their nests more easily. Where lemmings were found on lakeshores, I suspect that their burrows amongst the willow roots would be difficult to excavate.

Hersteinsson (1984) hypothesized that an arctic fox's movements were determined mainly by resource availability. "Availability" implies both the amount of prey present and the facility with which it can be captured. Avian prey seemed scarce on beach ridges, and lemmings in that habitat would require a prolonged and labourious effort to dig from their burrows. Prey also seemed scarce on unwooded shorelines, and goose eggs there seemed more difficult to capture. Thick willows may have discouraged extensive foraging on shorelines where they were present. In lowland areas, prey was plentiful, foxes could forage unimpeded and lemmings and goose eggs there were probably easier to capture. I suspect that these were the reasons why foxes hunted mainly in the lowlands.

Home Ranges

During the denning season, most arctic foxes occupy well-defined home ranges (Garrott and Eberhardt 1987), the size and shape of which depend on their location and on the abundance and dispersion of food (Skrobov 1958, Bannikov 1969). Arctic fox home ranges in the U.S.S.R. vary in size from 2 sq.km in the Bolshezemelska and Malozemelska tundras, to as large as 30 sq.km in the delta of Lena River (Skrobov in Bannikov 1969). Several other studies in Iceland, Greenland, Canada and Alaska have

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reported home range sizes within these extremes for both tundra and coastal habitats (Longstaff 1932, Speller 1972, Eberhardt et al 1982, Hersteinsson 1984, Burgess 1984). In Iceland, neighbouring home ranges varied widely is size, but they contained almost constant amounts of key foraging habitats (Hersteinsson and MacDonald 1982).

Neighbouring home ranges may overlap widely (Hersteinsson 1984). Within home ranges, territories exist "which are commonly used by members of the family group but are defended from other conspecifics" (Garrott and Eberhardt 1987). Such territories are believed to be maintained mainly through vocalizations and scent markings, but foxes occasionally engage in agonistic chases near territorial borders (Speller 1972, Eberhardt et al 1982, Hersteinsson and MacDonald 1982, Burgess 1984, Garrott and Eberhardt 1987).

Figures 10 and 11, and Table 4 detail the home ranges of two neighbouring foxes on Cape Churchill during the present study. The size of the home ranges were determined by connecting the outermost points of observation. This method was analogous to Hayne's (1950) minimum area method. Riewe (1971) notes that the minimum area method provides "an unrealistic view of the area actually utilized" because "there may be extensive areas which are never visited". However, this technique is widely used (Riewe 1971) therefore it was used here to allow for comparisons to other studies. Since the home range data were based on a fairly small number of observed hunts, no conclusions can be drawn concerning home range size or the amount of overlap, and the values in Table 4 are probably minimums.

Interactions between neighbouring foxes occurred in overlap areas and involved both vocalizations and agonistic chases. Vocalizations consisted of an exchange of staccato barks. When one fox heard another's bark, he typically replied in the same manner as he moved to the top of a hill or ridge. From that prominent position, he

Figure 10. The home ranges of two arctic foxes studied near Cape Churchill in 1985. The solid line delineates the observed home range of the fox from den A, while the dotted line delineates the observed home range of the fox from den B.

N

BASKETT
BAY

A

HUDSON
BAY

B

BEAR
BAY

● FOX DEN

BEACH RIDGE

LAKE

0   1   2
KILOMETERS
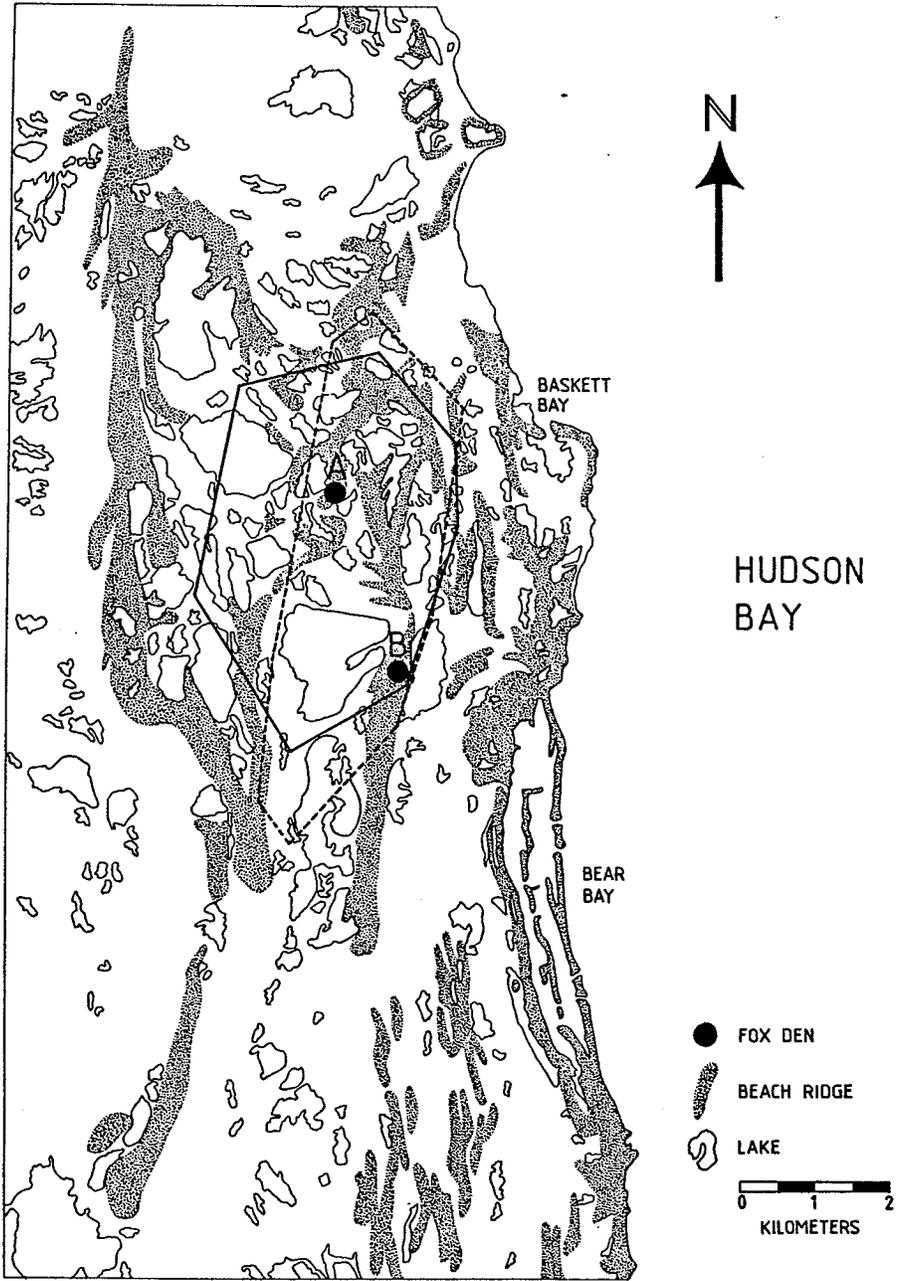
Figure 11. The home ranges of two arctic foxes studied near Cape Churchill in 1986. The solid line delineates the observed home range of the fox from den A, while the dotted line delineates the observed home range of the fox from den C.

N

BASKETT
BAY

A

HUDSON
BAY

C

BEAR
BAY

● FOX DEN

⬮ BEACH RIDGE

◌ LAKE

0   1   2
KILOMETERS
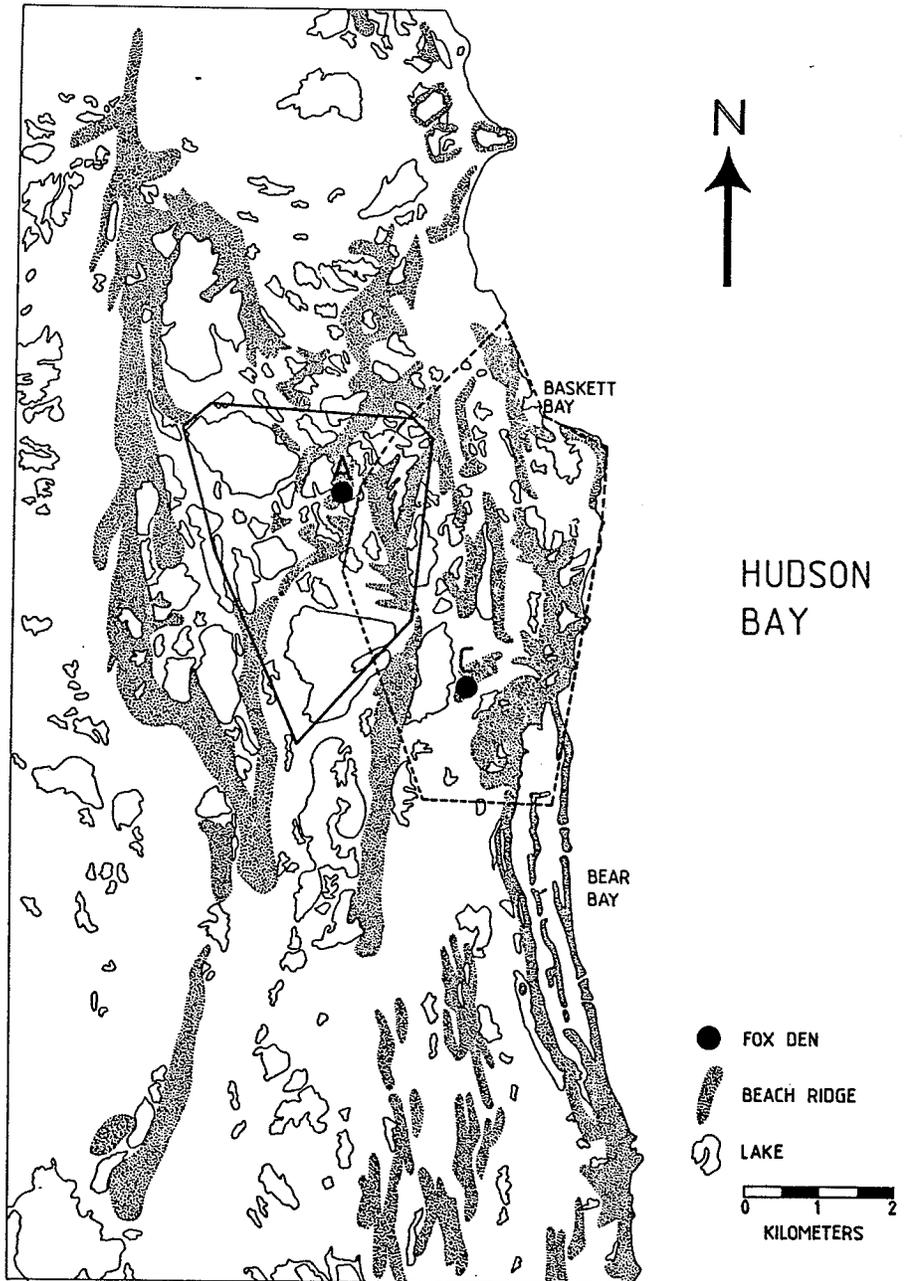
Table 4. The sizes and the amount of overlap for the home ranges of two

neighbouring arctic foxes on Cape Churchill in 1985 and 1986. Refer to Figures 10

and 11 for the locations of the dens listed.

Den	1985		1986	
	size	overlap	size	overlap
A	13 sq.km	65%	10.5 sq.km	21%
B	11 sq.km	77%	——	
C	——		15 sq.km	15%

sat and looked toward the other fox in the distance while the two foxes alternated barks. As the exchange came to an end, the fox would leave his high point and continue to forage, sometimes barking back over his shoulder while he descended the hill. In other cases, the fox continued to forage during the exchange, and he simply raised his head and barked in the direction of the other fox as he loped along. The foxes may have barked to announce their presence (Fine 1980) or to test whether or not another fox was in the overlap area (Hersteinsson 1984). In any case, these encounters seemed to result in mutual avoidance.

During agonistic chases, "the roles of the foxes...were unquestioned in all instances, and no fighting was observed" (Burgess 1984). The resident fox would run directly at the interloper and the interloper would run away. Chases can last from a few seconds to several minutes; the duration of the encounter may be determined by the interloper's actions during the chase (Burgess 1984).

Three agonistic chases were observed during the present study. In the simplest case, a resident fox sighted a neighbour about 200 m away and charged immediately. The neighbour ran away immediately upon sighting the charging resident. The chase extended for more than 200 m and was still on when I lost sight of the foxes. In another case, the male had returned to the den with food and was leaving when he saw the female running toward him from the direction in which he was heading. The male turned around abruptly and galloped in the opposite direction for about 400 m then sat down to watch the female. The female stopped her charge as she neared the den and she did not come within 100 m of the male. Both foxes loped away in different directions eventually. The female may have mistaken the male for a neighbour. However, I do not know why the male fox could be driven from his own den.

The third encounter was the most complex. A female fox encountered a neighbour, probably a male, about 350 m from her den. The neighbour chased the female toward

the den for about 20 m then stopped, whereupon the female stopped also, about 25 m from him. The neighbour stood broadside, facing the female, and gaping, with his head slightly lowered and his back and tail arched (Fig. 12). He then looked straight ahead, walked a few steps with his legs extended stiffly then stopped again to face the female. The female assumed the same posture, and the two foxes alternated the walk/stop sequence a few times. The foxes' paths were parallel and were across the path of the initial chase. After the foxes ended their display, the female shrieked at the neighbour then returned to the den, while the neighbour fox left in the direction from which he came. The female's shriek was a unique vocalization. With consideration to the female's behaviour during the encounter, I suspect that the shriek was a defensive/aggressive vocalization. On a subjective evaluation, it seemed to carry an undertone of distress. I do not know why the female could be chased so close to her own den. Mated pairs cooperate in establishing breeding territories (Fine 1980) but territories seem to be defended primarily by male foxes (Speller 1972). Since the encounter occurred in early June and the female had done little if any hunting to that point, the neighbour may have viewed her as a newcomer or transient. Perhaps also, rival males and females have a different relationship than do rival males. These conjectures aside, the last two encounters suggest that in some interactions, there may be subtleties beyond a strict rule of "resident ousts interloper".

Arctic foxes hunted over their entire home ranges both before and after goose hatch, and they did not appear to favour any particular region - for example, the northwestern corner of the home range. These observations refer to general areas but do not apply to specific habitats. The potential for the fox from den C to favour the eastern part of his home range occurred after hatch, when huge flocks of snow geese with goslings could be found predictably along or near the coast of

The Figure 12. The arched-back posture observed during an interaction between two neighbouring arctic foxes. A) the resident fox stands broadside and faces the interloper. B) the posture while the two foxes walk parallel to each other (see text). The arched-back and tail are reminiscent of the foxes' defaecation posture.

A
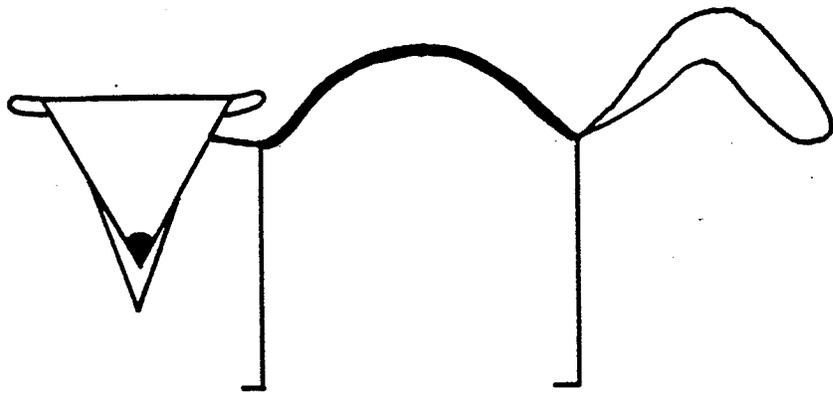
B
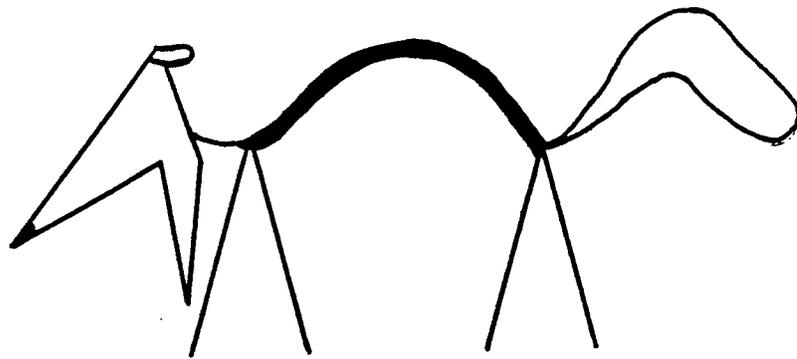
Hudson Bay, especially in saline meadow gosling-rearing areas. This fox travelled directly to large flocks of snow geese that he had sighted from his den but he was not observed to travel directly to the gosling-rearing areas, which could not be seen from the den. Foxes hunted "as they travelled...to places where they might expect successful hunting" (Speller 1972). As such, though the fox from den C hunted in all regions of his home range after hatch, I suspect that he hunted along routes that sooner or later included gosling-rearing areas.

After hatch, the whereabouts of geese seemed less predictable within the home range of the fox from den A. This fox foraged in all regions of his home range and he simply attacked geese as he encountered them. Snow geese seemed to frequent lowland areas to the west-northwest and to the north of his home range. Since this fox most often came from the north when he returned to the den with goslings, it may be that geese could be found reliably in the west-northwestern and northern parts of his home range. However, it is possible that his home range was larger than I observed it to be, and that it included those lowland areas in both 1985 and 1986.

The home range for the fox from den B was observed only before hatch. Though I did not see the fox hunt in lowland number 6 (Fig. 7), fox tracks along the beach ridge south of the den led to that area, and the male or female foxes from that den often brought a gosling when they returned to the den along that path after hatch. Therefore, I suspect that the home range of the fox from den B was larger than I observed it to be, and in particular, that it extended farther to the east than is indicated in Figure 10.

Capture Attempts for Lemmings

Speller (1972) describes several techniques that foxes use to capture lemmings. Stalking, lunging and dashing probably employed sight detection and predominated in

drier habitats and willow patches where the excavation of burrows was difficult and/or time consuming. They were important when lemmings were often exposed - during spring thaw when flooding of low-lying areas forced lemmings to higher ground, and as a cohort of young lemmings left their natal nests to seek or to dig their own burrows. Digging predominated in the moist hummocky habitats where foxes located lemmings in their nests by scent or by sound. Pounces and leaps were used to trap exposed lemmings, to break into the snow burrows of lemmings in spring and to collapse the entrances of burrows in hummocks during the summer (Speller 1972).

In this study, foxes captured all lemmings but one by digging them from their burrows. The exception occurred in early June of 1985 when a fox pounced on a lemming along the edge of a snow patch in a peat lowland.

Foxes found lemmings mainly by sniffing the entrances of lemming burrows. On occasion the fox seemed to follow a twisting and turning scent trail that led to a burrow entrance. Sometimes as the fox followed such a trail around a hummock, he tensed suddenly and tracked something visually for a moment then leaped to a burrow entrance and landed digging. The fox's behaviour suggested that as he rounded the hummock he suddenly saw a lemming outside its burrow. The moment of tensing and the direction and movement of the fox's gaze indicated that the lemming was probably within 40 cm of its burrow and that it just made it inside the burrow as the fox landed at the entrance.

If the fox detected a lemming inside a burrow he would dig into the burrow furiously and would often use his jaws to tear out and toss aside large chunks of moss from the hummock. The fox dug straight into the burrow with his nose at the entrance. His hind quarters sometimes drifted from side to side as he dug at the sides of the burrow to enlarge its diameter. The fox stopped digging periodically to jam his head into the burrow in an attempt to grasp the lemming.

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On prolonged capture attempts, the fox stopped digging occasionally to look around. When the fox stopped or slowed his digging at a one-entranced burrow, the lemming sometimes took that opportunity to escape from the burrow. The fox often caught the lemming immediately, but if the fox's attention was elsewhere then the lemming could run for about 15 cm to 30 cm before the fox reacted and made the kill. On a few occasions when the fox was looking around, the lemming ran between the fox's front legs. The fox seemed startled momentarily as the lemming ran about beneath him, but in such cases, the fox caught the lemming quickly.

As a fox dug into a burrow in a large multi-entranced hummock, he often stopped suddenly to listen with his head upraised and his ears cocked forward. While doing so he cocked his head from side to side as if to listen first with one ear then with the other. As the fox tracked the sound of the lemming inside the hummock he directed his gaze as if he could actually see the lemming. As the lemming approached an alternate entrance the fox leaped there, whereupon the lemming apparently ran back into the depths of the hummock. The fox sometimes dug at that entrance but he most often leaped back to the original one and continued to dig there until the lemming again moved to an entrance. Sometimes the lemming escaped from the hummock by way of an alternate entrance but in all cases, the fox heard it do so and caught the lemming with a short dash or a lunge before it could run one meter.

Foxes killed lemmings with two to four quick bites. The foxes' head motion suggested that the initial bites were to position the lemming for a final killing bite. After the kill, the fox always dropped the lemming for a few seconds, sometimes shook his whole body, then either cached the lemming, ate it or brought it to the den. Riewe (1971) noted that when rodent populations were large, red foxes sometimes skinned and eviscerated Microtus carcasses before eating them. In the

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present study, any lemmings eaten were consumed completly. On one occasion in 1985, however, a fox removed the stomach from a lemming and placed it to one side before he ate the lemming. The stomach was not eaten.

The fox was successful in 88% (n = 120) of capture attempts on lemmings in 1985 and in 57% (n = 7) of capture attempts in 1986. In all cases but one, the fox failed to dig lemmings out of large moss hummocks with more than one burrow entrance. In such instances, the attempt proceeded as usual but there came a point where the fox stopped digging, looked the hummock over then ended the attempt. The cues to end the attempt were unknown but they may have involved the depth and complexity of the burrows. It may have been that the lemming could not be trapped anywhere inside the burrow ie. it could always move out of the fox's reach, but it would not leave the hummock. I am less inclined to believe that fatigue was a factor in the failed capture attempts since the foxes successfully concluded several long and apparently labourious attacks. The exceptional instance of failure mentioned above occurred in 1985, when a fox ended a digging attempt for a lemming after he was harassed by a snowy owl (see Appendix 1).

In 1985, 62% of the lemmings caught were cached, 25% were eaten immediately and 12% were brought directly to the den (n = 106). Of the four lemmings caught in 1986, two were cached, one was eaten and one was brought to the den.

The methods that foxes used to detect lemmings in burrows merit further discussion. On several occasions, the fox sniffed a lemming burrow, began to dig at a relatively moderate pace, then tensed suddenly and dug furiously until he caught the lemming. The forward position of the fox's ears and the intensity of his gaze into the burrow when he tensed suggested that he had seen or heard the lemming. On a few other occasions when a fox investigated a large hummock, he started to dig for a moment at a moderate pace but then stopped and looked the hummock over. He

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started to dig again briefly but stopped again, examined the hummock and finally ended the attempt.

I suspect that if the scent of lemming is strong in a burrow then the scent alone is enough to indicate that a lemming in present, so the fox will dig. However, when the lemming scent may not be strong, the fox listens for activity inside the burrow to confirm the presence of a lemming, especially in large hummocks. Since lemmings will move about inside the burrow as the fox digs, the initial moderate digging may induce activity inside the burrow. Depending on the presence or absence of activity, the fox either continues or ends the attempt.

Capture Attempts for Geese

Table 5 shows the basic data for the foxes' attacks on goose nests in 1985 and 1986. Three of the 33 nests were undefended, ie. the geese were not present. In these instances the fox took and cached all the eggs one at a time. When all the eggs were gone, the fox sometimes defaecated in the empty nest before he continued to forage. During the incubation period, Canada geese leave their nests to feed for short periods of time in the morning and evening (Gillespie 1984). This was probably the case for two of the undefended nests. In the third case, the goose flushed from the nest when the fox was still about 100 m away, and she did not return while the fox emptied the nest.

During the incubation period, the female Canada goose (the goose) incubates the eggs while the male (the gander) stays close by, defends the territory and warns the goose of impending danger (Gillespie 1984). Canada geese on nests conceal themselves by lying flat with their necks extended and their heads on the ground. The foxes' behaviour while they foraged suggested that they first became aware of goose nests by scent if the goose remained concealed. In such cases, the fox seemed

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Table 5. A summary of the basic data for fox attacks on Canada goose nests near
Cape Churchill in 1985 and 1986.

	1985	1986	Total
Number of nests attacked	22	11	33
Number of nests defended by geese	20	10	30
Number of nests undefended*	2	1	3
Number of attacks on defended nests	24	15	39
Attack success rate on defended nests	62.5%	67%	64%
Average number of eggs taken per attack**	0.62	0.67	0.64
Average number of eggs taken per defended nest**	0.75	1	0.83

* the geese were not present. In 1985, the fox took three
  eggs from one undefended nest and six eggs from another.
  In 1986, the fox took four eggs from an undefended nest.

** these figures do not include undefended nests or one nest
   in 1985 where the fox killed the goose and took two eggs
   and three goslings.

to follow the scent to the nest, but he scanned the area ahead of himself until he saw the nest. If the goose moved or vocalized then the fox would notice the disturbance and lope directly to the nest.

During attacks on defended goose nests, foxes usually circled the goose on the nest rapidly, nipped at the goose's wing tips and lunged at her in an attempt to drive her from the nest. The fox circled at a fast lope to moderate gallop, and he stayed within two meters of the nest. In defense, the goose stood up with her wings outstretched and her head held high. She turned to face the fox at all times and she struck at him with her wings. When the fox could not use the circling attack, eg. if the nest was on a narrow peninsula, then he would approach the goose directly. As the goose stood up, on two occasions, the fox simply lunged forward, pushed the goose off the nest with his jaws and took an egg before the goose could recover her balance and retaliate. In most such instances, however, the goose stood up when the fox was still about one to two meters away. The fox sometimes hesitated or gaped, but if he lunged, then the goose would strike him with her wings. The fox would then back off slightly and perhaps side-to-side-fake but the goose was in a strong defensive position and the fox would soon end the attempt.

Geese usually vocalized as they defended their nests. The gander almost always returned to the nest to aid in the defense but he did not always do so immediately. On some occasions he did not return at all, and the goose was left to defend the nest on her own.

A few geese seemed very skilled at defending their nests solo. Their reflexes, turns and strikes were fast and precise. They did not falter when the fox lunged and they did not leave the nest. In such cases, the attack ended when the fox finally stopped or slowed his circling. Sometimes he stood back, looked at the goose then looked around as though he were trying to decide what he should do next.

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After a few seconds he loped away and continued to forage. In one instance the fox darted to the nest and defaecated in front of the goose before he left.

Some geese seemed less skilled in their defense. Their reflexes seemed less fast and the fox was sometimes able to run part way behind the goose's wings (Fig. 13) or to lunge a little closer before the goose struck at him. These geese were able to fend off the fox initially, but as the fox intensified his attack by circling faster and lunging and nipping more often, the goose's efforts proved inadequate and she was soon driven from the nest. In one case, the fox intensified his attack until finally, he lunged forward and pulled some feathers from the goose's breast with his jaws. The goose faltered and vocalized as though she were completely unnerved, then she fled from the nest. The fox hesitated for an instant as he watched the goose leave, then he pursued her and bit her on the hip. As the goose struggled to break free, the fox lunged over her back, bit her on the neck then head shook until she ceased to move. The fox bit off the goose's head and cached it, removed two eggs and three newly hatched goslings from the nest and cached them, then ate the goose's right breast, left the goose where it lay and continued to forage. The three goslings underfoot probably inhibited this goose's mobility and contributed to the failure of her defense. Though the killing of the goose on the nest does not seem to be the norm, the fresh remains of one other goose found during the incubation period, and the near capture of a gander during an attempt on a nest suggest that this incident of predation on an adult goose during incubation was not unique.

Geese may leave the nest to charge the fox during an attack. In such cases, the fox retreated typically along a curving or a hooking path until the goose was several meters away from the nest, then he darted to the nest and took an egg before the goose could fend him off. If the goose stayed close to the nest after her

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Figure 13. A fox attack on a Canada goose nest as would be seen from directly above the goose. The fox circles rapidly, and the goose rotates to remain facing the fox at all times. Some geese turned fast enough to keep the fox in front of themselves, ie. in region A. With other geese, the fox could sometimes run part way into region B before the goose could rotate.

A

B   B
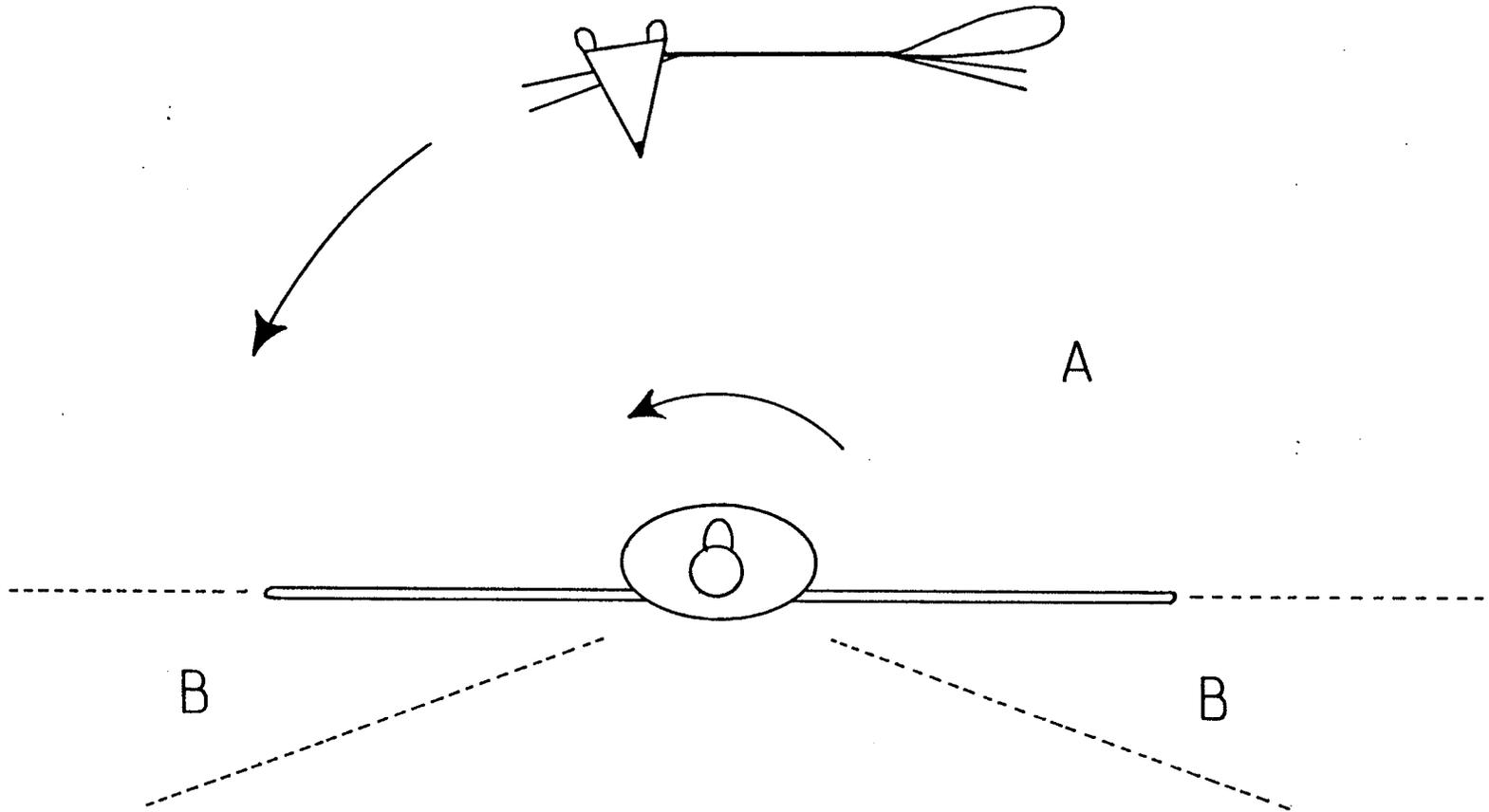
charge then the fox tried to work his way around her. However, his movements often suggested that he was trying to draw her away from the nest before he made his dash for an egg.

When the gander arrived at the nest during an attack, he became the chief defender while the goose stayed close to the nest. On several occasions, the fox ended the attack upon or soon after the gander's arrival. In most cases however, the fox pressed the attack and tried to outmaneuver both birds, though almost all of his trouble was with the gander.

During the attack, the gander typically charged the fox repeatedly as the fox tried to maneuver around the birds. The fox retreated at each charge but if the gander was right behind him then he sometimes end-swapped and gaped at the gander simultaneously. This seemed to startle or at least to slow down the gander momentarily and the fox was able to put a little more distance between himself and the bird. If the fox could not capture an egg even after a prolonged and intense effort then sometimes he simply stopped his maneuvering, looked the geese over, then continued to forage. Such failures, however, were usually associated with a final charge from the gander where the fox simply continued his retreat after the gander stopped. When he was so routed, the fox often glanced back at the geese as he loped away. On one occasion however, the fox charged straight up to the gander and defaecated in front of the bird before he left.

In two cases where foxes defaecated in front of geese, they did not squat in the usual manner. Rather, they turned around and simply lifted their tails as though they meant to defaecate at the bird instead of merely in front of it. It is tempting to anthropomorphize about the significance of such defaecations. However, other instances where foxes thoroughly investigated objects then defaecated, eg. beside a box of electronics from a weather balloon, on top of a white plastic

container in the camp outhouse, on the lawn chair from which I observed den B, suggest that such defaecations do hold some meaning. Defaecations may be directed at unusual objects, and faeces may act as signals for other foxes (Kleiman 1966).

Though the gander was usually an effective defender of the nest, such was not always the case. In one instance, the fox darted past the gander but was blocked from the nest by the goose and was subsequently routed. On rare occasions the fox succeeded in driving the gander away momentarily. At first the gander seemed to hesitate in his return, but he came back when the fox turned his attention to the nest and the goose started to vocalize intensely. On some occasions the fox was able to outmaneuver both birds and to capture an egg.

If the fox captured an egg on his first attempt, he cached it then most often left the vicinity as he continued to forage. In all such cases, either the gander arrived at the nest during or just after the attack, or the lone goose returned to the nest while the fox cached his egg. The presence of the geese may have deterred the fox from a second attempt but in many instances, the fox showed no signs of wanting to attack again. He may have glanced at the geese and the nest as he loped away, but he often left without looking back.

On some occasions the fox made a second or even a third attempt in quick succession, with mixed results (Table 6). The reasons why the fox finally ended his attempts in such cases ranged from a goose's successful solo defense of the nest during the fox's second attempt, to no more eggs left in the nest. It is unknown why foxes attacked most nests only once while they attacked others several times even with the gander present. I suspect that the fox treated each situation individually and that the decision for or against multiple attempts was based partly on the presence of the geese and on the strength of their defense.

After goose hatch, foxes attacked flocks of geese and they killed both adults

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Table 6. Results of fox attacks on defended Canada goose nests near Cape Churchill in 1985 and 1986. In all successful attempts but one, the fox took only one egg. All eggs were cached.

Number of Nests	Number of Attacks at each Nest	Result of each Attack
10	1	failure
13*	1	success
3	2	success on first, fail on second.
2	2	both successful
1	3	success on first and second, fail on third.
1	3	all successful

* at one of these nests, the fox killed the goose and took three newly hatched goslings and two eggs. The goose was eaten while the goslings and eggs were cached.

and goslings. A fox usually made attempts for geese as he encountered them while he foraged. On three occasions, the fox sighted a flock of snow geese close by as he crested a beach ridge, and he charged the flock immediately. In one case the geese reached a lake before the fox reached them. In another case, the flock huddled together in a tight group with the goslings in the center and the adults at the periphery. The fox cut short his charge but he eyed the geese as he decelerated and loped past the flock. Snow geese are aggressive defenders, and if the fox pressed the attack then the adult geese would have pummelled him with their wings (R. Rockwell pers. comm.). In the third case, the fox reached the geese and caught a gosling from the rear of the flock as the geese ran to a lake.

Foxes often scanned adjacent lowland areas as they sat on their dens. On two such occasions, the fox from den C (Fig. 1) sighted a large flock of snow geese in the distance to the east, left the den and loped quickly and steadily towards the flock with his head held low. The fox's lope was not relaxed and springy as it was when he foraged. Rather, the lope was deliberate and stealthy as though the fox was trying to approach the geese quickly but still maintain a low profile. In the first instance, the fox broke into a gallop when he was about 200-300 m from the geese. I was astounded by the fox's acceleration and velocity as he rocketed toward the flock. The geese were fleeing to a lake by the time the fox reached them. The fox had approached the flock from the side, and when he reached the geese, he killed a gosling, dropped it then wheeled on his hind legs and killed another gosling as it ran past him toward the lake.

The one incident where a fox was observed to kill a goose in a gosling-rearing area occurred at Bear Bay (Fig. 1). The fox walked through the tall grass and scrub along the edge of the more sparsely vegetated saline meadow where snow geese were feeding on low-growing sedges. The fox charged from the edge of the tall grass and

caught an adult goose near the middle of the saline meadow. The fox's charge created a disturbance and many geese ran toward the seashore. However, the geese returned and started to feed again within about 20 min. after the fox left with his goose. Foxes killed geese with a bite to the neck. A simple bite was sufficient to kill goslings but foxes may also head shake as they bite adult geese.

Foxes were successful in six of nine observed attacks on geese. In each of two successful attacks, the fox killed two goslings. Speller (1969) reported an incident where a fox killed four young geese during a single attack before the flock could reach the safety of a river. Captured geese and goslings may be eaten on the spot, brought to the den for the fox pups or cached either near the capture point or near the den. One such cache contained three newly hatched goslings. Larger goslings seemed more difficult to hide completely in a cache. Though the fox tried to stuff the bird into the cache hole as best he could, part of the bird remained showing. Beside one den, one gosling was simply placed in a shallow depression on the side of a hummock.

Table 7 shows Canada goose nest data and data for fox predation on goose nest eggs. Undefended goose nests were not included in the calculation of predation rates because in two of the three cases where foxes preyed on undefended nests, my presence may have caused the geese to abandon their nests. The incident where a fox killed the goose and took three goslings and two eggs was also excluded from the calculations since it was probably a rare event.

Table 8 gives estimates for the foxes' impact on the goose egg crop within their respective home ranges. The estimates are subject to the following conditions:
1) Only one fox hunted within each home range. This condition serves to show the minimum impact on the egg crop within a particular home range. Female foxes did not hunt before goose hatch since they were still caring for the pups inside the dens.

Table 7. Data for Canada goose nests and predation rates on Canada goose eggs in the study area in 1985 and 1986.

	1985	1986
Number of nests per square kilometer*	16	14
Average clutch size*	3.4 eggs	4.2 eggs
Percent nest failure*	55%	48%
Number of observation hours for the calculation of predation rates	26.1	7.7
Number of nests attacked/hour/fox**	0.8	1.4
Observed predation rates (#eggs/fox/hour)	0.6	1.2

*Rusch (1987)

**includes undefended nests.

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Table 8. Estimates of the foxes' impact on the Canada goose egg crop within their home ranges near Cape Churchill in 1985 and 1986.

	1985			1986		
	Total # eggs available*	# eggs taken**	Percent of total	Total # eggs available*	# eggs taken**	Percent of total
Den A	705	100	14%	570	200	35%
Den B	600	100	17%			
Den C				815	200	25%

* ie. in the home range. Calculated from the goose data in Table 7 and from the home range data in Table 4.

** calculated from the predation data in Table 8 under the specified conditions.

Because home ranges overlapped, however, the percentage of eggs taken by foxes may have been higher than that indicated in Table 8 since more than one fox hunted in overlap areas.

2) Each fox hunted for six hours per day. Speller (1972) and Burgess (1984) saw that arctic foxes' activity periods ranged from 4-16 h in duration, but that not all of the time in an activity period was spent hunting. These authors did not provide data for the foxes' actual hunting time in a 24 h period. Data from the present study show several days where foxes hunted for 2-6 h during the daylight hours before contact was lost. Given that arctic foxes have a chiefly nocturnal activity pattern, I believe that six hours of pure hunting time per 24 h period is a reasonable minimum.

3) Predation rates on goose eggs were constant throughout the defined sampling period (see below).

4) The incubation period for Canada goose eggs is 28 days (Gillespie 1984), therefore, the calculated predation rates were applied for a 28 day period.

5) Goose nests were uniformly distributed throughout the study area.

A comparison of values for the foxes' impact on the goose egg crop (Table 8) with those for the percent nest failure (Table 7) indicate that foxes were not responsible for all the eggs taken in either year of this study. This was expected since gulls and jaegers also prey on goose nests (D. Rusch pers. comm.). Some egg loss may not have been due to predation. MacInnes and Misra (1972) suggest the possibility that the small egg loss they observed at McConnell River was due to scavenging by predators after the geese had deserted their nests.

The higher calculated predation rate in 1986 was probably due to the relatively low number of observation hours in that year. Of the 7.7 hours of observation, 1.7 h occurred during one hunt where a fox captured one egg from each of five nests then

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captured two eggs from a sixth nest. A similar hunt occurred in 1985 where a fox captured four eggs in 0.93 h. However, the fox's good fortune during that hunt was put into perspective by 25.17 h of previous and subsequent observation.

The decreased availability of lemmings in 1986 (see Food Habits) may have influenced the foxes' predation rates on goose nests. However, foxes simply attacked goose nests as they found them, and they did not appear to seek out goose nests specifically. Therefore, the number of nests attacked per unit time probably depended on nest density. Since nest densities were almost equal in the two years of this study (Table 7), the greater number of nests attacked per hour in 1986 (Table 7) supports the suggestion that the higher predation rate calculated for that year was due to the combination of the fortunate 1.7 h hunt and the low number of observation hours.

The predation rates in both years are also functions of the foxes' attack success rates (Table 5). It is possible that my presence on hunts facilitated the capture of goose eggs, but in almost all instances, any effects of my presence were not obvious during the attack. The two attacks on undefended nests were notable exceptions. In the case where the goose flushed, I suspect that she did so because of my presence. In the other case, the geese returned to their nest as the fox and I left the area, and I suspect that my presence kept the geese away as the fox preyed on the nest. These instances are in contrast to an incident where the geese returned to defend their nest successfully even though I was in view nearby.

Foxes seemed to detect goose nests of their own accord. If geese reacted to my presence then they did so by lying flat on the nest to remain inconspicuous. Lone geese did not vocalize until the fox closed to within a few meters of the nest. When a gander was present, he vocalized when the fox was still several meters away. In those cases, I could not rule out the possibility that my presence elicited the

ganders' vocalizations. By that point, however, the fox was already closing on the nest and had obviously detected it, so I probably did not aid in the nest detection.

When the gander was not present at a nest, he was on a lake nearby, but he did not return until the goose vocalized. The gander sometimes came to the nest immediately, but on occasions when he did not come immediately or did not come at all, I do not know whether he had simply strayed too far from the nest or if my presence inhibited his return. In one case, a gander who was more than 100 m away flew to his nest quickly and directly even though I was in plain view.

During an attack on a nest, the geese seemed to have their attention fixed on the fox, and there were no instances where my presence had an obvious effect on the proceedings or on the outcome of the encounter. As a fox left to cache an egg, the geese would return to the nest even if I was in view. Geese appeared to turn their attention to me only after an attempt ended and/or when the fox was out of sight.

These observations suggest that my presence did not facilitate the capture of eggs from defended nests. However, Canada geese are wary and they are sensitive to human disturbance (Gillespie 1984). It is unclear why a lone goose could successfully fend off a fox even during prolonged and intense attempts, while in other cases, the fox could capture several eggs even when the gander was present. The location of a nest may influence defense by restricting the foxes' mobility, eg. as on a narrow peninsula, or by providing a large area in which the fox can maneuver. The reasons may also be related to the geese' physical condition, to their experience in nest defense or perhaps to their individual temperment. Some geese leave the nest when humans are still far away, while other geese will sit tight on the nest even as a human comes to within 15 m. As such, I do not discount the possibility that the varying success in nest defense was due at least in part to varying sensitivity to disturbance or distraction caused by my presence. Therefore,

the attack success rates shown in Table 5 are probably higher than they would be without human disturbance.

Overall, an accurate assessment of the egg loss due to foxes cannot be given due to the arbitrary though necessary conditions imposed for the calculations, and to the possible biases discussed above. MacInnes and Misra (1972) suggest that since Canada goose nests are widely dispersed, they have a fairly low susceptibility to widespread destruction unless foxes are numerous in the nesting area.

Predation on Birds Other than Geese

Foxes preyed on duck, shorebird, passerine and ptarmigan nests by simply approaching the nest and taking or eating the eggs. Eggs were taken and cached one at time until all the eggs were gone. In all cases, the adult birds vacated the nest just as the fox arrived. Ducks either flew away or swam about near the nest. When ducks flushed, foxes sometimes lunged in an attempt to catch the bird but they were not observed to be successful. As the fox took and cached eggs from shorebird and ptarmigan nests, the adult birds vocalized and walked about near the nest, beside the fox and away from the nest in an apparent attempt to catch the fox's attention and draw him away from the nest. The fox always ignored such attempts. Passerines ie. Lapland longspurs, flushed from the nest, fluttered along the ground then watched silently from a few meters away as the fox preyed on the nest. All nests of the four types of birds mentioned were emptied completely. All duck and ptarmigan eggs were cached. All shorebird eggs were cached in 1985, while 36% were eaten and 64% were cached in 1986. All passerine eggs were eaten on the spot. Passerine eggs were eaten shell and all, while all other types of eggs were opened neatly at one end and the contents licked out.

FOOD HABITS

Methods and Materials

The arctic foxes' food habits were observed directly by following adults on hunts and by observing fox dens. Indirect observations were made through scat collection and analysis, through the collection of goose feet on fox dens and through observations of other prey remains on dens.

The methods used to follow adult foxes on hunts have been described previously (see Hunting Ecology). The locations of kills and meals were recorded on 1:50,000 maps in 1986. Kills and meals were recorded in a notebook in 1985.

From 31 May to 5 June of 1985, den B (Fig. 1) was observed with a 20X spotting scope from an observation platform at camp, about 250 m to the northwest. From 5 June to 1 July, dens A and B were observed as I waited for the male fox to return from a hunt. The dens were observed with the naked eye or with a 20X spotting scope, without a blind from a distance of 30-60 m. From 1 July to 17 August I stopped following foxes on hunts and I observed den B as I sat on a lawn chair about 60 m away. Food items brought to the den were recorded in a notebook.

In 1985, I examined scats as they accumulated on dens A and B, and I checked for prey remains when I began observations for the day at those dens. Dens D and F (Fig. 1) were checked infrequently on an ad libitum basis. In 1986, prey remains were observed, and scats and waterfowl feet were collected periodically from dens A,C,D and E (Fig. 1) between 9 July and 1 August. These materials were brought to Winnipeg where the scats were autoclaved, then teased apart while they were submerged in water. Scats were analysed on a presence/absence basis with regard to their components ie. mammal, bird, insect and plant remains.

Waterfowl feet were identified to species by Colleen Nelson. Thereafter, I paired the feet on the basis of size and toenail morphology. Gosling and adult feet were separated on the basis of toenail wear. Feet where toenails had sharp clean edges were considered gosling whereas toenails that were worn and/or blunted were considered to be from adults.

Differences in lemming population densities between 1985 and 1986 were observed with a small mammal trapping plot. One hundred trapping stations were set out in a 90 m x 90 m grid that extended from hummocky peat lowland to lichen-heath vegetation on a beach ridge. There were ten rows with ten trap stations per row, all ten meters apart. At each trap station, one Museum Special snap trap was attached to a wooden stake by a one meter long string to allow for subjectivity in trap placement. The traps were baited with peanut butter and were checked morning and evening for three days and three nights in each trapping period. There was one trapping period per month in late June and late July of 1985 and 1986. Standard data and measurements were recorded for each small mammal captured. The carcasses were cleaned in an enzyme bath and are now stored at the University of Manitoba.

Results and Discussion

Status of Goose and Lemming Populations

Table 7 shows the Canada goose nesting density within the study area in 1985 and 1986. In addition to the Canada geese, 7-8 snow goose nests were found in the study area in both years (D. Rusch, pers. comm.).

Nest density data (Rusch 1987) combined with data from aerial surveys conducted after hatch in 1977 and 1978 (Didiuk 1979), produce an estimate of less than 10 Canada geese (adults and goslings) per square kilometer after hatch in 1977 and

1978. In those years, Canada goose nest densities were from 25-55% higher than they were in 1985 and 1986. Also, nest success was about 30-55% higher in 1977 and 1978 than it was in 1985 and 1986. Since mean clutch sizes were similar between the two sets of years, the differences between nest densities and nest success suggest a densities of far less than 10 adult Canada geese and goslings per square kilometer in 1985 and 1986.

After hatch, an estimated 4000-5000 adult snow geese and goslings moved into the study area in 1985 and 1986 (D. Rusch, pers. comm.), producing an estimated snow goose density of more than 40 individuals per square kilometer.

These density estimates indicate that Canada geese are the predominant species in the study area before hatch, while snow geese predominate after hatch.

In 1985, 3.2 lemmings were caught per 100 trap nights, while 1.2 lemmings were caught per 100 trap nights in 1986. Though these values show that the lemming populations were lower in 1986 than in 1985, the difference in the populations between the two years was also reflected by other observations. The presence of snowy owls is an indicator of lemming abundance (Fine 1980, Bent 1938). At least three snowy owl nests were active in the study area in 1985, and snowy owls were seen regularly during that summer. No snowy owls were sighted in 1986 and no active nests were found. Also, the number of lemmings that foxes caught per hour (see below) showed marked differences between the two years, and they suggest that differences in lemming populations between the two years was larger than the results of the small mammal trapping program indicated.

Captures and Meals During Hunts

Arctic foxes are opportunistic predators and scavengers that will utilize any food source (Garrott and Eberhardt 1987). During the summer, their food habits

reflect the availability of the prey species within their home ranges (Chesemore 1968, Fine 1980, Hersteinsson 1984). In tundra regions, birds and small mammals - especially lemmings - are the primary summer prey, but berries and other plant matter, fish, caribou faeces and carrion, muskox carrion, frogs, insects, snails, Arctic hares and Arctic ground squirrels may also be eaten (Barabash-Nikiforov 1938, Braestrup 1941, Shibanoff 1958, Gunderson et al 1955, Sdobnikov 1958, Underwood 1975, Chesemore 1968, Macpherson 1969, Speller 1972, Riewe 1977, Fine 1980, Kennedy 1980, Garrott et al 1983, Burgess 1984, Hersteinsson 1984). In general, lemmings are the predominant prey when they are abundant, while birds become important when lemmings are scarce (Speller 1972, Burgess 1984, Macpherson 1969).

In coastal regions, arctic foxes prey heavily on products of the sea. These include marine invertebrates and the carrion of marine birds, fish and mammals. However, small mammals from adjacent tundra regions may also be eaten. Where sea-bird colonies exist, foxes prey heavily on that abundant food source (Barabash-Nikiforov 1938, Murie 1959, Stephenson in Fine 1980, West and Rudd 1983).

Around human settlements, foxes take advantage of garbage and of human handouts. In an oil-developed area in northern Alaska, Fine (1980) noted that fox pups even "sat near the kitchen door on steak nights". However, foxes sometimes also ingested non-digestible items such as rope, rubber and bits of plastic and wire insulation (Seton 1929, Chesemore 1968, Underwood 1975).

When lemming populations are high, arctic foxes may remain in inland tundra regions during the winter and prey mainly on lemmings (Chesemore 1968, Sdobnikov 1958), but they also eat carrion (Banfield 1977, Underwood and Mosher 1982), eggs left over from the previous summer (Soper 1944), arctic hares (Banfield 1977) and ptarmigan (Sdobnikiv 1958, Banfield 1977). Arctic foxes may also follow caribou herds and eat the remains of wolf kills (Manning 1943, Banfield 1977).

Foxes that denned in tundra regions during the summer may move to the seashore for the winter (Shibanoff 1958) where they, and the foxes that inhabited the coastal regions during the summer subsist on foods of marine origin (Chesemore 1968, West and Rudd 1983). Foxes also move out onto the sea ice where they stay close to polar bears and scavenge the remains of bear kills or even eat the bear faeces (Banfield 1954, Bannikov 1969, R. Riewe pers. comm.). Arctic foxes will eat conspecifics caught in traps set by trappers (Banfield 1977). In spring, foxes on the sea ice may prey on seal pups by digging into the pups' subnivian birth lairs (Smith 1976, Riewe 1977). For foxes living in areas of human development, food scavenged from dumps and from around housing facilities may be the primary source of sustenance during the winter (Eberhardt et al 1982, 1983, Garrott et al 1983).

Foxes kill and cache more than they need immediately during times of food abundance, then they utilize their food caches when fresh food becomes scarce (Riewe 1977, Burgess 1984). Caches may contain from one to more than one hundred food items (Murie 1959, Burgess 1984).

Tables 9 and 10 list all prey items that foxes captured and ate during hunts in 1985 and 1986. The importance of lemmings in both captures and meals reflected their availability during the two summers. Both tables show that avian prey items compensated for the low lemming populations in 1986. Sdobnikov (1958), Riewe (1977) and Tomkovich (in Summers 1986) saw that arctic foxes preyed heavily on birds when lemming populations were low. Although lemmings are a preferred prey item (Burgess 1984) and they were abundant in 1985, foxes preyed upon birds whenever the opportunity arose. In contrast, Kennedy (1980) thought the availability of lemmings was the reason for an observed lack of predation on birds.

Table 9 also shows the rates at which foxes caught each prey type in both years. The difference in the capture rates for lemmings was attributable to the

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Table 9. All prey items captured during hunts near Cape Churchill in 1690 min. of observation in 1985 and in 1070 min. of observation in 1986.

Prey type	1985		1986	
	Total # items captured	# items captured/ hour/fox	Total # items captured	# items captured/ hour/fox
lemmings	104	3.7	4	0.2
goose eggs	26	0.6	14	1.2
adult geese	1	<0.1	-	-
goslings	3	< 0.1	4	< 0.1
duck eggs	11	0.4	26	1.5
shorebird eggs	8	0.3	23	1.3
ptarmigan eggs	-	-	7	0.4
passerine clutches	9	0.3	3	< 0.1

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Table 10. The number and type of food items consumed by adult arctic foxes near Cape Churchill during 1690 min. of hunt observations in 1985 and in 1070 min. of hunt observations in 1986.

	1985	1986
Fresh items:		
lemmings	27	1
adult goose or gosling	1	1
shorebird eggs	-	13
passerine clutch	9	3
Cached or scavenged items:		
goose remains	-	3
goose egg	-	1
duck eggs	-	3
shorebird egg	-	1
lemming	1	-
Meals from fresh items (%)	97	63
Meals from caches (%)	3	37
Meals from mammalian items (%)	74	5
Meals from avian items (%)	26	95

differing lemming populations. The capture rates for goose eggs were discussed previously (see Capture Attempts for Geese).

Speller (1972) thought that foxes discovered passerine nests fortuitously as foxes hunted for lemmings. In the present study, passerine, shorebird and ptarmigan nests were detected when the fox seemed to stumble across them, or when the incubating adult flushed from the nest. If an adult bird does not flush then the nest may go unmolested, apparently unnoticed (this study and R. Riewe pers.comm.).

Avian nest densities may show large variations between years (Burgess 1984), and Hersteinsson (1984) saw that the importance of passerines in a fox's diet was proportional to the birds' nest densities. In the present study, the differing rates of predation on shorebird and passerine nests between the two years may have been due to changes in the detectabilities of the nests, to different nest densities or, as Burgess (1984) suggested, "to a change in the behaviour of...foxes in response to decreased availability of preferred small mammal prey". No conclusions can be drawn as to which of these possibilities applied in the present study because avian nest densities were not studied. However, the foxes' foraging patterns and hunting intensities, and their behaviour immediately before they preyed on nests seemed to be consistent between the two years. Therefore, hypotheses for the differing rates of predation on passerine and shorebird nests based on nest detectability and behaviour changes in the foxes are less attractive than a hypothesis based on nest densities.

The low rates of predation on ptarmigan nests in both years suggest that such rates were normally low. Therefore, I suspect that the one observation of predation in 1986 was due to chance rather than being indicative of a higher predation rate in that year.

The predation rate on duck nests in 1986 is attributable to one hunt, part of which was along the sea coast where a fox found three duck nests. The foxes' home ranges in 1985 were not observed to extend to the sea coast. Therefore, if the three nests found along the coast in 1986 are ignored then the rates at which foxes found duck nests along freshwater shorelines were identical for the two years.

Table 10 shows the food items that adult foxes ate during hunts in 1985 and 1986. The major difference between the two years was that foxes ate mostly fresh lemmings in 1985 whereas they ate mostly eggs in 1986. Most notably, the foxes ate shorebird eggs in the nest in 1986 whereas all shorebird eggs were cached in 1985. As with all items captured during hunts, the change in the foxes' diet was attributable to the decreased lemming availability in 1986.

No comparisons can be made between the two years concerning differences in the foxes' use of cached food because hunt observations ended on 1 July in 1985, and the first meal from a cache in 1986 occurred on 29 June. Burgess (1984) found that foxes used cached food to maintain constant rates of consumption as the availability of fresh food decreased. Thus, the almost total lack of meals from caches in June of 1985 may have resulted from the abundance of fresh food at that time. The one meal from a cache in that year occurred while a fox was recaching several lemmings, and the consumption of one of the lemmings seemed to be more a matter of convenience than of necessity.

The use of cached and scavenged food items in July of 1986 was surprising because goslings were available. No conclusions can be drawn on this matter due to the paucity of data, but it may be that the adult foxes did not kill enough goslings for both themselves and the pups. With the low lemming populations, it may have been necessary for the foxes to use their food caches and to scavenge food items. The items scavenged ie. a goose foot and the almost bare remains of a gosling, were

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very meager fare. The foxes' consumption of such items may have indicated a decreasing availability of fresh food. Fine (1980) noted that available caribou carrion was not utilized in an oil-developed area where other food items were readily available.

Table 11 shows the average times and distances between attempts, kills and meals in both years. The values in the table were calculated from total hunting times and distances, and they reflect the times and distances between individual lemmings and nests that foxes encountered, or between meals that foxes ate. If a fox made several attempts on a goose nest in quick succession, then these were counted as only one attempt. A single feeding bout was recorded as one meal regardless of the number of individual items eaten. The 1985 data were not suitable for a statistical treatment, so the data for both years were analysed in a non-statistical manner for more accurate comparisons between the two years. A statistical treatment of the 1986 data is given in Table 12. For those calculations, the times and distances between the start of the hunt and the first kill/meal, and between the last kill/meal and the end of the hunt were not included so that the quantities of time and distance used were strictly between attempts, kills and/or meals. I suspect that the differences between the two years (Table 11) were due mainly to the differences between the lemming populations, though possible differences in avian nest densities may also have been a factor. With the large lemming populations in 1985, the foxes encountered more prey items per unit time than they did in 1986 when lemming populations were low.

Table 13 shows the estimated total number of kilocalories of food energy that foxes accumulated during hunts in 1985 and 1986. The weights and caloric values of birds' eggs were gleaned from the literature (see below) or were calculated with equations from Bergtold (1929) where egg dimensions were obtained from Reed (1904)

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Table 11. Average times and distances between capture attempts, kills and meals during hunts near Cape Churchill in 1985 and 1986. The distance measures for 1985 were based on an estimated total distance of 150 km.

	1985	1986
Average time between attempts (min.)	11 (n = 155)	26 (n = 41)
Average time between kills (min.)	13 (n = 133)	31 (n = 35)
Average time between meals (min.)	44 (n = 38)	56 (n = 19)
Average distance between attempts (km)	0.95	2.15
Average distance between kills (km)	1.15	2.5
Average distance between meals (km)	3.95	4.65

Table 12. Average times and distances between capture attempts, kills and meals during hunts near Cape Churchill in 1986 according to a statistical treatment of the data.

Average time between attempts (min.)	14 (S=12, n=34)
Average time between kills (min.)	18 (S=16, n=23)
Average time between meals (min.)	37 (S=26, n=8)
Average distance between kills (km)	1.35 (S=1.05, n=23)
Average distance between meals (km)	2.1 (S=1.8, n=8)

Table 13. The caloric values of food items captured by foxes during hunts near

Cape Churchill in 1690 min. of observation in 1985 and in 1070 min. of observation

in 1986.

	weight (gm)	Kcals per gm** '	Total Kcals captured	
			1985	1986
Canada goose egg	145*	1.73	6020	3512
duck egg	37*	1.95	794	1876
shorebird egg	6.5*	1.48	77	221
ptarmigan egg	18.5*	1.6	–	207
passerine clutch	12**	1.16	125	42
lemming	16.5***	5.0	8580	330
gosling	30***	5.4	810	324

* weight without shells.

** based on 5 eggs per clutch. Weight without shells.

*** dry weight.

**' Kcal/gm fresh weight for eggs and Kcal/gm dry weight for lemmings and goslings.

and/or were measured personally. The weights, water contents and caloric values for other food items were obtained from Romanoff and Romanoff (1949), Pattie (1977) and Riewe (1977). If weights or caloric values were not available for specific species, then the data for similar species were used, eg. partridge egg caloric values were used for ptarmigan eggs. These data were used to calculate standard weights and values that were assumed to be constant for the two years. Since larger goslings were not captured by foxes during observations in June 1985, then large goslings were excluded from the calculations for 1986 so that comparisons could be made for the two years based on similar prey types.

Tables 13 and 14 show that lemmings accounted for the majority of calories that foxes captured and consumed during hunts in 1985. Also, fresh prey items accounted for almost all calories consumed in meals (Table 14). In 1986, avian prey items became the predominant source of calories, lemmings became an insignificant food source, and cached or scavenged items provided more calories in meals than did fresh food items.

Food Items Brought to Dens

Table 15 shows all food items that I observed foxes bring to their dens during 263 h of observation between 31 May and 17 August in 1985, and during 164 h of observation between 3 June and 30 July in 1986. All observations were made during the day.

During June of 1985, lemmings were the only food item that male foxes brought to their dens, and they brought 5-6 lemmings at a time. Though lemmings were brought occasionally during July and August, avian prey items, especially goslings, were the predominant item brought to the dens during that time. Fewer observations were made in 1986 because the adult foxes returned to their dens less frequently during the

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Table 14. The caloric values of food items consumed by foxes during hunts near Cape
Churchill in 1690 min. of observation in 1985 and in 1070 min. of observation in
1986.

	1985 Kilocalories		1986	
	fresh items	cached or scavenged items	fresh items	cached or scavenged items
lemmings	2228	82	82	-
goose* or gosling	162	-	162	-
goose remains**	-	-	-	270
goose egg	-	-	-	251
duck egg	-	-	-	216
shorebird egg	-	-	125	10
passerine clutch	125	-	42	-
Totals	2515	82	411	747

* the fox ate the right breast only; therefore, the standard gosling weight was used (see Table 13).

** estimated as 15 gm dry weight each @ 5.4 Kcal/gm dry weight.

Table 15. Food items brought to dens A and B during 263 h of observation in 1985, and to dens A and C during 164 h of observation in 1986.

	1985	1986
lemmings	101	3
adult geese	2	-
goslings	15	11
goose remains*	1	2
adult ducks	3	-
adult shorebirds	7	-
passerine nestlings	2	-

* portions of fresh carcasses.

daylight hours. However, on two occasions where foxes brought lemmings to their dens, a single lemming was brought in the first case, and two lemmings were brought in the second case.

The most striking difference between the two years is in the number of lemmings brought to the dens. Macpherson (1969) and MacFarlane (1908) observed that arctic foxes stored large numbers of lemmings in their dens. In the present study, the male foxes were probably feeding the female and storing lemmings during June of 1985. In 1986, however, I suspect that the males were bringing only enough food to meet the females' needs.

Table 16 identifies the remains of food items found on fox dens. Underwood (1975) found empty eggs on fox dens in Alaska, but "all signs of the eggs had disappeared 24 hours after their discovery". The short time in which eggs are visible on dens suggest the possibility that more eggs could have been brought to the dens than were or could have been observed.

The ten whole lemmings found in 1985 were just inside den entrances where the male fox had placed them. The presence of lemming remains on the surface of dens in 1985 may have been a reflection of the large lemming populations, but the low number of remains found gave no clue as to the large number of lemmings brought to dens in that year.

The time in which gosling remains, ie. carcasses and feet, were visible on dens varied from overnight to a few days. Therefore, an accurate value for the number of goslings brought to dens was be difficult to obtain. In 1985, however, 28 carcasses appeared on one den during a 23 day period, while 24 carcasses appeared on another den during a 16 day period. At the latter den, seven of the carcasses appeared within two days. R. Rockwell (pers. comm.) estimated that 90% of the snow goslings in the study area could fly by 11 August in 1985. Despite this, new

Table 16. Prey remains found on dens A,B,D and F in 1985 and on dens A,C,D and E in 1986. Refer to Figure 1 for the locations of the dens.

	1985	1986
whole lemmings	10	-
lemming remains*	3	-
goose egg shell	1	1
gosling remains*	59	91
adult goose remains*	1	4
ptarmigan remains*	2	-

* each item of remains corresponded to a single live
  individual.

gosling carcasses continued to appear on dens until observations ended on 17 August.

The gosling feet collected in 1986 revealed wide variations in the rates of appearance of fresh gosling remains. These rates ranged from one pair of feet in six days, to 33 pairs of feet in 16 days. The lower rates were observed during the first half of July whereas the higher rates were observed during the latter half of that month. The differences in the rates may have been related to the changing food demands of the pups and/or to the pups' activity patterns. Sargeant (1972) noted that food remains on red fox dens were often located underground during the period immediately after the first den emergence, when pups restricted their movements to the immediate den vicinity. As the pups matured and dispersed their activities more widely in the den area, most, but not all, food remains occurred on the den surface (Sargeant 1972). For these reasons, the rates of accumulation for goose remains on dens in the present study should be considered minimums.

Of all goose remains found on dens in 1985, 3.3% were of Canada geese while the remainder were from snow geese. The low percent of Canada goose remains observed represent only those remains that were identified positively. I could not distinguish between Canada goslings and snow goslings as they were brought to the dens because the adult foxes moved quickly and only a few seconds were available to make the identification before the gosling was taken into the den. When carcasses appeared, they typically lacked heads. Therefore, an identification through bill morphology was not possible. Also, I did not have the expertese to make identifications based on foot morphology. The analysis of gosling feet collected in 1986 showed that 7% of the remains were from Canada geese. This low percentage was expected in light of the large number of snow geese and goslings in the study area. In 1986, all Canada goose feet were those of goslings. Of the snow geese feet, 4% were from adults while 96% were from goslings. These results show that goslings

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were the preferred prey type with regard to geese, but adults were also taken on occasion.

Scat Analysis

In 1985, 22 adult fox scats were analyzed in the field between 3 June and 27 June, while 34 scats were analyzed between 1 July and 18 August. All the scats in June consisted almost entirely of small mammal remains, eg. lemming fur; however, four scats each contained a few feathers. On 1 July, one scat consisted entirely of feathers, one was a mixture of fur and feathers while ten others were entirely fur. To that point, all scats were from adult foxes. During the remainder of July and August, all scats but one that were found on the dens were from pups. These consisted entirely of feathers. The one scat voided by an adult consisted of lemming fur and lemming bones.

Though the scats were subject to gross analysis only, they reflected the observation that lemmings were the predominant food source for adult foxes during June 1985. They also indicated that birds were eaten occasionally during that month. At the end of June, the scats indicated that the foxes began to prey on goslings as that food source became available. During July and August, the scat contents reflected the pups' diet, which consisted mainly of goslings. The one adult scat voided on 18 August indicated that foxes were eating lemmings at that time. That observation, along with the observation of goose and gosling carcasses in the field indicated that adult foxes ate both geese and goslings during hunts. However, the proportion of these food items in the adult foxes' diet were unknown.

Table 17 shows the results of analysis for 108 pup scats collected during July ie. after goose hatch, 1986. As was expected from visual observations of the pups' diet, the majority of the scats consisted either mostly or entirely of goose

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Table 17. The contents of fox pup faeces collected during 1986. Mammal remains consisted of fur, teeth and bones while bird remains consisted of feathers, large bone fragments, toenails, beaks and large pieces of gristle. Bile was an amorphous brown material that dissolved in water in the petri dish. The underlined word (below) is the main component of the scat.

	% of total # of scats (n = 108)
entirely bird remains	62
bird remains w/ mammal remains	13.9
equal parts mammal and bird remains	9.3
bile w/ mammal and bird remains	6.5
mammal remains w/ bird remains	4.6
entirely mammal remains	3.7
total frequency of bird remains	96%
total frequency of plant material	60.2%
total frequency of mammal remains	38%
total frequency of insect remains	14.8%

feathers. Bits of vegetation, eg. grass, were typically found in scats consisting of feathers. I suspect that these plant materials were ingested accidentally as the pups picked, plucked and tore off pieces of flesh from gosling carcasses. This was also the conclusion of Chesemore (1968) who found plant material in "almost all" of 200 summer scats that he analyzed. Fine (1980) saw that pups occasionally chewed on grass on the den. The insect material, eg. maggots and adult flies, were probably also ingested accidentally as pups fed on gosling carcasses of varying ages. Both Macpherson (1969) and Underwood (1975) found insect remains in fox scats. Macpherson saw that though such remains were rare in fox scats, some scats were more than half composed of bee remains "indicating that the foxes were hunting the insects selectively, or perhaps digging out or lying in wait at nests" (Macpherson 1969). Though pups may chase and even capture insects during play, Shibanoff (1958) found that insects were an unimportant component in the diet of young arctic foxes.

The high percentage of scats that contained lemming fur in July of 1986 was not expected from the low number of lemmings that I observed adult foxes bring to the dens. Macpherson (1969) saw that the frequency of lemming remains in scats decreased as lemming populations decreased. However, the relative importance of each prey type in a fox's diet is difficult to determine through scat analysis because "Prey such as lemmings, which contain a high proportion of indigestible material, tend to be overrepresented, whereas larger prey such as waterfowl tend to be underrepresented because they contain a smaller proportion of indigestible material" (Garrott and Eberhardt 1987).

Methods and Materials

Nine pups of one den were observed between late June and mid-August 1985. The den (den B)(Fig. 1) was a stage 2 (mature) den according to Macpherson's (1969) classification scheme, and was located on a level section of sandy beach ridge about 250 m southeast of Nestor 1. The surface of the beach ridge around the den was irregular due to wind erosion of the sand between patches of _Dryas integrifolia_ and other vegetation. The den overlooked a large lake to the east.

Observation timing, duration and structure were ad libitum (Altman 1974). The pups were observed with the naked eye or 20X spotting scope, without a blind from a distance of 50-60 m. In each observation period, new developments in physical features, locomotor ability and behaviour were recorded. Between observation periods, trends in these characters were noted and indicated with descriptions such as "more frequent", "decreasing amounts of", etc. However, since structured observations were not taken, these trends are general impressions and are not substantiated quantitatively. Most periods began when a pup emerged from the den and ended when no pups were visible on the den. However, nine periods began and 14 ended when I started and ended, respectively, observations for that day. The observations presented here are not intended for rigorous analysis due to the limitations of ad libitum sampling. Their value is strictly illustrative, suggestive and heuristic (Altman 1974).

Results and Discussion

The following sections describe the chronology of specific aspects of the pups' development. The dates given are those on which specific behaviours were first observed and are not necessarily the dates on which they first occurred. Underlined words are defined in Appendix 2.

The pups first emerged from the den on 28 June. This date is designated Day 21 in keeping with Frafjord (1986). By calculating from life history data in Bekoff et al (1981), the pups' conception date and birth date were estimated as April 15 and June 7 (Day 0), respectively.

The distribution of observation hours is shown in Figure 14. The pups were observed for a total of 52.45 hours. Observation periods averaged 35.36 min. in length (n = 89) and ranged in length from 2 min. to 3.59 hours. Figure 15 shows the distribution for the length of the observation periods. On the 30 days that pup observations were taken, an average of three observation periods occurred per day.

Body Colouration

On Day 21, the pups were entirely greyish-brown in colour. By Day 36, their undersides and the sides of their necks and torsos were a slightly lighter shade of greyish-brown than were their heads, backs, tails, limbs, shoulders and rumps. A light/dark colour pattern was evident but not sharply defined. By Day 53, the lighter-shaded areas had lost their grey tint and were light tan. The light/dark colour pattern was distinct but the borders between colour areas were still slightly blurred. By Day 70, the dark areas had lost their grey tint and were brown. The borders between light tan and brown areas were about as sharply defined as in the adult foxes.

Figure 14. The distribution of pup observation hours through the day. The pups were observed at Den B in 1985.
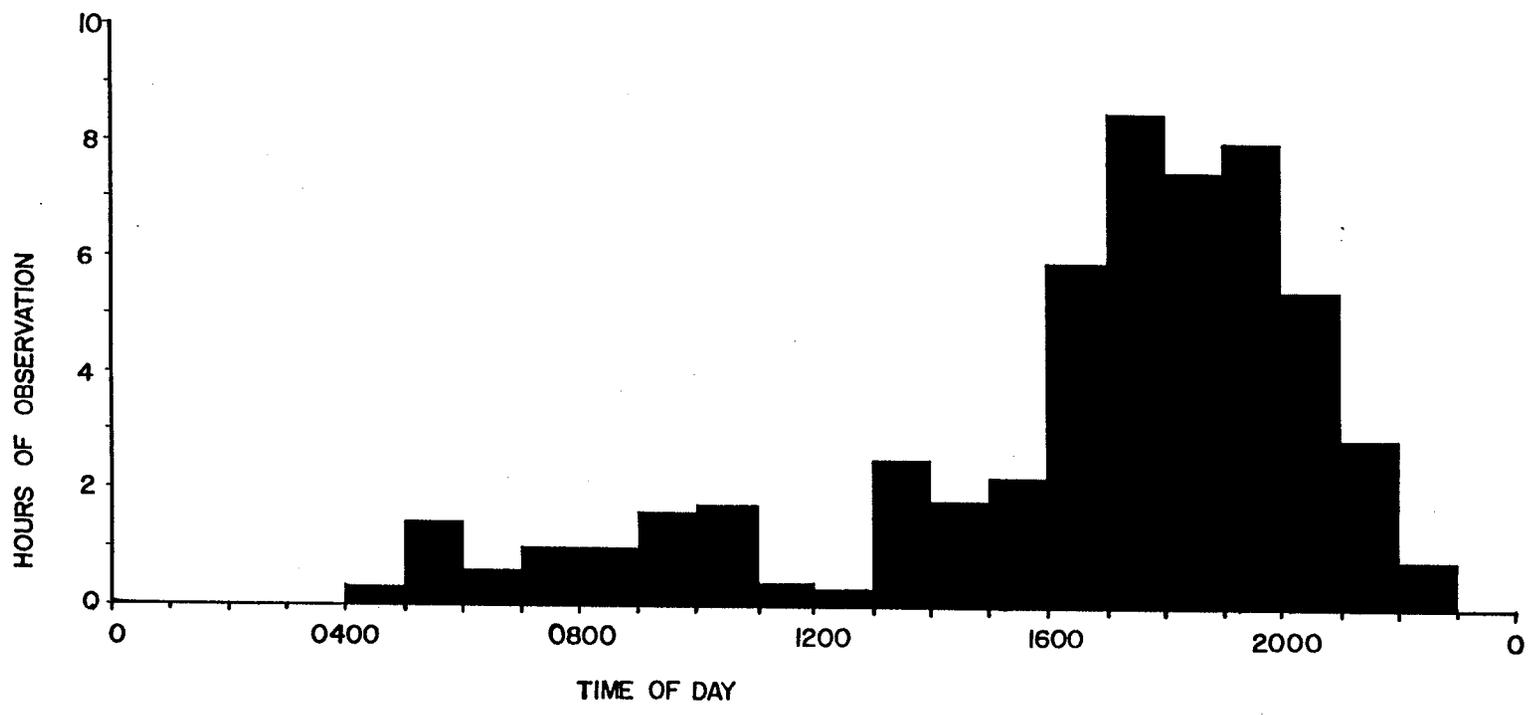
Figure 15. Histogram for the length of pup observation periods. The pups were observed at Den B in 1985.
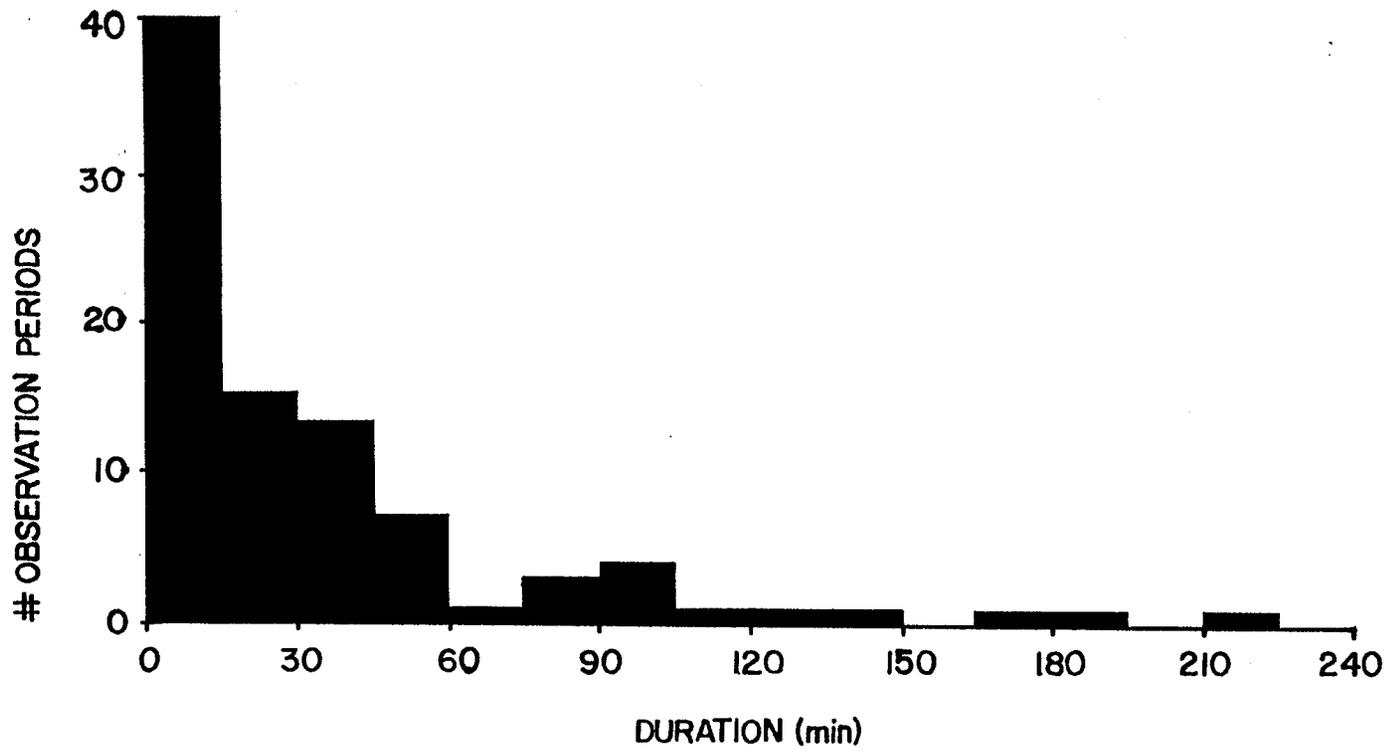
Novikov and Stroganov (in Fine 1980) identified three stages of pup colouration. Newborn pups have short brown fur that becomes longer and lighter at about two weeks of age. After their first emergence from the den, the pups develop a dark dorsal stripe that forms a crosslike pattern at the shoulders. The pattern becomes more and more distinct until the pups, at about four months of age, disperse from the den.

Response to Unusual Stimuli

Between Days 21 and 39, the pups showed two distinct levels of response to unusual stimuli.

From Days 21-33 the pups showed little or no apparent response as I approached the den or stood motionless on the den. They continued their activities seemingly heedless of my presence. If I walked slowly about the den surface, they moved from my path but did not seem alarmed. Their first evident investigation of me occurred on Day 33, when a pup approached and looked at me for several seconds from a distance of one meter.

As I approached the den on Day 35, all the pups withdrew to the entrances when I was still several meters from the edge of the den. They lingered momentarily to watch me then ran down the entrances. The cause of their sudden change in response was unknown, but from that day on the pups were wary, alert and quick to respond to unusual stimuli: on Day 36 the pups bolted down the den entrances instantly when the adult female barked and later that day, as a gull flew over the den. As on Day 35, the pups withdrew to the entrances when I approached the den. As I stood near the den on Day 39, three pups about 8 m from me tried to catch my scent by sniffing the wind with their noses in the air. They watched me as they walked crosswind and sniffed until they were directly downwind of me, then they stood there and continued

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to sniff and look for several seconds. A pup not among the three barked and all the pups bolted down the entrances. The three pups' cautious investigation at a distance was in sharp contrast to the lone pup's direct approach on Day 33. Several times in the following weeks, as I approached the den, a pup would see me and bark when I was more than 25 m from the edge of the den.

On several days leading up to Day 65, several pups seemed to become more curious about me as I sat in a lawn chair about 60 m away. They sniffed the wind as they watched me, and they approached ever closer to investigate. There seemed to be a threshold distance from me beyond which they would play, apparently undisturbed, but if they approached that threshold then their attention turned to me. The combination of investigation and play brought them ever closer to me until on Day 65, three pups sniffed, watched and approached until they were within one meter of me. I sat motionless during the pups' close-up inspection. After about 1.5 min., they loped back to the den and continued to play. Sdobnikov (1958) described a similar incident where a young arctic fox approached a human and "looked him over with curiosity, jumping aside whenever he (the human) made a movement". When I arrived at my observation position the next day, there were many new fox tracks there, and there was a pup scat on top of my folded lawn chair. This defaecation behaviour was also observed in adult foxes (see Capture Attempts for Geese).

Fine (1980) observed that arctic fox pups did not react to stimuli that occurred beyond about 40 m from the den. In the present study, it was difficult to determine when the pups actually became aware of my presence because they may have been aware without reacting noticably. However, the ever-increasing distance at which they reacted noticably, and the changes in the ways in which they reacted suggested a maturation in their skills of self preservation.

Behavioural Maturation

On Day 31, the pups begged from the adult male upon his return from a hunt. The pups handled solid food on Day 33: when the adult male returned to the den with food, one pup secured a lemming and ran down a den entrance. These behaviours, begging and securing, suggest that the pups were eating solid food by Day 33 rather than merely handling it. In southern Norway, Frafjord (1986) saw the pups from one litter first handle solid food on Day 28 and first eat solid food on Day 34. Pups from a second litter both handled and ate solid food for the first time on Day 27.

The first recorded pup vocalization was a rapid series of yips (Table 18). On one occasion, I heard this vocalization as the adult male fox was leaving the den. He turned around and poked his nose into the den entrance as though he were nudging the pups back into the den. This observation, and the context in which the pups yipped while I was taking care of them, suggests that the pups yipped to call their parents to them and perhaps to indicate distress.

One pup yelped during a wrestling bout on Day 33. A pup barked as I stood near the den on Day 39 and all the pups bolted down the den entrances. On Day 44 a pup watched me from beside a den entrance and barked repeatedly, just as the adult female did when she returned to the den and saw me there. The pups first staccato barked on Day 48. The bark of one pup seemed to stimulate the others to bark. Sometimes two or three pups on different parts of the den sat barking more or less in turn, apparently in response to one another. On Day 51, I heard the pups rumble inside the den after they had secured food from an adult.

Fox (1969) observed that the different vocalizations of coyote pups first appeared on different days. The appearance of a specific vocalization may be linked to innate factors. However, I suspect that learning was also a factor in the use of some vocalizations, eg. the alarm bark, because the pups were exposed to, and

Table 18. Pup behaviours and the days on which they were first recorded. See Appendix 2 for definitions of the behaviours. The Behavioural Maturation column contains important events in the pups' maturation and some of the behaviours listed may appear in other columns.

Day	Vocalizations	Locomotor Abilities	Predatory, Agonistic and Play Behaviours	Bahavioural Maturation
?*	yip	crawl, stand unsteadily		
21		walk		
29				play with adults.
30			playfight	follow adults on den surface.
31			pounce	beg from adults
33	yelp	trot, gallop	lunge, scruff-bite, head-shake	secure food, investigate me, follow adults off den surface.
35				withdraw as I approach the den.
36				bolt when the adult barks.
38		lope	side to side fake, back-arch	emerge from the den without the presence of an adult, play off the den surface.
39	bark (alarm)		dig	follow an adult away from the den, pup alarm barks.
40		smooth sprint	ambush	
41			leap	
44	bark (information)			pups rest on the den surface, pup repeatedly information barks.
45			zig-zag, stalk	
48	staccato bark		dodge, weave, 90 degree turn, cut-back, cut off angle, hip-slam	
51	rumble			meandering
54				pup digs rodent out from under a rock.
58			end-swap	
61				pup stalks and charges a small bird
65			cache	pup caches an object
70				pups explore several hundred meters away from the den without the presence of an adult.

* see the definition of yip for an indication of the pups' age.

even reacted to some vocalizations before they actually used them.

Between Days 21 and 38, the pups would emerge from the den only if an adult were present. At first they would re-enter the den as the adult departed, but they soon began to linger outside by themselves after the adult had gone. On Day 38, the pups emerged from the den on their own for the first time.

Between Days 21 and 44, all the pups' time on the den surface appeared to be spent in social play. Solo play and parallel play probably also occurred but did not become obvious until Day 39 when the pups started digging. Solo object play on Day 47 was followed by social object play on Day 48 when feathers or sticks were incorporated into play chases. A pup was first seen lying on the den on Day 44. Thereafter, resting on the den surface became common.

During the first few weeks after Day 21, the pups seemed to emerge, play and re-enter the den more or less as a group. As they matured, they began to emerge and re-enter the den more independently. After Day 51, social play was gradually, though not completely, replaced with solo and parallel activities, especially meandering, resting and solo object play.

The pups began to play with the adults and to follow them on the den surface early (Table 18). They first followed an adult off the den for a short distance (< 20 m) on Day 33, and thereafter followed the adults for increasingly longer distances (< 200 m) until on Day 39, a pup followed an adult away from the den.

The pups first played by themselves off of the den surface on Day 38, though they did not stray farther than 5 m from the edge of the den. By Day 41, they played anywhere within 35 m of the den and by Day 70, at least two pups were venturing farther than 400 m from the den.

The occurrence and/or order of appearance of the pups' behaviours and activities generally agreed with the observations of Fine (1980), Garrott et al (1984) and

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Frafjord (1986). Discrepancies in the time of appearance of specific behaviours could have been due to natural variation between litters as Frafjord (1986) observed, and to the limitations of ad libitum sampling where an observer may make subconscious sampling decisions (Altman 1974), eg. some behaviours may attract attention while other behaviours are less conspicuous.

Fine (1980) noted that the pups' rapid behavioural maturation closely paralleled their rapid physical growth. I believe that the two are strongly interdependent. The pups' progression from den emergence only when an adult was present, to solitary investigations away from the den seemed to occur through a process of learning: the pups' investigations led to familiarity with an ever larger number of stimuli and situations and with an increasingly larger area around their den. The pups' forays away from the den with their parents were probably a catalyst in this process. Also, improvements in the pups' locomotor abilities may have encouraged play at increasingly greater distances from the den.

The pups' increasing independence from their parents and from their fellow siblings, and the changes in their behaviour from social play to solitary activities, may have been facilitated by the above processes and maturations. I suspect that innate factors as discussed by Brown (1975), Morse (1980) and Gould (1982) played an important role in the pups' progression from sociable infants to solitary hunters. However, the relative importance of innate factors and learning was beyond the scope of this study.

Strength, Coordination and Locomotor Ability

These three aspects of the pups' development are strongly related. Since strength and coordination were not measured directly, their development was inferred from changes in the speed and agility of the pups' movements.

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From Days 21 to 33, the pups' locomotor abilities improved from a slow, unsteady walk on Day 21 to a fast walk, steady trot and a laboured gallop on Day 33. The pups could rear up on their hind limbs momentarily then fall down onto all fours in a manner that suggested a weak pounce (Fig. 16). During this period, gains in strength and/or improvements in coordination seemed to result in the development of a new gait.

From Days 33 to 38, the pups appeared to gain strength and improve coordination rapidly. They could pounce with greater agility and gallop faster and more smoothly than they could previously. The increased speed in the gallop allowed the slower, more relaxed lope to become distinguishable.

From Days 38 to 70, continued development of strength and coordination was evident through the "fine tuning" of, and power apparent in locomotor abilities. Movements became faster and more precise than they were previously. Play chases now included sharp turns and other maneuvers performed at a gallop (Table 18). The gallop further differentiated into a fast, smooth sprint with strong acceleration from a standstill. Leaps and pounces were graceful, controlled and were even performed in quick succession or were combined with other movements.

Fine (1980) saw that the pups' activities became more precise as the pups matured. In theory, strength, endurance and skill might mature to an optimal end-point on their own without the exercise gained through play (Fagen 1981). However, play activities develop these attributes through the effects of physical training and practice (Fagen 1976, 1981, Smith 1982).

Maturation of Predatory and Play Behaviours

The maturation of these behaviours was inferred from an increase in repertoire through time and from the in-context application of behaviours.

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Figure 16. Two techniques that arctic foxes use to secure prey. A) the pounce:
the fox arches over the prey (i) then immobilizes it with a forelimb stab (ii). B)
the leap: the fox jumps off the ground (iii) and lands with all four paws together
(iv). The fox may not land with all four paws on the prey as depicted.

A   i   ii

B   iii   iv
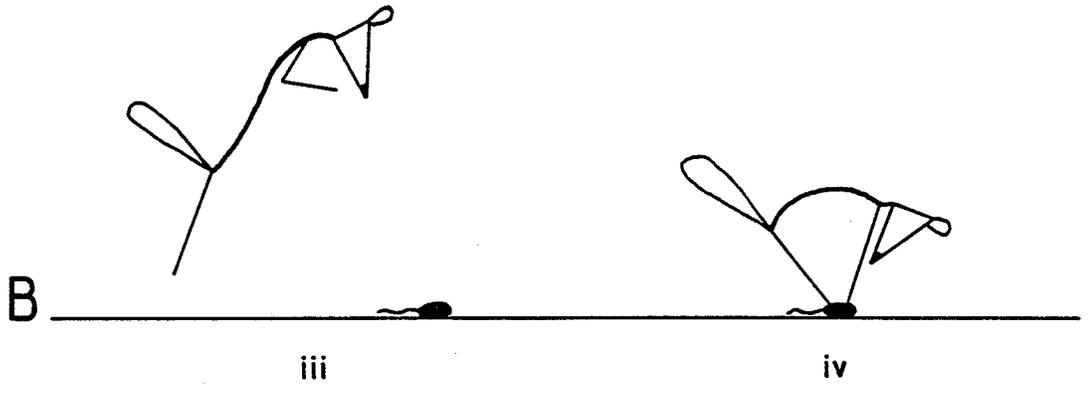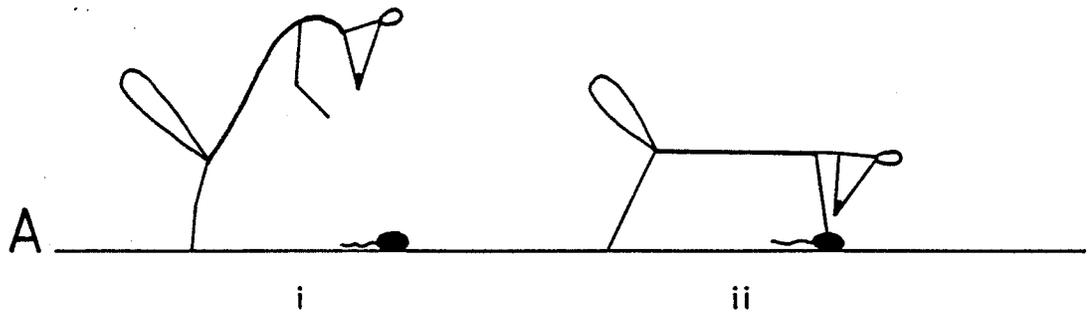
The pounce first recorded on Day 31 later differentiated into a second jumping motion, the leap (Fig. 16) on Day 41. During solo play on Day 58 the leap was combined with a downward head thrust and a biting motion upon landing.

A few pups started to dig on Day 39. The rest of the pups soon followed suit and within a few days the den surface, the ground around the edges of large rocks and the bases of some Dryas-topped sand knobs around the den were pock-marked with small, shallow holes. On Day 54 a pup ate a rodent it had just dug out from under a large rock beside the den. I could not determine whether the rodent was a cache or if it was live. On day 65 a pup cached a piece of rubber tubing on the den by using the same sequence of actions observed in adults.

During play, the pups were first seen to ambush each other on Day 40 and to stalk each other on Day 45. The ambush or stalk ended with either a lunge or a charge that usually resulted in a playfight unless the "victim" noticed the "attacker" in time to avert the attack. On Day 61 a pup stalked and charged a small bird but did not catch it.

The pups were playfighting vigorously by Day 30. They lunged, scruff-bit and head shook during wrestling bouts on Day 33 though they probably had done so previously. I noticed hip-slamming around Day 33 but did not recognize it as a purposeful action until Day 48 when a pup hip-slammed a playmate three times in quick succession. Back-arching was first recorded on Day 38.

Early play chases followed straight or arcing paths where the chaser exactly followed the path of the chasee. As a chase seemed imminent on Day 38, a pup side-to-side-faked (Fig. 17) then galloped away with its playmate in pursuit. Chasees began to zig-zag (Fig. 18) across a more or less straight path on Day 45, and a few days later, further complicated chases with dodges, weaves, cut-backs and quick 90 degree turns when not zig-zagging (Figs. 17, 18 and 19)(Table 18). If a pup was

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Figure 17. Maneuvers that fox pups use to avoid being captured. A) dodge, B) side to side fake. The circle is the chasee and the triangle is the chaser. In B) the short solid arrow shows the direction of the feign. In both A) and B) the pups are facing each other.
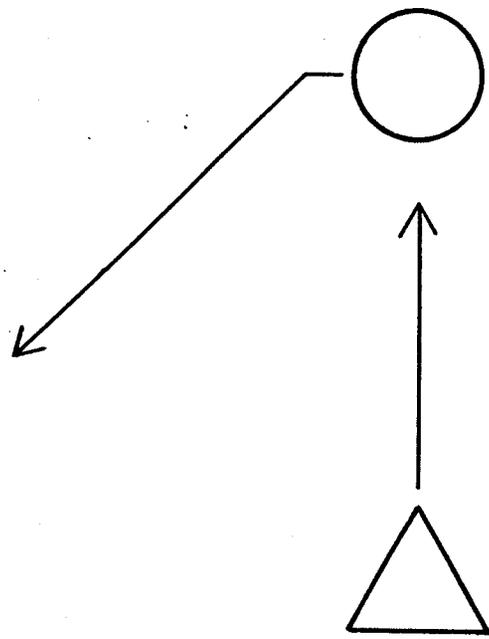
A
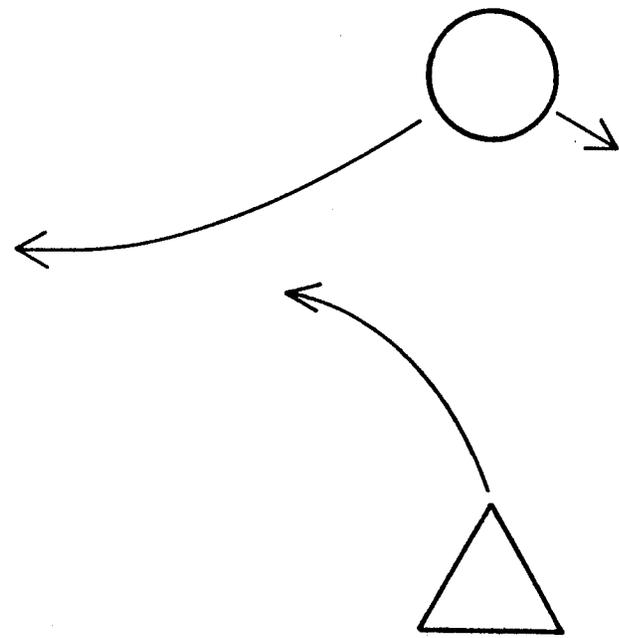
B

Figure 18. Maneuvers that fox pups use to avoid being captured. A) zig-zag, B) weave, C) 90 degree turn. The circle is the chasee. The chaser (not shown) follows closely behind and in the same path as the chasee.

A   B   C

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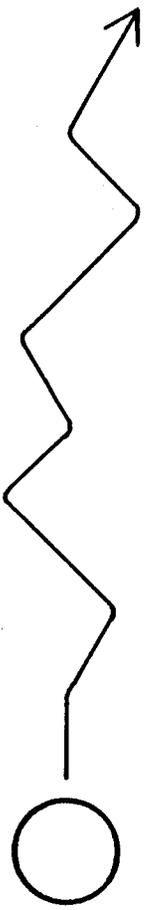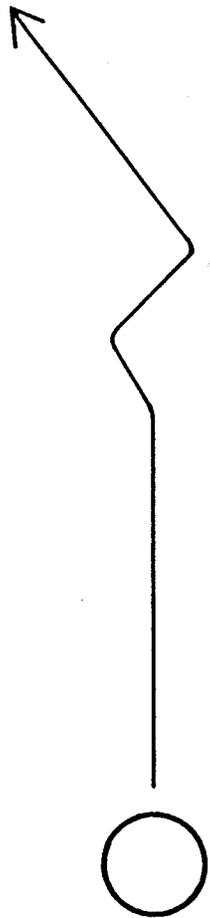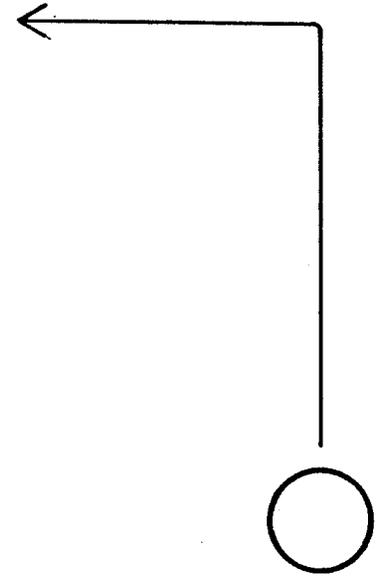
Figure 19. A maneuver that fox pups use to avoid being captured: the cut back. The circle is the chasee and the triangle is the chaser. The dotted line is the original path of the chase. As the pups run in a straight line (i), the chasee dodges and stops suddenly (ii). The chaser overshoots the chasee slightly (iii) who then runs across the original path behind the chaser (iv). The chaser changes direction and continues the pursuit.

101
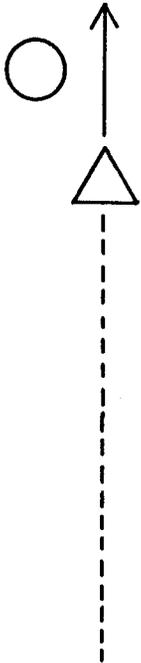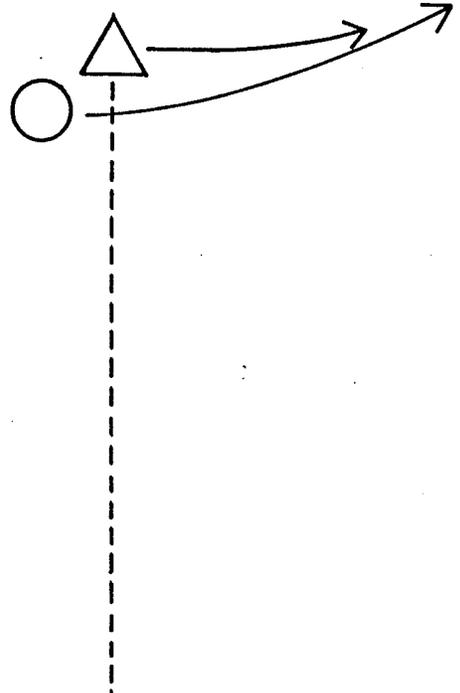
i   ii   iii   iv

performing these complex maneuvers then the chaser was bound to follow exactly the path of its playmate if there was to be any chance of a capture. During smoothly arcing playchases, however, the chaser cut off the angle (Fig. 20) rather than follow directly behind its playmate. On Day 58 a pup's end-swap (Fig. 21) appeared to startle the chaser momentarily. This maneuver was previously performed only by adults as geese chased them away from nests (see Capture Attempts for Geese).

Around Day 51 the pups started to spend more and more time meandering. In some instances they appeared to be following scent trails. As two pups loped away from the den on Day 70, they held their noses close to the ground for much of the time though they raised their heads frequently to look around.

As with the vocalizations and the pups' maturation into solitary adults, innate factors seem to play an important role in the development of the pups' behaviours. Fox (1969) saw that many behaviours, even apparently complex behaviours such as hip-slamming, appeared on their own at a very early age. Personnel at the Winnipeg zoo saw the pups cache objects without the benefit of observing adult foxes beforehand. These observations, along with the universality of many behaviours amongst arctic foxes, suggest that these behaviours are indeed innate.

Learning may be a catalyst to the expansion of a pup's repertoire of behaviours. Fine (1980) noted that "pups often incorporated new patterns into solitary play after being led away from the natal den by adults". One pup was observed to cache objects for the first time immediately after it returned from one such foray (Fine 1980). The quick spread of digging amongst the pups in the present study also suggests that information is spread through observation. I suspect that the appearance of some maneuvers, eg. end-swapping, 90 degree turns, also depends on the pups' locomotor skills. The execution of such maneuvers may not be possible until the pups develop the necessary strength and coordination.

Figure 20. A technique that arctic foxes use when chasing prey: cut off the angle. The chaser takes the "inside" path during arcing chases. The circle is the chasee and the triangle is the chaser.
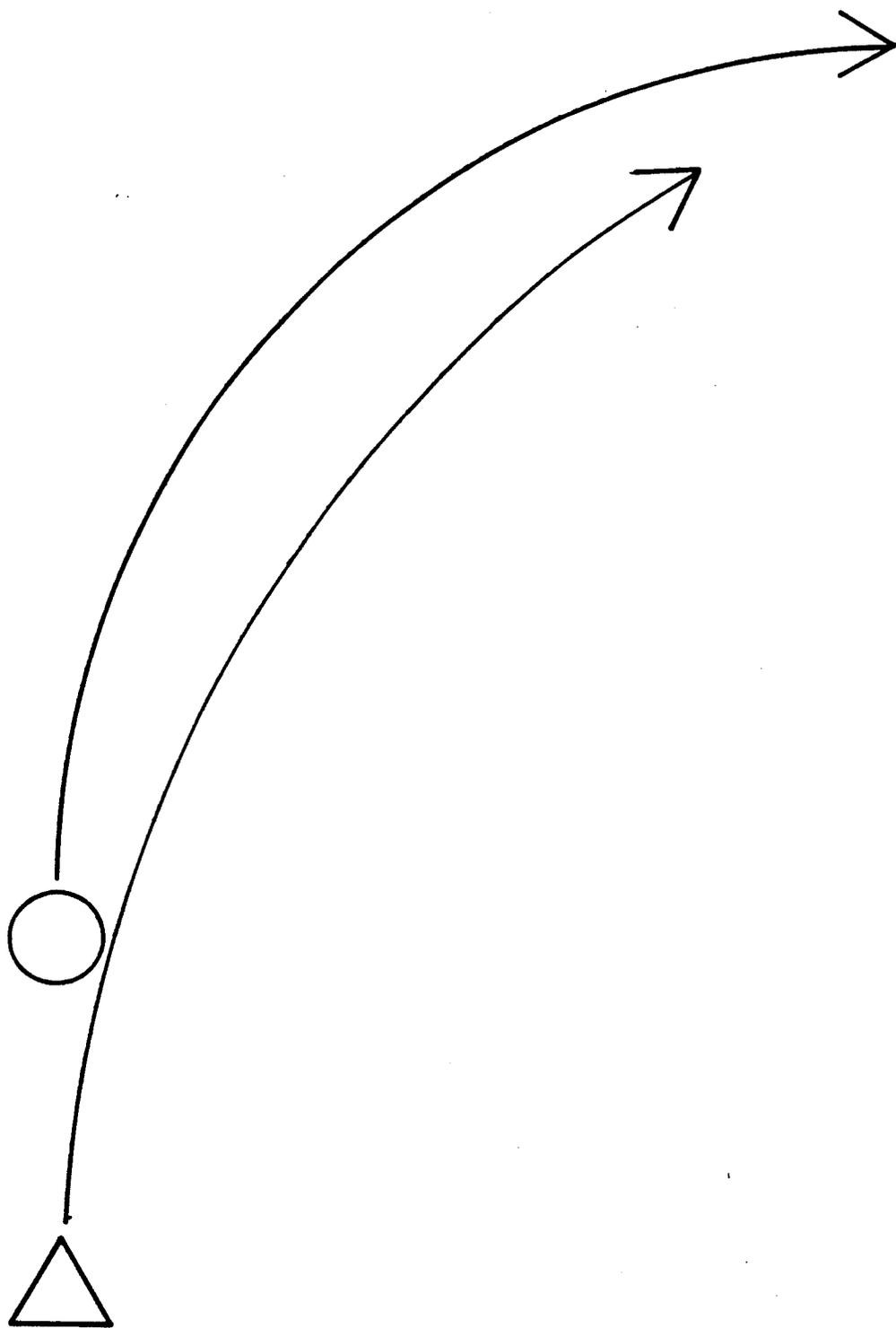
Figure 21. A defensive maneuver of arctic foxes: the end-swap. As the fox gallops (i) it pivots 180 degrees on its front feet at point A (ii). It then pivots on its hind feet at point B (iii) and continues to gallop in the original direction (iv).

i)

ii)

iii)

iv)
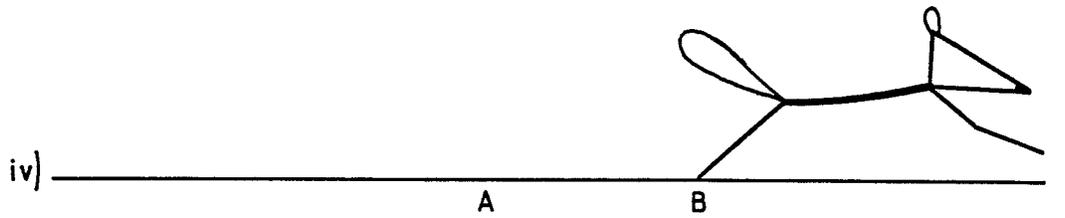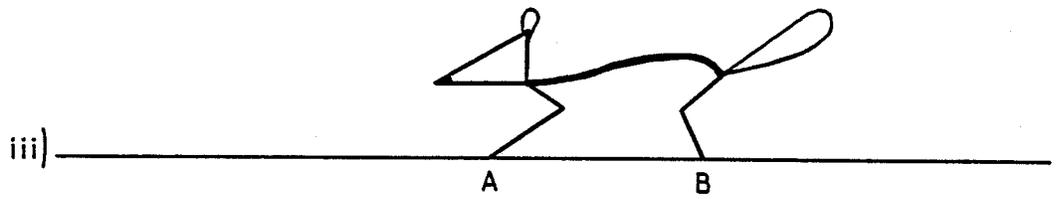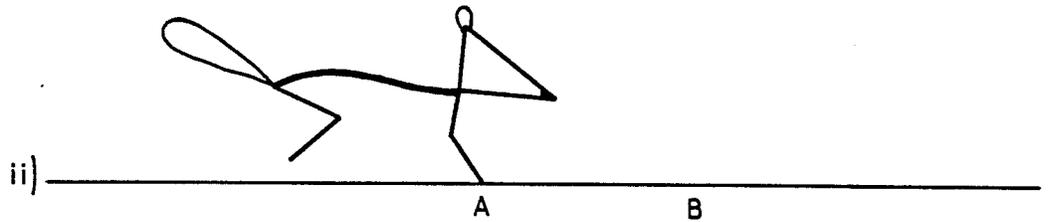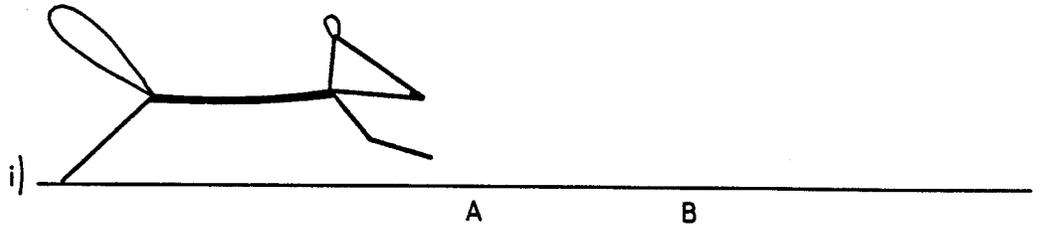
SUMMARY AND CONCLUSIONS

Arctic foxes were studied near Cape Churchill in summers 1985 and 1986 primarily to examine their hunting ecology and food habits, and to estimate their impact on the local Canada goose population. Goose defenses to fox predation, and fox pup development were also observed, while lemming populations were assessed through a small mammal trapping program.

Observations of pup development were strictly illustrative and suggestive due to the limitations of ad libitum sampling. Nevertheless, the observations in this study agreed with previous work in the literature.

The pups' body colouration changed from entirely greyish-brown on Day 21 to the sharply defined colouration of adults by Day 70. Their responses to unusual stimuli developed from little or no apparent response before Day 33, to decisive responses indicative of wariness and alertness after Day 35.

The pups begged from an adult on Day 31 and were probably eating solid food by Day 33. Their repertoire of vocalizations increased with time, and I suspect that both learning and innate factors were involved in the process.

The pups' locomotor abilities developed as they grew. Their repertoire of physical maneuvers and predatory behaviours expanded with time and I suspect that the expansion was due to learning, innate factors and to increases in strength and coordination.

During the period immediately following the pups' first emergence from the den, the pups played together only on the den surface and only when an adult was present. With time, the pups showed increasingly greater independence from their fellow siblings, the den and the adults.

The pups' rapid behavioural maturation closely paralleled their rapid physical growth, and I suspect that the two were strongly interdependent.

Adult foxes from two dens were followed on hunts during the summers of 1985 and 1986. Fewer observation hours were accumulated in 1986 due primarily to the foxes' infrequent visits to their dens during the day.

Entire hunts ranged from 15-220 min. in duration and from 2.3 km to an estimated 18 km in length. All hunts extended farther than one kilometer from the den due to the distribution of productive hunting grounds within the foxes' home ranges. The total distance covered during a day of hunting was not determined, but a fox covered an estimated 25-30 km during 5.67 h of hunting on one day in 1985.

Foxes travelled at an average speed of 5.3 km/h during hunts in 1986, but this figure includes time spent on capture attempts and investigations. Their actual lope speed was estimated to range from 7-11 km/h. Foxes zig-zagged and loped at various speeds as they foraged, but they loped quickly and steadily towards distant goals. Investigations ranged from a quick head turn and simultaneous sniff to sudden stops where the fox investigated a spot for several seconds. Other foraging behaviours, eg. jumping, swimming were also described.

During the course of a hunt, foxes travelled in a loop that began and ended at the den. Within 100-300 m of the den, the foxes followed fairly specific routes that led them to lowland areas where their paths were less specific. Foxes may go on several hunts per day, but on consecutive hunts they typically loop through a part of their home range other than the part they had just traversed.

During hunts, foxes covered the most distance and made the majority of kills in the peat lowlands, where a wide variety of prey existed. Prey in that habitat seemed more accessible and abundant relative to other habitats. Foxes investigated shorelines but they did not forage extensively in that habitat. Beach ridges were

not hunting grounds. They were used only for direct travel to or from the den, or in crossing from one lowland area to another.

Home range sizes varied from 10.5 sq. km to 15 sq. km and the amount of overlap between neighbouring home ranges varied from 15% to 77%. These values are probably minimums because they were based on a fairly small number of observations. Foxes hunted over their entire home ranges even when conspicuous prey was fairly concentrated in certain areas. Though foxes were not observed to travel directly to distant areas of prey concentrations, I suspect that they hunted along routes that sooner or later included such areas.

Interactions between neighbouring foxes included vocalizations, chases, and agonistic displays in overlap areas.

The foxes' methods for detecting and capturing lemmings were described. The foxes were successful in 88% of capture attempts for lemmings in 1985 and in 57% of attempts in 1986. In 1985, 62% of the lemmings caught were cached, 25% were eaten immediately and 12% were brought directly to the den. Of the four lemmings caught in 1986, two were cached, one was eaten and one was brought to the den.

The foxes' methods for detecting and capturing goose eggs and goslings were described. Foxes were successful in 62.5% of attempts to capture goose eggs in 1985, and in 67% of attempts in 1986. Foxes sometimes attacked a goose nest more than once in quick succession. By doing so, they sometimes captured more than one egg from the same nest. Geese showed variations in their abilities to defend their nests. The bases for the variations were undetermined but they may have been related to the goose's physical condition, experience in nest defense, individual temperment and sensitivity to a human presence or to the location of the nest. All goose eggs captured were cached.

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Foxes may capture more than one gosling during a single attempt on a flock of geese. Captured geese and goslings may be eaten on the spot, brought to the den for the fox pups, or cached either near the capture point or near the den.

Estimates for the foxes impact on the Canada goose egg crop within their home ranges varied from 14% to 35% of the eggs available. These values are lower than the percent nest failures recorded by goose researchers. Such was expected because gulls and jaegers also prey on goose nests. However, an accurate assessment of the egg loss due to foxes cannot be given due to the arbitrary conditions imposed for the calculations.

Foxes preyed upon duck, shorebird, passerine and ptarmigan nests by simply approaching the nest and taking or eating the eggs. All duck and ptarmigan eggs were cached. All passerine eggs were eaten on the spot. All shorebird eggs were cached in 1985, while 36% were eaten and 64% were cached in 1986.

Direct observations of the foxes' food habits were made during hunts and at fox dens. Indirect observations were made through the collection of scats and goose feet on fox dens. and through observations of other prey remains on dens.

The small mammal trapping program, along with observations of snowy owls, the number of lemmings caught per hour and the number of lemmings brought to dens, indicated that lemming populations were high in 1985 and lower in 1986. Lemmings were the predominant food source when they were abundant in 1985, though foxes preyed on birds whenever the opportunity arose. Meals from caches were rare in that year. Avian prey became the predominant food source when lemming populations were low in 1986, and cached food items became a larger part of the adult foxes' diet.

Foxes attacked, killed and ate more prey per time and per distance in 1985 than in 1986. This was probably due to the abundance of lemmings in 1985 that allowed the foxes to encounter more prey per time and per distance than they could when

lemmings populations were lower in 1986.

Lemmings were the only food item brought to dens during June 1985. During July and August of that year, ie. after goose hatch, avian prey items, especially goslings, were the predominant items brought to dens though lemmings were still brought occasionally. Foxes brought fewer lemmings to their dens in 1986. When they did so, they brought fewer lemmings at one time than they did in 1985. During July 1986, avian food items again became the predominant prey type brought to dens.

Observations of goose remains on dens showed that most remains were from snow goslings, while a small percentage were from adult geese. Canada geese accounted for a low percentage of goose remains found on dens. This observation was expected in light of the large number of snow geese available within the foxes' home ranges.

Scat analysis reflected the direct observation that lemmings were the predominant food source for adult foxes in June 1985, and that foxes began to eat goslings when that food source became available after hatch. During July and August, scat contents reflected the pups' diet, which consisted mainly of goslings.

More detailed analysis of pup scats from July 1986 revealed an almost universal frequency of bird remains and a high frequency of plant material. Most plant material was probably ingested accidentally. The fairly high frequency of lemming remains in scats was not expected from the low number of lemmings that I observed adult foxes bring to their dens. Insect remains were present in pup scats, but insects were probably ingested along with other food or perhaps in play.

Due to the limitations inherent in the methods, some data could not support strong conclusions concerning the foxes' hunting ecology and food habits. Nevertheless, the observations in this study were consistent with the arctic foxes' opportunistic foraging strategy. When lemming populations were large in 1985, foxes encountered more lemmings than other prey types and so took mostly lemmings. When

lemming populations were low in 1986, foxes encountered more nests than lemmings, and so took eggs. When an influx of snow geese and goslings into the study area occurred after hatch, the foxes took advantage of the new food source but they did not abandon previously used prey types or foraging patterns. Quite simply, the foxes took prey as they found it.

The foxes' impact on the Canada goose population was limited largely to the period before hatch, when eggs were available. After hatch, the influx of snow geese and goslings relieved predation pressure on the Canada geese.

Interactions between snowy owls and adult foxes were described. An owl appeared to take a food item from a fox on one occasion. During most interactions, the owl seemed to have been simply harassing the fox, though it may have been trying to capture the fox.

Observations of pup mortality included those of pup remains in a snowy owl nest, and of a decomposing carcass near one den. At one den, a pup seemed to have been impaired mentally and was found dead a few days later. In 1985, six pups whose eyes were not yet open were found scattered about a den area. The reasons for this event were unknown. It seemed unlikely that the pups crawled from the den on their own, and it may have been that the parents or some other fox removed them from the den.

Interactions Between Arctic Foxes and Snowy Owls

In 1985, I observed two ways that snowy owls approached hunting arctic foxes. In four cases, the owl was standing on top of a beach ridge or hill when he sighted the fox. In one case, the owl was already in the air when I sighted it. At the time, the fox was either excavating a lemming burrow, foraging or carrying food back to the den, and he was apparently unaware of the approaching owl.

In cases where the owl approached the fox from above (Fig. 22) the fox was carrying food to the den. In one instance that occurred during the evening, I saw the owl silhouetted against the sky as it approached from the rear and glided slowly about 10 m above the fox. I could barely see the fox lope along with a large light-coloured object in its mouth - probably a gosling or an adult snow goose. The owl suddenly folded its wings back and dropped straight down toward the fox. I heard the fox scream, and as the owl rose above the horizon and became silhouetted again, it had a large object in its talons. The fox watched the owl fly away then loped towards lowland area number 6, with nothing in his mouth. In two similar instances, the owl again approached from the rear and glided about five meters above the fox, who was carrying a mouthful of lemmings. The owl folded its wings and dropped toward the fox. In one case, the fox noticed the owl just in time to drop his lemmings and to duck. The owl missed the fox and flew away. In the other case, the fox noticed the owl as the bird started to drop. The fox dropped his lemmings, leaped up at the owl and tried to bite it but the owl veered upwards and flew away.

Owls also approached foxes by gliding just above the ground, and again from the rear (Fig. 23). In one case, the fox noticed the owl when the bird was still several meters away. He cowered and screamed at first but he became aggressive as

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Figure 22. Interaction between an arctic fox and a snowy owl. The owl approaches the fox from above (A) and glides into position without flapping its wings. B) the owl folds its wings and drops towards the fox.
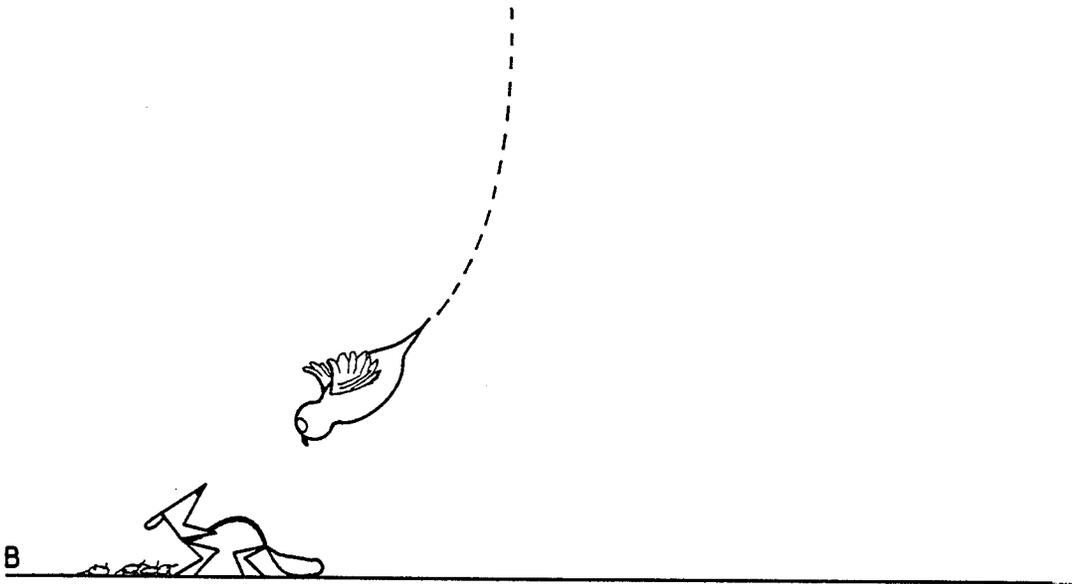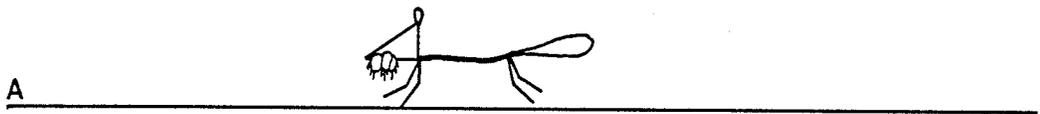
Figure 23. Interaction between an arctic fox and a snowy owl. The owl approaches the fox from behind by gliding just above the ground without flapping its wings (A). B) the fox detects the owl and cowers. C) the owl veers upwards as the fox turns to defend itself.

A

B

C

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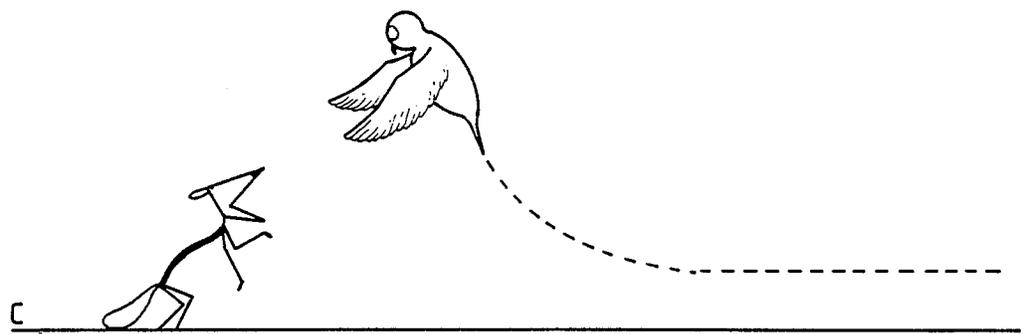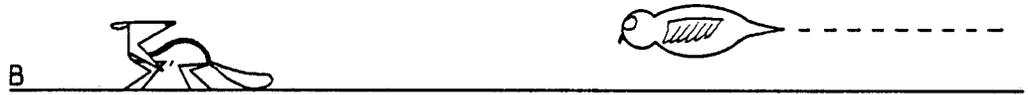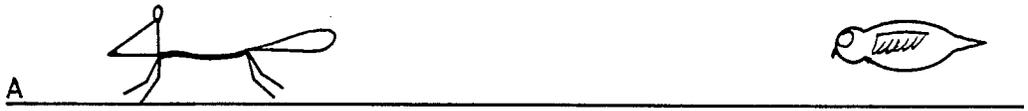
the owl neared. The owl veered upward at the last moment, the fox leaped at the owl and the bird flew away. In another case, the owl had almost reached the fox when the fox noticed the bird. The fox ducked and gaped and again the owl veered upward and flew away. The foxes' screams in these instances had a nasal quality, and they were "somewhat like the scream of a domestic cat" (Sdobnikov 1958).

Snowy owls will kill arctic fox pups (Barabash-Nikiforov 1938, Bannikov 1969). Bent (1938) reported an incident where a snowy owl attacked and severely wounded an adult arctic fox that was caught in a trap before human intervention ended the attack. As A.M. Bailey (in Bent 1938) and his dog approached a snowy owl nest, the resident owl dropped " from the sky on folded wings" repeatedly in an attempt to drive the intruders away. Several other authors in Bent (1938) described similar encounters.

In the present study, the reasons for the attacks were unknown except for the case where the owl took the fox's object. The owl may have been trying to take the lemmings in the cases where the foxes were carrying lemmings. In the other cases, the owls' single swoop and stealthy approach suggested that the owl may have been trying to capture the fox. However, all these attacks occurred in the same area. Therefore, the owl may have been simply harassing a fox that had entered its territory or who was nearing the owl's nest.

Definitions of Underlined Terms in Pup Development

The definitions come from several sources and some are my own. RHCD is the Random House College Dictionary and WCTD is Webster's Clear Type Dictionary.

alert: keenly aware of surroundings; keen active observation (RHCD 1982). Quick to perceive and act (WCTD 1976).

ambush: the act of lying concealed so as to attack by surprise (RHCD 1982). While lying concealed, the pup was fully crouched with its belly on or almost on the ground.

back-arch: a posture where the pup arches its back and tail, extends its legs stiffly and faces its antagonist broadside. Adults additionally gaped, lowered their heads and ears and walked with a stiff-legged or stilted gait. This posture is an agonistic posture (Fox 1969).

bark: a quick bark that is used in two contexts (Fine 1980):

1) a single alarm bark to which the pups always responded by bolting down the den entrances.

2) an information or announcement bark that was often repeated. "Other foxes generally responded to this call by facing the danger, and perhaps barking themselves. The announcement bark sounded less sharp than the alarm bark, indicative perhaps of a less imminent danger (Fine 1980).

beg: a pup was considered to be begging when it tried to touch another fox's mouth with its own (Frafjord 1986).

bolt: the strongest flight reaction (Frafjord 1986). The pups sprinted to the den and most often ran down the entrances. In the early weeks, the pups stayed inside the den for a while after bolting, but as they matured, a few pups would sometimes emerge again almost immediately and look around.

cache: caches are used to hide or store food items. The fox selects a cache site, pulls the vegetation aside with its front paws then places the item in the hole thus created. The fox then covers the item by using its nose to push back and tamp down the displaced vegetation.

cut-back: during a chase, the leader dodges and stops suddenly. The chaser overshoots the leader who then runs across the chaser's path behind the chaser.

cut off the angle: when a pup gallops in an arcing path, the chaser gallops along the "inside" path rather than follow directly behind the chasee.

dig: the pups would dig a small hole, usually not more than about 4 cm deep, with their front paws. The apparent purpose was not so much to dig a hole as to perform the act of digging.

dodge: to move aside suddenly (RHCD 1982). Sometimes a stationary pup appeared to wait until a charging playmate was close, then dodge and gallop. The playmate usually could not change directions in time to catch the pup.

end-swap: during a chase, the leader makes a sudden 180 degree turn and stop followed immediately by another 180 degree turn to continue galloping in the original direction.

follow the adult away: pups followed adults away from the den. The adult may lope ahead of the pups then stop and wait for the pups to catch up before moving on again.

gallop: the fastest gait where the animal can move at its maximum speed. There is a period during the cycle of footfalls where all four feet are off the ground. The sequence of footfalls is: right hind, then left hind and right fore simultaneously, then left fore (Coggins 1984). Carrington (1967) gives a sequence of footfalls where all the feet strike the ground individually: right hind, then left hind, then right fore, then left fore.

handle solid food: manipulate solid food without eating it.

head-shake: violent side to side shaking of the head while grasping prey in the jaws. During playfights, head-shaking while delivering a play bite sometimes brought a yelp from the playmate.

hip-slam: a blow delivered with the hips by quickly moving them laterally to slam into the playmate. Pups often hip-slam while turning away from playmate to avoid a play bite (Fox 1969).

leap: "Jumping...off the ground, tail held high; four paws together upon landing, head snaps down quickly after landing" (Speller 1972).

lope: a medium paced gait that is really a slow gallop. There is a period during the cycle of footfalls where all four feet are off the ground. The sequence of footfalls is: right hind, then left hind and right fore simultaneously, then left fore (Coggins 1984).

lunge: a sudden forward thrust (RHCS 1982). The fox thrusts forward with its hind legs and may or may not keep its front paws on the ground.

meandering: "A pup seems to move relaxed and at random around in an area, exploring with all its senses" (Frafjord 1986). This activity was "opportunistic rather than purposeful..." and "typically ended in play with found objects or other pups" (Fine 1980).

90 degree turn: a very sharp right-angle turn performed at a lope or a gallop.

parallel play: "This behaviour is intermediate between solo and social play, and is most often observed in two pups running alongside each other or digging under the same tussock. Pups are primarily playing solo, but one responds to the other's acts by doing the same as his play partner (Frafjord 1986).

playfighting: social play that consists of both chasing and wrestling. Chasing and wrestling were closely related (Frafjord 1986) in that one often ended in the other.

pounce: "Rearing up on hind quarters, tail up and landing with both front paws together" (Speller 1972).

resting: pups rested on the den surface by lying down fully recumbent with their eyes closed or by lying down with their eyes open and head upraised. The pups also either sat motionless with their eyes closed for short periods of time or sat and looked around.

rumble: "Arctic foxes gave a throaty rumble when threatening other foxes. Adults frequently rumbled at pups and pups rumbled at siblings during disputes over food" (Fine 1980).

scruff-bite: a bite specifically directed towards the scruff of the neck. During playfights, pups also direct bites towards the shoulder, cheek, tail and occasionally the muzzle (Fox 1969). Bites delivered in play are not delivered with full force (Fagan 1981).

secure: "Pups ran as fast as they could toward adults carrying prey, and collected as many prey items as possible. Then they most often ran away from other individuals to a place where they could eat their food undisturbed" (Frafjord 1986).

side to side fake: to feign a movement in one direction then move in a different direction.

social object play: "Social object play is nearly the same as playfighting, with the main difference being that an object is handled by one of the play participants. The object seemed only to be a means of playing and not a goal in itself" (Frafjord 1986).

social play: play where pups play with each other or with adults. Chasing, wrestling, ambushing and stalking siblings are forms of social play.

solo object play: "A pup would orient itself toward a dead object with locomotor-rotational movements, or manipulate the object. This kind of playing was not intense and only occurred in short bouts" (Frafjord 1986).

solo play: play where a pup plays alone and other pups are not involved in the activity. Solo object play and digging are examples of solo play.

sprint: the sprint is a gallop, but "sprint" implies maximum acceleration to a top speed that is sustained for a short(er) distance whereas "gallop" implies a slightly slower speed that may be maintained for a longer distance. Sprinting pups seemed to be running as fast as they could while galloping pups seemed to have a slightly more relaxed stride. Pups galloped or sprinted during play chases but they always sprinted in response to an alarm bark.

staccato bark: a "musical Cooo-co-co-co-co-coo" (Fox 1970). Foxes seemed to staccato bark as an announcement of their presence to other foxes (Fine 1980). While I followed a fox on a hunt, I observed the fox exchange staccato barks with a distant, unseen fox.

stalk: to approach quarry stealthily (WCTD 1976). While stalking, a pup moved slowly in a semi-crouched position.

trot: a medium paced gait where the legs move in diagonal pairs; a front foot and the opposite hind foot strike the ground simultaneously. There is a brief period where all four feet are off the ground. The feet move in the sequence: right hind with left fore, then left hind with right fore (Coggins 1984).

unusual stimuli: any stimuli not frequently encountered on the den, eg. a passing caribou, an approaching human, a gull calling overhead.

walk: a slow gait where each foot strikes the ground separately and where there are always at least two feet touching the ground. The feet move in the sequence: right hind, then right fore, then left hind, then left fore (Coggins 1984).

wary: regarding with suspicion and caution.

withdraw: the pups move toward the den entrances and often enter the den. "The stimulus was considered as average frightening" (Frafjord 1986).

yelp: "Pups occasionally emitted a single shrill yelp, apparently in pain...during bouts of rough play and (the yelp) surprisingly did not always stop the activity" (Fine 1980). Such vocalizations let play partners know when tolerance limits have been overstepped so that play does not become too rough (Fagan 1981).

yip: a rapid series of yips in much the same pattern as the staccato bark. In July of 1985. my temporary field assistant and I came upon a den where six very young pups were scattered about the den area (see Appendix 3). Two were dead but four were alive. During the following three days as we took care of the pups until they could be flown to the zoo in Winnipeg, the pups yipped when they became restless and seemed to want to be fed. We fed them, whereupon they stopped yipping and fell asleep.

weave: a zig and a zag performed suddenly while galloping in a straight line.

zig-zag: a line, course or progression characterized by sharp turns first to one side and then to the other (RHCD 1982).

Observations of Pup Mortality

Several factors may cause pup mortality during the denning period. In years of low food availability, male foxes may not be able to supply the female with enough food during the suckling period. This may force the female to begin hunting sooner than she would normally and lead to starvation of some pups or to a total den abandonment (Speller 1972). If the pups are weaned successfully then the parents may have difficulty in meeting the pups' ever increasing food demands. The parents may then abandon the den unless "Sibling aggression reduces the food demand to the level which the adults can supply" (Speller 1972). Macpherson (1969) suggested that sibling aggression was responsible for the death of six pups from one litter. Even when an adequate supply of fresh food is available, pups may eat siblings that are weak or that have died from disease (Shibanoff 1958). Adult foxes may also kill and eat pups (Chesemore 1975). In one year at Prudhoe Bay, Fine (1980) saw that 18 of 53 recognized pups were known to have died. "Most simply disappeared" (Fine 1980), but three carcasses that were examined showed no external wounds and Fine implied that in these three cases, distemper or perhaps rabies was responsible. Frafjord (1986) saw a red fox kill an arctic fox pup, but snowy owls are probably a more significant "enemy" of young arctic foxes (Barabash-Nikiforov 1938, Bannikov 1969).

Four cases of pup mortality were observed in the present study. In June 1985, the remains of at least two pups were found in a snowy owl nest. Observations of snowy owls standing on fox dens suggest that the owl had killed the pups rather than just scavenged carcasses. In late July, a largely decomposed and dried-out carcass of a fox pup was found about 100 m from an active den. The cause of death was not determined but the skull was intact.

On 11 July 1985, I found a den where six very young pups were scattered about and lying motionless within about 10 m of their den. Two of the pups were dead but four were still alive. I took the four pups back to camp and took care of them for three days until a plane could take them to Winnipeg. The two dead pups each had several narrow, linear bruises about 3-4 cm long scattered over their bodies. One of the live pups had a gaping skin tear on one of its shoulders. These wounds suggested that gulls had pecked and bit the pup as they lay outside the den. These wounds were the only signs of trauma found on the pups. The eyes of the four live pups were not yet open. The pups could drag themselves around on their bellies but they could not stand up. On the third day, the largest of the pups could remain standing if I stood him up, but his legs were shakey. Also, the eyes of this and of one other pup were opening. I estimated that these pups were at least one week younger than the pups at den B, who had already emerged from their den on 28 June. The reasons why the pups were scattered about their den were unknown. It was unlikely that they crawled out of the den by themselves, so I conjecture that the parents or some other fox removed them from the den. The four pups are now alive and well at the Winnipeg zoo.

The final instance of pup mortality was observed in late July 1986. I noticed that one pup from den C was not as coordinated, wary or alert as the other pups. If I approached it, it moved to a den entrance and looked toward me but its gaze was not intense. The movements, actions and responses of the pup gave the distinct impression that the pup was mentally impaired. I returned to the den a few days later and found the pup dead.

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