The Arctic Fox, *Alopex lagopus*, as a Marine Mammal; Physical Condition and Population Age Structure.

by

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The Arctic Fox: Physical Condition and Population Age Structure

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Abstract

Methods of age determination and the assessment of physical condition of trapped arctic foxes, Alopex lagopus, were examined.

The presence or absence of primary incremental lines in tooth cementum is related to physical condition of juveniles and to month of capture for both juveniles and adults. A combination of femur marrow fat plus kidney or omentum fat index are the best indices of physical condition. Arctic foxes trapped in March and April are in better condition than foxes trapped in November. The proportion of juvenile animals in the harvest ranges from a low of 17.4% to a high of 95.8% in different years. Reproduction by females in their first year is positively correlated to their physical condition. Female mortality rates are higher than male mortality rates and may be related to reproduction. Arctic fox populations appear capable of quickly adjusting their numbers in response to changes in availability of critical resources. This might be accomplished by maximizing recruitment possibly at the expense of increased adult female mortality.

Résumé

Plusieurs méthodes employées pour déterminer l'âge et la condition physique des renards arctique ont été examinés. La présence de bandes annuelles dans le ciment des dents est relié à la condition physique des renards juvéniles, et à la date de capture des juvéniles et adultes. Une mesure basé sur la teneure de gras de moelle dans le fémur avec l'index de gras des reins ou de l'omentum est la plus utile pour décrire la condition des renards. Les renards trappés en mars-avril étaient en meilleurs conditions que ceux prient en novembre. La proportion de juvéniles dans la récolte annuelle a varié de 17.4 à 95.8 pourcent durant différentes années. Le statut reproductif des femmelles juvéniles démontre une corrélation positive avec leur condition physique. Une taux de mortalité plus élevé chez les femmelles pourrait être relié à l'effort de la reproduction. Les populations de renard arctique semble avoir la capacité d'ajuster rapidement leur nombre en répondant à une baisse des ressources sur lesquelles ils dépendent. Ceci est peut-être accompli en augmentant la croissance, même si il aurait une hausse de mortalité chez les femmelles.

Introduction

The arctic fox is the most important source of cash revenue derived from a harvested renewable resource in the Northwest Territories (Tinling 1982). The majority of arctic fox pelts harvested in North America are trapped from the communities surrounding Amundsen Gulf, notably Sachs Harbour, Holman and Coppermine (Usher 1971 a,b). It is also in this region that the arctic fox is a major predator on ringed seal, Phoca hispida, pups and may be a significant factor in controlling ringed seal populations (Smith 1976a).

In spite of its importance to the northern economy and northern ecosystem, detailed studies on the arctic fox in Canada with respect to its basic biology, ecology and its role as a rabies vector have been few (Macpherson 1969; Speller 1972; Urquhart 1973; Smith 1976a; Secord, Bradley, Eaton and Mitchell 1980; Bradley, Secord and Prins 1981).

In Alaska researchers have examined its denning ecology, seasonal movements, feeding, behaviour and growth (Chesemore 1968a, b, 1969; Fine 1980; Garrott 1980); bioenergetics (Underwood 1971); home range and long distance movements (Eberhardt, Hanson, Bengston, Garrott and Hanson 1982; Eberhardt and Hanson 1978).

Additional material has been published on; age determination (Klevezal and Kleinenberg 1969; Grue and Jensen 1976); its biology in the U.S.S.R. (Lavrov 1932; Boitzov 1937; Dementyeff 1951; Tchirkova 1951; Smirnov 1967) in Greenland (Braestrup 1941); its distribution and movements in Finland (Pulliainen 1965) and in Norway (Ostbye, Skar, Svalastog and Westby 1978).

This study was undertaken in order to determine the characteristics and population structure of the arctic fox population being harvested by the Holman trappers along the western coast of Victoria Island. An effort was made to develop a method of assessing the physical condition of individual foxes and to record the changes in the condition of foxes during the trapping season (November to April). Factors causing changes in the physical condition of foxes were examined and the effect of these changes on the vital parameters of the population are discussed.

The Study Area

The study was based on the village of Holman located on the west coast of Victoria Island, N.W.T. (70°10'N, 115°30'W). A description of the geology, climate and economy of the study area can be found in Abrahamson (1963), and Usher (1965). Usher (1971a, b) in particular gives an excellent description of the history, methods and economics of the fox trapping industry on nearby Banks Island. Previous biological studies in the area surrounding Holman have been limited. Porsild (1951) and Smith (1973) have described the avifauna of the region. Macpherson (1969) identified the locations of fox dens. The most extensive biological studies have been carried out on the ringed seal in Prince Albert Sound and in Amundsen Gulf (Smith and Stirling 1975, 1978).

Materials and Methods

Data collection

Fox specimens were purchased from Inuit trappers in the village of Holman during January to May in 1973, 1974 and during November to May in 1979-80 and 1980-81. A total of 29 different trappers provided samples, and three of these provided samples throughout the entire study. Only fox heads were obtained during the first two years of the collection program along with information on sex, date trapped and name of trapper. In 1980-81 whole carcasses minus pelts were purchased from the trappers along with the appropriate documentation.

Age determination

Four different methods were examined for their usefulness as indicators of age.

A canine tooth was extracted from the upper jaws of 2700 foxes; it was then cut in half using a bench mounted jeweller's slotting saw (7.62 cm diameter) and the crown was discarded. The remaining root was placed in a 30% buffered formic acid solution (Humason 1967). Decalcified teeth were then stored in 70% ethanol before further processing occurred. Sections 15-20μm thick were cut on a cryostat (Ames Lab-tek) at a temperature of -18°to -20°C, mounted on slides and stained with Harris' haematoxylin (Humason 1967). Age could then be determined by counting the dark staining incremental lines in the cementum (Kleinenberg and Klevezal 1966; Grue and Jensen 1976). Each tooth was examined twice to determine age and the time of year that formation of the dark staining line began. Age determined by this method was used as the reference age to which ages derived from the other techniques were compared.

One hundred and seventy-five teeth were selected to include all the age classes encountered. These were read six times to determine the precision of the cementum line technique. Precision was expressed in terms of the average percent error (APE), $APE=\frac{1}{R}\cdot\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}$ (Beamish and Fournier 1981), where X_{ij} is the ith age determination of the jth tooth, X_j is the mean age for the jth tooth and R is the total number of times the jth tooth is aged. A coefficient of variation (V), $V=S_j/X_j$ where S is the standard deviation of the jth tooth and X_j is the mean age of the jth tooth and an index of precision, D=V/R, were also calculated (Chang 1982). The estimates for each tooth were then averaged to determine the precision involved in ageing each age class.

A subsample of 744 teeth was examined to determine age at which closure of the pulp cavity occurred. Diameter of the root canal opening was measured using an optical micrometer.

The length of one upper canine tooth was measured along the anterior edge of the tooth from the alveolus to the proximal edge of the enamel, as in the technique employed by

Macpherson (1969). Regression analysis was used to relate tooth length to age in years.

Closure of skull sutures as a means of separating juveniles from adults was also examined. In 185 cleaned skulls the basisphenoid-presphenoid and basisphenoid-basioccipital sutures were examined and classified as open, closing or closed.

Physical condition and body measurements

All specimens minus pelt were weighed to the nearest 250g. Body length was measured from the tip of the nose to the base of the tail. Anterior girth was measured as the maximum girth immediately posterior to the forelimbs. Posterior girth was measured as the minimum girth immediately anterior to the hind limbs. A body weight index expressed in kg/cm was determined by dividing body weight by body length.

One femur from each of 110 carcasses was cracked open and all marrow removed and freeze-dried at -80°C for 24 hours. Prior to analysis samples were oven dried at 65°C for 12-24 hours. Percentage of marrow fat was determined gravimetrically following extraction with a microsoxhlet apparatus (chloroform: methanol 2:1) (Giese 1967). The crude extract was washed with 0.9% NaCl (Folch, Lees and Scoane-Stanley 1957). Two samples from each specimen were analysed using dried marrow weights of 50-150 mg each.

A kidney fat index (100× perinephric fat weight(g)/kidney weight (g) was calculated using the method of Hanks, Cumming, Orpen, Parry and Warren (1976). Indices were calculated for each kidney and the two values averaged.

An omentum fat index was determined by weighing the greater omentum to the nearest 0.01 g and dividing by body length.

Physical condition was assessed subjectively, based on the method of Kistner, Trainer and Hartmann (1980). The method involves assigning subjective scores of 0, 5, 10 or 15 based on the amount of fat present at six target sites; heart and coronary groove, pericardium, omentum, kidneys, rump and chest. Summing the scores for the six sites plus a score of 0 or 5 if the body musculature appears bony or full, respectively, gives a possible maximum total of 95. Four indices were used to determine the changes in condition occurring during the trapping season from November until April. All foxes examined were caught in leg hold traps. Animals which had spent 10 days or less in the trap were selected from the catch returns of five trappers. Because traps are checked at irregular intervals during December, January and February I was restricted to comparisons of body condition for the months of November, March and April. Significant differences in condition were accepted if these differences occurred in two or more of the condition indices considered.

Discriminant function analysis

Information on sex was incomplete for the 1973 collection. From this sample adults were sexed using discriminant function analysis. Twelve measurements were taken from the skulls of foxes after they had been cleaned in a dermestid beetle colony. Each measurement was taken twice to the nearest 0.01 mm using vernier calipers. Measurements differing more than 0.5 mm were repeated and the pair of measurements with the least difference were kept. The 12 measurements were: 1) total skull length measured from the posterior edge of the sagittal crest to the anterior edge of the premaxillary over tooth I_1; 2) zygomatic width measured as the maximum width of the zygomatic arches; 3) braincase width measured as the maximum width of the braincase taken at the parietal-temporal suture; 4) least cranial width measured as the minimum width across the frontal bones posterior to the postorbital processes; 5) interorbital width measured as the minimum width across the frontal bones anterior to the postorbital processes; 6) palatal length measured as the maximum length along the midline from the anterior edge of the premaxillary to the posterior edge of the palatine bone; 7) postpalatal length measured as the maximum length from the posterior tip of the palatine to the posterior edge of the occipital condyle; 8) crown length, (C-M_2) measured as the length from the anterior edge of the canine to the posterior edge of the maxillary; 9) palatal width measured as the width taken from the external surfaces of the posterior root of the carnassial teeth; 10) palatal width measured as the width taken from the external surfaces of the maxillary at the posterior root of P_2; 11) palatal width measured as the distance between the external surfaces of the canine teeth; 12) carnassial tooth length measured as the maximum length of the carnassial tooth.

Analysis of reproductive tracts

Reproductive tracts were collected from females only. Maximum length and width of each ovary and the maximum diameter of each uterine horn midway between the ovary and cervix were measured using vernier calipers to the nearest 0.1 mm. These were recorded as a mean ovary diameter for each reproductive tract. Ovaries with a mean diameter of 5 mm or less were not examined. These were from immature animals and did not show any sign of follicular activity.

Each ovary with a mean diameter greater than 5 mm was sectioned into four or five parts with a scalpel blade and examined under a dissecting microscope. The number of follicles greater than 0.4 mm were counted and the two maximum perpendicular diameters of the largest follicle were recorded using an optical micrometer. These were combined from each reproductive tract and expressed as the mean number of follicles and the mean follicle diameter per ovary. The number of corpora lutea and the two maximum perpendicular diameters of the largest corpus luteum were also recorded from each reproductive tract and are expressed as mean number and mean diameter of corpora lutea per ovary.

Placental scars were divided into two categories depending on whether the scars were black or grey in colour. Grey placental scars represent embryos that may have died in the early stages of gestation or they may remain from previous pregnancies. Dark placental scars remain from successful pregnancies or from embryos that died late in gestation (Englund 1970). The number of scars of each type occurring in each uterine horn were recorded.

Estimates of fox predation

Ringed seal birth lairs and other seal structures were detected by olfaction using a trained Labrador retriever bitch (Smith and Stirling 1975). Seal density was calculated from the number of seal structures found per minute searched. Evidence of fox predation was noted and the successful predation of foxes on seal pups, indicated by the presence of blood or pup remains in the birth lair is expressed as a percentage of birth lairs found (Smith 1976a).

Statistical treatment of the data

Multivariate analysis of the morphometric measurements was carried out using the discriminant function procedure of the Statistical Analysis Systems package (SAS Institute Inc., P.O. Box 8000, Cary, N.C., 27511, U.S.A.). The procedure computes a generalized squared distance (D^2) value which provides a measure of how much each skull deviates from the mean of each known group. Based on the criterion developed from samples of known sex, specimens are classified into the group which produces the smallest D^2. The non-parametric Kruskal-Wallis k sample test was used to test for differences in frequency distributions between two or more variables. A Chi-square test to determine if two characteristics occurred independently of each other was also used (Siegel 1956). All test statistics were tested for significance at $P<0.05$.

Age Determination

Various methods have been used to determine the age of Canids including: counting incremental lines in tooth cementum (Kleinenburg and Klevezal 1966; Jensen and Nielsen 1968; Grue and Jensen 1976), the extent of closure of skull sutures (Dolgov and Rossolimo 1966; Gurskii 1973) and the measurement of tooth length (Churcher 1960; Macpherson 1969; Allen 1974).

Very few attempts have been made to calculate the accuracy or precision when using these techniques (Dapson 1980; Beamish and Fournier 1981). I measured the precision of several techniques and discuss the influence of factors such as physical condition, reproductive state and month of capture on the age estimates. Throughout the remaining text all animals referred to as adults were greater than one year of age; younger animals are called juveniles.

Age from cementum lines

The cementum consists of alternating very narrow opaque (dark) staining lines and much wider translucent (pale) bands. These dark narrow lines will be referred to as primary incremental lines or simply the incremental lines (fig. 1). Counting the number of primary incremental lines gave the age of the animal.

In many teeth a narrow staining line or lines of intermediate intensity (secondary line) in addition to the incremental line and a translucent band of cementum, was detected. These secondary lines are not continuous across the root end or down the side of

Fig. 1. Photograph of the root section of the canine tooth of a female arctic fox caught in April. Two primary incremental lines are visible with a third incremental line beginning to form at the tooth edge.

the root, or they appear as a double line alongside the primary incremental line.

The dark staining incremental lines are detected most easily at the root end of the tooth. However, this region is most likely to be cluttered with secondary lines. In the cementum extending towards the distal portion of the tooth the dark lines are more regular, fewer secondary lines are present, but the alternating translucent bands are narrower making it difficult to count the incremental lines if the animals are old. Because of these difficulties, dark lines were considered primary incremental lines if they extended from the apex of the root and along at least one side of the tooth. Alternatively, age was assigned if agreement could be found in the number of primary incremental lines from two different regions of the tooth.

Intensity of the stain of the dark line was most variable for animals aged 1+ years. In the animals 2+ years of age or older the intensity of the stain forming the dark line was more consistent beginning at the second incremental line. The width of the translucent band of cementum was greatest in the first layer of tooth growth. In successive layers the bands became progressively smaller.

Estimates of precision of the cementum line technique are presented in table 1. Precision is greatest in animals aged 0+ years and least in animals aged 1+ years. Precision decreased from age 2+ to 6+ but was still greater than the precision estimated for 1+ animals. Reasons for this observed decrease in precision assocated with aging animals one year of age or older are discussed below (p22).

Table 1. Average precision of age estimates for each age class using six replicate counts for each tooth examined. Age determination is based on counts of cementum lines.

Age (Years)	Sample Size	Average Percent Error	Coefficient of Error	Index of Precision
0+	96	.0283	.0232	.0104
1+	13	.2279	.2932	.1236
2+	49	.0590	.0820	.0329
3+	7	.1251	.1740	.0739
4+	1	.0731	.1066	.0435
5+	5	.0680	.0929	.0396
6+	4	.1136	.1412	.0594

Factors possibly affecting the presence of the primary incremental line at the outer edge of the tooth were investigated using a Chi-square test. Presence of the primary incremental line for juveniles (0+ years) and adults (≥1+ years) was significantly related to the month of capture (table 2; $\chi^2=16.8$ and 184.9, respectively; df=6, $p<0.05$ for both cases). The presence of the incremental line at the outer edge of the tooth was related to good physical condition in juvenile foxes, but not in adults (table 3; $\chi^2=12.47$, df=4, $p<0.05$ and $\chi^2=1.75$, df=3, $p>0.05$ respectively). There was no relation between the presence of the incremental line at the tooth edge and the reproductive status of either juvenile or adult foxes (table 4; $\chi^2=7.1$ and 1.75, df=3 and 2, $p>0.05$ in both cases).

Age from root canal closure

Closure of the pulp cavity results from the extension of the cementum around the outer edge of the dentine and across the bottom of the tooth forming a narrow root canal. Three different patterns of closure of the root canal were observed. The most simple was the formation of a regular, cylindrical shaped opening; the second, a hole with a scalloped edge, and the third, a regular shaped opening developed at the bottom of a concave depression. In 100 animals aged 1+ to 8+ years, the diameter of the largest root canal was 0.375 mm. To reduce the possibility of error it was decided that, any tooth having a root canal ≤0.5 mm in diameter would be classified as closed (adult tooth).

Table 2. Percentage of juveniles and adults with the primary incremental lines present at the tooth edge and total number of animals caught during each month of sampling.

Month	November		December		January		February		March		April		May	
Age (years)	<1	≥1	<1	≥1	<1	≥1	<1	≥1	<1	≥1	<1	≥1	<1	≥1
Foxes with incremental line present	0%	26%	1%	4%	4%	13%	6%	23%	17%	31%	27%	49%	26%	33%
Number in sample	276	19	97	31	142	16	222	40	465	131	663	160	77	43

Table 3. Percentage of juveniles and adults with the primary incremental line present at the tooth edge and total number of animals sampled in each physical condition class.

	Juveniles		Adults	
Condition Class	Foxes with line present	N	Foxes with line present	N
Emaciated (0-10)	6%	121	42%	92
Poor (11-30)	13%	24	--	--
Fair (31-50)	17%	71	50%	2
Good (51-70)	21%	89	50%	4
Excellent (71-95)	18%	157	0%	2

Table 4. Percentage of juveniles and adults with the primary incremental line present at the outer tooth edge, total number of animals sampled and reproductive state. Reproductive state was indicated by the number of follicles greater than 0.4 mm in diameter.

	Juveniles		Adults	
Number of follicles	Foxes with line present	N	Foxes with line present	N
0-5	49%	82	67%	6
6-10	30%	60	56%	9
11-15	27%	11	0%	1
16-25	0%	2		

In the total sample of 744 teeth no root canals of animals ≥1+ years (n=238) were open. Table 5 shows the number of animals aged 0+ with open root canals by month of capture. As many as 65% of juveniles could be aged by closure of the root canal from a sample caught during November. This figure was reduced to as low as 6% in the sample from March.

Age from skull suture closure

The basisphenoid-presphenoid suture was open in 10 skulls and closed in one skull aged 0+ caught before March. In juveniles caught during March-April (n=87) 46%, 18% and 36% of the skulls had open, closing and closed sutures respectively. The basisphenoid-presphenoid suture was open in two out of 70 skulls from animals ≥1+ years of age. Both animals were 2+ years of age. In all animals examined, the basisphenoid-basioccipital suture was closed.

Age from tooth length

Age from counts of cementum annuli was regressed on tooth length for each sex. No significant difference was found between their respective regression coefficients. The data were then combined producing the regression equation: $Y=0.880X-0.228$ ($F=197.9$, $df=1, 231$, $p<0.05$), where Y is the predicted age in years and X is tooth length in mm. Confidence limits for individual teeth based on the predictive equation were never less than ±2 years, showing that the ability to determine age accurately using tooth length is very poor.

Table 5. Percent of juveniles caught by month with open root canals.

	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY
Foxes with Root Canal Open	75	22	6	19	4	24	2
Total	115	46	22	46	66	150	19
% Open	65	48	27	41	6	16	11

Discussion

The counting of incremental lines in tooth cementum has been established as a valid technique for determining the age of arctic foxes based on known age material from fur farms (Kleinenburg and Klevezal 1966; Grue and Jensen 1976). An assessment of the precision of the method was required because of the subjective nature of defining primary and secondary cementum lines.

The use of a percentage agreement technique assumes that precision is independent of age (Beamish and Fournier 1981). A better measure of precision, used in this study, incorporates the effects of age into the estimate (Beamish and Fournier 1981; Chang 1982). Excluding animals aged 1+ precision decreased with age. This can be attributed to increased error resulting from the need to identify and count increasing numbers of primary incremental lines.

An explanation of the low precision associated with animals aged 1+ is more difficult. The first incremental line is the most difficult to determine because of the large variation in the intensity of the stain. This agrees with the findings of Kleinenburg and Klevezal (1966) but contrasts with the findings of Grue and Jensen (1976). Since detection of a faintly stained primary incremental line standing alone at the outer edge of the tooth is difficult, the precision of age determination of animals in the 1+ age class will be lower. In animals aged 2+

or older the last forming incremental lines are stained more intensely. These lines are classified as primary incremental lines with relatively greater ease and provide a standard to which the first forming incremental line can be compared. In these cases even if the first forming incremental line is faint, if it is regular and parallel to those of later years, it is then easily identified.

Primary incremental line formation in tooth cementum is the result of both endogenous and exogenous factors (Grue and Jensen 1979). My findings that incremental line formation is not linked to reproductive state of the females agree with Grue and Jensen (1979). Incremental line formation is linked with physical condition for juveniles only. The number of juveniles with an incremental line present increased as physical condition improved. Formation of a faint, indistinct first incremental line has also been reported for juvenile caribou, Rangifer tarandus, in poor physical condition (Reimers and Nordby 1968). In this study the proportion of foxes with an incremental line at the edge of the cementum increased from November until May. A seasonal effect is obviously present but no factors associated with the time of year at which the translucent cementum was laid down have been identified. Month of formation of the incremental line in the arctic fox has previously been stated as December to March (Klevezal and Kleinenberg 1969) or during February to May extending into the summer months (Grue and Jensen 1976). Bradley et al. (1981) working in the western Canadian Arctic report that line formation began as early as November in adults and continued until February, the last month that samples were available. This agrees with my results showing line formation continuing to May when my last samples were obtained. No doubt formation of the incremental line can extend into the summer months but samples are required from these months to confirm this. With such large variability in the time when formation of the incremental line begins, a knowledge of the date of capture is essential in order to assign animals to particular age classes.

Use of the basisphenoid-basioccipital skull suture to separate juveniles from adults was not successful since it closes at age six months (Dolgov and Rossolimo 1966; Macpherson 1969) and all animals in my sample were at least eight months old.

Macpherson (1969) stated that the basisphenoid-presphenoid suture was closed but still visible by age 12 months while Dolgov and Rossolimo (1966) reported that the basisphenoid-presphenoid suture began closing at age 10-12 months with closure complete by 18-24 months. Use of this criterion in my study to separate adults from juveniles incorrectly classified two of 70 animals aged 2+ years as juveniles for an error rate of three percent. This type of error in separating adults from juveniles is acceptable when dealing with arctic fox populations.

Regression of tooth length on age has been used to age red fox, Vulpes vulpes, (Churcher 1960; Allen 1974) and arctic fox (Macpherson 1969). Predictive equations developed using this method in my study had confidence limits which were too wide to make this a useful method.

Arctic fox harvests contain a large number of juveniles (Smirnov 1967; Macpherson 1969; Bradley et al. 1981). The decalcification and staining of teeth for age determination is expensive and time consuming. This coupled with the large variability in month of incremental line formation means that special care must be exercised when determining the age of wild foxes with the cementum line technique. Information on date of capture and relative growth rates of the dark staining lines and translucent bands of the cementum are required to estimate the age of wild foxes accurately from their teeth. A method which eliminates juveniles from further examination would remove much of the workload and expense in determining the age of fox samples.

Separation of animals aged 0+ from adults on the basis of closure of the basisphenoid-presphenoid skull suture or closure of the root canal of a canine tooth is recommended. Closure of skull sutures and the tooth root canals would have eliminated 90% and 53% respectively of the juveniles from foxes captured before March. These methods are inexpensive and require little sample preparation before use.

Assessment of Physical Condition

Fat content has often been used as a measure of physical condition because it is the primary source of energy for the body during periods of starvation (Harris 1945; Young and Scrimshaw 1971), and has been related to the onset of puberty and fertility in man (Pond 1978) and in ungulates (Thomas 1982). Determination of body fat content has involved either direct measurement or the development of an index of body fat content from one of several sites in the body. Methods used include, percentage body fat calculated from carcass fat density (Anderson, Medin and Bowden 1972), weight-length relationships (Bailey 1968), femur marrow fat (Ransom 1965), kidney fat index (Riney 1955; Finger, Brisben, Smith and Urbston 1981), omentum weight (Woodall 1978) and a subjective physical condition index (Kistner et al. 1980). This section discusses the development of quick and reliable methods for assessing the physical condition of trapped foxes. These methods are applied to animals caught during 1980-81 to determine seasonal changes in condition.

Age, size and weight relationships

In the initial subsample 87 of 93 animals, whose age could be determined, were less than 12 months old. No significant difference in length between adults and juveniles was found.

Significant differences were found between males and females for body weight (χ^2=90.5, df=1, n=1399, p<0.05) and body length χ^2=151.95, df=1, n=515, p<0.05). Mean weights for males and females were 2.5 kg and 2.1 kg respectively. Mean body lengths were 56.0 cm for males and 53.3 cm for females.

Weight could be related to anterior girth, posterior girth and body length by the regression equation: $WT=0.09838X_1+0.08822X_2+0.03104X_3-3.1852$ (WT= body weight (kg), X_1=anterior girth (cm), X_2=posterior girth (cm), X_3=body length (F=165.1, df=3, 43, p<0.05)).

Relation of condition indices to femur marrow and kidney fat

Spearman correlation coefficients were calculated between the indices used to assess body condition. Sample sizes for all correlations range from n=45 to 108. The strongest correlations were observed between kidney fat index and the body measurements as well as with the subjective score method. These had a range in value from R=0.77 to 0.94, (p<0.01). Weaker correlations were observed between femur marrow fat and the body measurements as well as the subjective score method. These had a range of R=0.58 to 0.71, (p<0.01).

Mobilization of visible fat reserves began in the subcutaneous areas followed by the fat around the kidneys and omentum and finally fat around the pericardium and heart. Fat mobilization occurred in an overlapping fashion, fat being mobilized around the kidneys before subcutaneous fat reserves had been exhausted.

Visible changes in body musculature did not occur until body fat had been exhausted.

Animals in excellent condition as seen by maximum values of 95% for femur marrow fat had corresponding values of 68% for kidney fat index, 2.8 g/cm for omentum fat index and 95 for the subjective score. These animals had a maximum subcutaneous fat thickness of 1.5 cm over the rump. Maximum values recorded for posterior girth were 38.0 cm and 25.0 cm, for anterior girth 39.0 cm and 30.0 cm and for body weight 4.2 kg and 3.8 kg for males and females respectively.

In animals of intermediate condition where the percentage femur marrow fat ranged from 75-95%, the kidney fat index exceeded 15%, the omentum fat index exceeded 0.309 g/cm, the subjective score exceeded 40, the posterior girth exceeded 16.0 cm for both sexes and body weight exceeded 2.5 kg for both sexes. The kidney fat index and omentum fat index reached a value of 0 when the percentage femur marrow fat was 35% or less. The subjective score decreased to 0 at a femur marrow value of 10%. At this level of femur marrow fat, posterior girth decreased to an average of 14.6 cm and 12.9 cm for males and females respectively. Body weight decreased to an average of 2.1 kg and 1.7 kg for males and females respectively.

Values for femur marrow fat, kidney fat index, omentum fat index and subjective score for 16 to 18 foxes found dead in the traps were significantly lower than those of animals found alive (χ^2=35.4, 30.8, 31.8 and 34.9, respectively, df=1, $p<0.05$). Mean values were 16.2% for femur marrow fat, 1.0% for kidney fat index, 0.01 g/cm for omentum fat index, and 6.4 for the subjective score.

Arbitrary condition classes were created using the subjective score method. Table 6 shows how these condition classes relate to mean percentage femur marrow fat, omentum and kidney fat indices. Posterior girth and body weight for male and female skinned carcasses are also shown for these condition classes.

Trapline and seasonal differences in condition

Comparisons of the condition indices were made between trappers to see if differences in physical condition occurred between foxes taken from different traplines. These differences would indicate the presence of possible sampling biases. Location of the traplines are shown in figure 2 (trappers 1-5).

There were no significant differences in the condition of male foxes between the samples from the five trappers for the indices; body weight, body weight index, posterior girth and subjective score. For female foxes no differences were found between the catches of trappers for all condition indices except subjective score (χ^2= 18.9, df=4, $p<0.05$). With the catches of all trappers pooled, comparisons of the condition indices showed significant differences ($p<0.05$) between the months November, March and April in all condition indices in

Table 6. Mean values for the measured condition indices of each subjective score class.

Subjective score class	Femur marrow fat (%)		Kidney fat index (%)		Omentum fat index (g/cm)		Male body weight (kg)		Male posterior girth (cm)		Female body weight (	
	n	x̄	n	x̄	n	x̄	n	x̄	n	x̄	n	
Emaciated (0-10)	20	10.18	21	0.00	20	0.00	9	2.12	9	15.11	7	1
Poor (11-30)	2	33.95	2	6.85	2	0.24	1	2.30	1	15.50	1	2
Fair (31-50)	30	72.94	28	10.42	23	0.30	12	2.63	15	17.33	6	2
Good (51-70)	24	87.22	24	31.03	18	0.83	5	3.02	8	22.06	5	2
Excellent (71-95)	31	85.17	33	51.12	27	1.57	8	3.56	14	25.06	8	3

the measured condition indices of each subjective score class.

arrow	Kidney fat index (%)		Omentum fat index (g/cm)		Male body weight (kg)		Male posterior girth (cm)		Female body weight (kg)		Female posterior girth (cm)	
x̄	n	x̄	n	x̄	n	x̄	n	x̄	n	x̄	n	x̄
0.18	21	0.00	20	0.00	9	2.12	9	15.11	7	1.69	11	13.00
3.95	2	6.85	2	0.24	1	2.30	1	15.50	1	2.40	1	16.00
2.94	28	10.42	23	0.30	12	2.63	15	17.33	6	2.15	7	16.29
7.22	24	31.03	18	0.83	5	3.02	8	22.06	5	2.24	9	17.58
5.17	33	51.12	27	1.57	8	3.56	14	25.06	8	3.11	12	22.02

males: subjective score (χ^2=28.96, df=2), posterior girth (χ^2=6.15, df=2), body weight (χ^2=13.68, df=2) and body weight index (χ^2=7.20, df=2). In females significant differences were found only for the subjective score (χ^2 =18.29, df=2, $p<0.05$) and posterior girth (χ^2 =10.67, df=2, $p<0.05$). Table 7 shows mean values for the condition indices considered. Indices of condition for both males and females are higher during March and April than during November. Males were significantly higher than females in November ~~for the~~ body weight index (χ^2=6.52, df=1, $p<0.05$), but not for the subjective score. In March males had a significantly higher subjective score (χ^2=8.44, df=1, $p<0.05$), but no significant difference was found for body weight index. Posterior girth was then divided by body length to remove the effect of sexual dimorphism in size. Differences in condition between sexes using this method were significant for November only (χ^2 =5.93, df=1, $p<0.05$), showing males to be in better condition. During April condition levels for both sexes were similar. There were no significant differences in condition between adults and juveniles caught in November, March and April.

Discussion

Very little information is available on the seasonal changes in condition in the arctic fox. A physical condition index for trapped arctic foxes can provide a means of assessing the health of arctic fox populations from year to year. This might lead to a better understanding of the factors causing the large oscillations seen in arctic fox populations (Macpherson 1969).

Table 7. Mean condition values of arctic foxes trapped during November, March and April.

	November			March			April		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Males									
Body weight (kg)	89	2.73	0.71	61	3.20	0.88	93	2.73	0.80
Body weight index (kg/cm)	45	0.05	0.01	25	0.06	0.01	31	0.05	0.01
Subjective score	92	48.70	31.39	64	73.05	24.52	109	67.04	24.74
Posterior girth (cm)	48	19.65	4.66	23	22.38	4.71	45	21.04	5.62
Females									
Body weight (kg)	43	2.31	0.64	34	2.37	0.64	61	2.36	0.70
Body weight index (kg/cm)	21	0.04	0.01	11	0.05	0.01	23	0.05	0.01
Subjective score	47	40.53	31.82	33	54.24	29.50	67	66.34	25.87
Posterior girth (cm)	26	16.36	3.09	11	20.35	4.30	25	20.09	5.29

Arctic foxes attain full size by the age of five or six months (Fine 1980). Therefore the large number of juveniles in the sample is not thought to have affected the validity of the different fat indices used in this study. From my results I was able to determine critical values at which death occurred in trapped foxes. These values must be considered only as upper limits because my samples were taken from extremely stressed animals.

Bone marrow fat is the best method for assessing the physical condition of animals in a poor state (Ransom 1965). For animals in good shape both the kidney fat index and the omentum fat index are better indicators of body condition. However, all these methods require equipment which may not be available in a field camp. The combination of the subjective score method and body measurements provide a suitable index of condition for animals ranging from poor to good condition. They are easy to use and require little experience.

This study has shown that male arctic foxes are in better condition than females caught in November. This might be explained by the larger home range of males which tend to disperse earlier than do females from the den site (Fine 1980). Such access to a larger area might decrease competition for food and increase its availability to individual males.

A definite improvement was documented in the body condition of foxes harvested during March and April in comparison to those taken during the fall months. This has also been demonstrated in the studies of Boitzov (1937) and Segal, Popovich and Vain-Rib (1976). Underwood (1971) reported a diminished condition in Alaskan arctic foxes trapped from December to March, but appears not to have taken trap stress into account during his assessment. Several factors appear to be involved in influencing the seasonal condition of foxes. It is not thought that the improvement in condition is related simply to the increased hunting experience of the young foxes which form a large part of the stock. Gross energy requirements of the arctic fox in the winter have been found to be only 50% of those in summer. The difference is attributed to the decrease in energy required for thermoregulation, a result of the exceptionally good insulative properties of the winter pelt (Underwood 1971). This adaption of the arctic fox to low temperatures coupled with the possibility that there might be elevated food resources at this time of the year, such as winter born lemmings (Mallory, Elliot and Brooks 1981) and ringed seal pups (Smith 1976a), probably results in the improved condition documented here. This improvement in condition may be of great importance for successful mating and the ultimate reproductive success of the fox population.

Population Dynamics

Sex determination by discriminant function analysis

Information on sex was incomplete for the 1973 collection of fox skulls. In order to determine the sex of these samples discriminant function analysis was used. Discriminant function analysis presupposes that two or more classification groups exist. Sexual dimorphism in arctic fox skulls has been confirmed by Bisaillon and DeRoth (1980).

To eliminate the effects of differential growth rates in young foxes collected at different times of the year, only animals that had completed skull growth as indicated by the fusion of the basisphenoid-presphenoid suture, were included in the analysis. The discriminant function was developed from the 12 measurements of 10 males and five females of known sex. Mean and standard deviations for the 12 skull measurements from the animals of known sex are listed in table 8. The discriminant function classified 247 skulls as male or female.

Analysis of the harvest of individual trappers

Samples were collected from areas to the north and to the south of the village of Holman. Age structures and sex ratios of the catch of each trapper were compared to see if the population could be described adequately in the future by the catch of one trapper, or if many samples would be required from different trappers because of possible sampling biases.

Figure 2 shows the approximate trapline location on Victoria Island of the seven Holman trappers who supplied large samples or participated in the collecting program over more than one year. In 1973, samples were obtained from trappers 1, 4, 5

Table 8. Mean and standard deviations of the 12 measurements (mm) from 10 males and five females used to construct the discriminant function.

	Males		Females	
	$\bar{x}$	s	$\bar{x}$	s
Total skull length	127.12	4.76	122.34	4.89
Zygomatic width	70.55	2.77	67.53	2.77
Braincase width	46.07	1.38	45.22	1.23
Least cranial width	23.30	0.77	24.29	1.07
Interorbital width	28.12	2.10	27.89	2.47
Palatal length	62.70	2.37	60.42	3.45
Postpalatal length	58.88	2.37	56.86	2.20
Crown length ($C-M_2$)	55.27	1.55	52.44	2.74
Palatal width (P_4)	40.64	1.90	39.23	1.49
Palatal width (P_2)	24.11	1.43	23.12	1.04
Palatal width (C)	23.39	0.95	22.16	1.40
Carnaissal tooth length	13.81	0.66	13.36	0.66

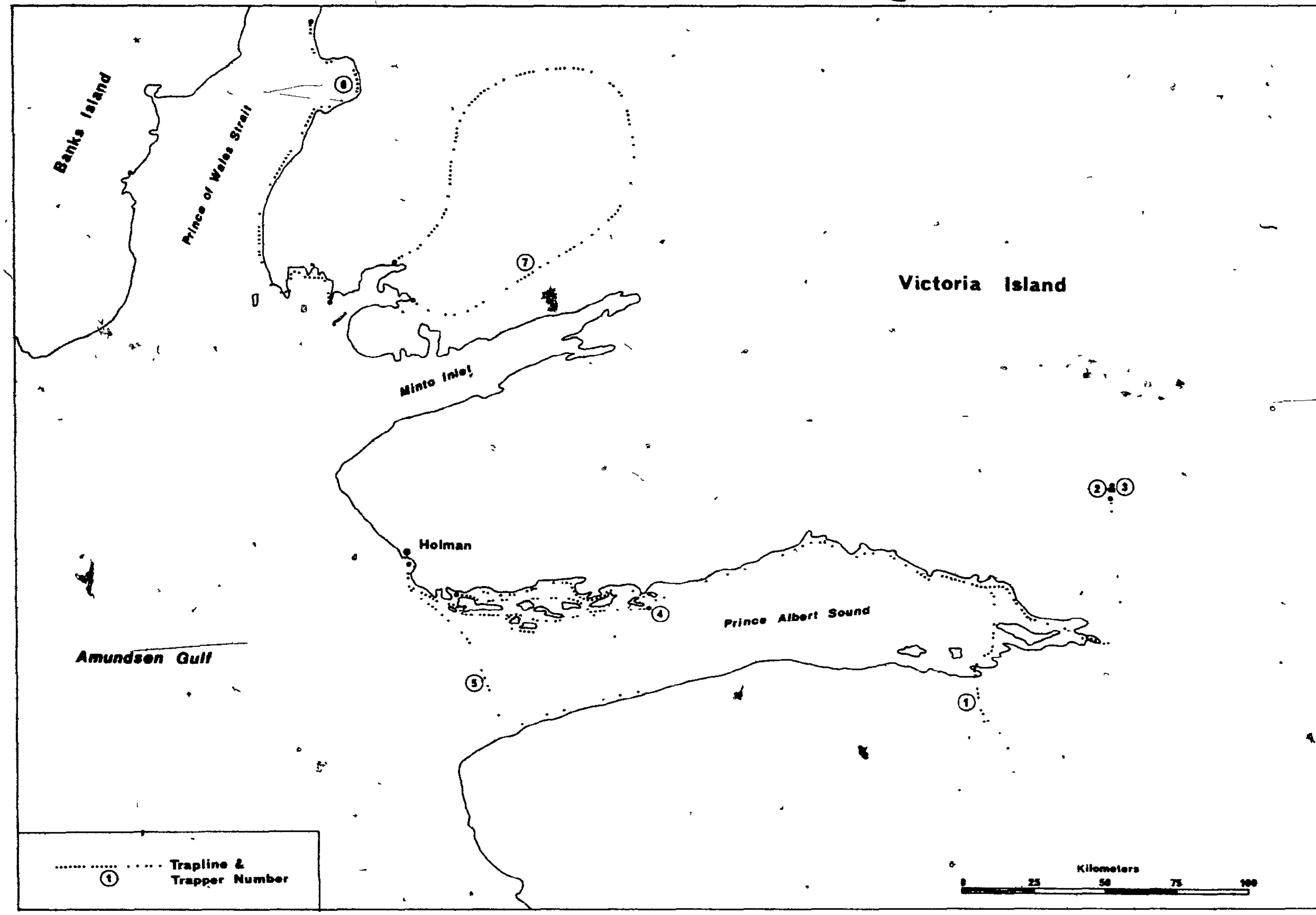

Fig. 2. Trapline locations on western Victoria Island of the seven trappers who provided the largest samples during this study.

and 6. Significant differences between the age frequency distributions of the catch of difference trappers were found for females only (χ^2 =13.16, df=3).

In 1979-80 significant differences were found between the catches of trappers in the age frequency distributions of both males (χ^2=31.97, df=4) and females (χ^2 =17.73, df=4). No significant differences were found in the age frequency distributions between trappers in the samples obtained in 1974 and 1980-81.

Significant differences in the sex ratios of catches between trappers were found only in the sample from 1974 (χ^2 =62.24, df=6).

Age structure of the annual harvests

Significant differences were detected between the age frequency distributions of the pooled annual harvests from the four different years of sampling (χ^2 =409.95, df=3). These differences resulted from large variations in the proportion of juveniles in the harvests which ranged from a high of 96% in the 1981 harvest to a low of 17% in 1973 (table 9).

The age structure of the harvest of the 1979-80 trapping season showed monthly changes. The proportion of juveniles was greatest in samples obtained in November and least in the month of April. The percentage of juveniles in the harvest with total number of animals collected in brackets was; 81%(75), 74%(42), 81%(75), 76%(144) and 45%(123) for the months November, December, January, February and April respectively. In the harvest

Table 9. Age frequencies of catches of arctic fox, *Alopex lagopus*, for four different years presented as a percentage of the total catch for each year.

Year	1973	1974	1980	1981
Age (years)				
0	17.4	90.8	65.5	95.8
1	22.2	2.2	10.2	0.7
2	48.5	2.6	9.9	0.6
3	2.6	2.6	5.0	0.6
4	1.0	0.4	3.2	0.6
5	4.1	0.4	3.2	0.3
6	2.6	0.9	0.6	0.5
7	1.1	--	0.6	0.7
8	--	--	0.9	--
9	--	--	0.9	--
10	--	0.2	--	--
N=	270	578	342	965

from the following year, 1980-81, only a slight change in the proportion of juveniles in the harvest was recorded through the year. For the months of November through May the percentage of juveniles with total number of animals collected in brackets was; 98%(219), 97%(68), 96%(83), 97%(119), 95%(270), 96%(454) and 97%(35) respectively.

Comparisons of the mean age between the two sexes showed significant differences only for the 1973 sample. In this sample the mean age for males was 1.97 years (n=69) and for females 1.60 years (n=95) (χ^2=4.54, df=1, $p<0.05$). The mean age for males was also higher for the 1980 sample, the only other sample with relatively large numbers of adults. Mean ages for males and females were 1.22 years (sd=1.96, n=129) and 0.81 years (sd=1.62, n=213) respectively (χ^2=3.0, df=1, $p>0.05$).

Sex ratio of the harvests

Adult sex ratios did not differ significantly from 1:1 in the annual harvest of foxes for the four years of sampling. Similarly, juvenile sex ratios were 1:1 for the samples collected in 1974 and 1980. However in the 1981 sample juvenile males significantly outnumbered females by a ratio of 544:377 (χ^2=30.3, df=1, $p<0.05$).

Monthly changes in the sex ratio of the catch are listed for the 1979-80 and 1980-81 catches in table 10. In 1979-80

Table 10. Adult and juvenile sex ratios of arctic fox harvests by month for the 1979-80 and 1980-81 trapping seasons. Chi-square values for departures from a 1:1 sex ratio are listed in brackets. An asteri
denotes significance at p<0.05.

	November	December	January	February	March	Apri
	Males:Females	Males:Females	Males:Females	Males:Females	Males:Females	Males:F
1979-80						
Juveniles	24:37(1.4)	19:12(1.6)	26:35(1.3)	38:71(10.0)*	---	13:42
Adults	12:2 (8.7)*	2:9 (4.17)*	8:6 (0.3)	13:22(2.3)	---	31:37
1980-81						
Juveniles	138:76(9.0)*	33:33	44:68(5.14)*	68:47(3.8)	173:85(30.0)*	239:19
Adults	2:3	1:1	1:1	1:4 (1.8)	3:9 (3.0)	15:5

e sex ratios of arctic fox harvests by month for the 1979-80 and 1980-81 trapping
are values for departures from a 1:1 sex ratio are listed in brackets. An asterisk
nce at $p<0.05$.

r	December	January	February	March	April	May
ales	Males:Females	Males:Females	Males:Females	Males:Females	Males:Females	Males:Females
.4)	19:12(1.6)	26:35(1.3)	38:71(10.0)*	---	13:42(15.3)*	---
.7)*	2:9 (4.17)*	8:6 (0.3)	13:22(2.3)	---	31:37(0.5)	---
.0)*	33:33	44:68(5.14)*	68:47(3.8)	173:85(30.0)*	239:195(4.5)*	20:14(1.1)
	1:1	1:1	1:4 (1.8)	3:9 (3.0)	15:5 (5.0)*	1:1

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significant departures from a 1:1 sex ratio were found in favour of juvenile females caught during the months of February and April. In the harvest from 1980-81 the sex ratio ~~was~~ reversed; significant departures from a 1:1 sex ratio were found in favour of juvenile males collected during November, March and April.

In the adult segment of the catch, significant departures from a 1:1 sex ratio were found in the 1979-80 November and December catch. The disparity in sex ratio favoured males by a ratio of 12:2 in November but was reversed to favour females in December by a ratio of 9:2. In 1980-81 a significant departure from a 1:1 sex ratio was found in favour of males in the April harvest.

Female reproductive data

A total of 545 reproductive tracts was collected during 1980-81. Of these, 524 were from juveniles, 362 of which showed no signs of follicular activity.

Mean diameters of the pairs of ovaries, uteri, largest follicle, largest corpus luteum, number of follicles and corpora lutea are listed by month in table 11. In both juveniles and adults the mean diameters of the ovaries, uteri and largest follicle increased from November to April. The mean number of follicles larger than 0.4 mm in diameter was greatest in foxes caught during March and decreased in foxes caught during April. The largest follicle recorded, from a juvenile caught in April had a mean diameter of 3.2 mm. The

Table 11. Mean statistics for the juvenile and adult arctic fox reproductive data from each month of the trapping season.

	November			December			January			February			March			A
	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄
Juvenile																
Ovary diameter (mm)	7.2	1.4	3	7.7	--	1	8.4	0.8	5	7.4	1.0	11	8.9	1.7	35	9.2
Uterus width (mm)	1.5	0.7	2	1.3	--	1	2.0	0.0	2	1.6	0.5	5	1.8	0.4	24	2.0
Mean no. of follicles/ovary	2.9	4.0	5	0.5	--	1	3.2	4.4	6	3.0	3.5	11	5.1	5.8	37	3.9
Largest follicle diameter (mm)	0.7	0.1	2	--	--	0	0.8	0.0	2	0.6	0.1	11	0.8	0.2	19	1.0
Mean no. of corpora lutea	0.0	--	5	0.0	--	1	0.0	--	5	0.0	--	11	0.0	--	37	3.5
Diameter of largest corpus luteum (mm)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.7
Adult																
Ovary diameter (mm)	10.2	4.3	2	6.7	--	1	9.5	0.1	2	8.3	1.6	3	10.0	1.5	6	11.8
Uterus width(mm)	2.2	1.1	2	--	--	--	2.6	--	1	4.3	3.0	2	2.4	0.5	7	3.0
Mean no. of follicles/ovary	3.0	3.5	2	0.0	--	1	3.8	4.6	2	4.0	4.9	3	6.8	2.5	7	2.8
Largest follicle diameter (mm)	0.6	--	1	--	--	--	1.0	--	1	1.8	1.8	2	1.1	0.2	7	1.2
Mean no. of corpora lutea	0.0	--	2	0.0	--	1	0.0	--	2	0.0	--	3	--	--	--	4.0
Diameter of largest corpus luteum (mm)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.8

ics for the juvenile and adult arctic fox reproductive data from each month of the
son.

vember		December			January			February			March			April			May		
s	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s	n
1.4	3	7.7	--	1	8.4	0.8	5	7.4	1.0	11	8.9	1.7	35	9.2	2.7	94	6.1	--	1
0.7	2	1.3	--	1	2.0	0.0	2	1.6	0.5	5	1.8	0.4	24	2.0	0.8	64	--	--	--
4.0	5	0.5	--	1	3.2	4.4	6	3.0	3.5	11	5.1	5.8	37	3.9	3.3	101	0.0	--	1
0.1	2	--	--	0	0.8	0.0	2	0.6	0.1	11	0.8	0.2	19	1.0	0.5	56	--	--	--
--	5	0.0	--	1	0.0	--	5	0.0	--	11	0.0	--	37	3.5	0.7	2	0.0	--	1
--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.7	1.1	2	--	--	--
4.3	2	6.7	--	1	9.5	0.1	2	8.3	1.6	3	10.0	1.5	6	11.8	--	1	--	--	--
1.1	2	--	--	--	2.6	--	1	4.3	3.0	2	2.4	0.5	7	3.0	--	1	--	--	--
3.5	2	0.0	--	1	3.8	4.6	2	4.0	4.9	3	6.8	2.5	7	2.8	3.3	4	--	--	--
--	1	--	--	--	1.0	--	1	1.8	1.8	2	1.1	0.2	7	1.2	--	1	--	--	--
--	2	0.0	--	1	0.0	--	2	0.0	--	3	--	--	--	4.0	--	1	--	--	--
--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.8	--	1	--	--	--

largest follicle found in an adult female had a mean diameter of 3.1 mm. Comparisons were made between adult and juvenile animals. Significant differences were found only for follicle diameter, adult reproductive tracts having significantly larger follicles than juveniles ($\chi^2=7.01$, df=1).

Corpora lutea were found in both ovaries of two juveniles and one adult captured 14 April. Diameters of the largest corpora lutea for the two juveniles and one adult were 5.5, 3.8 and 4.8 mm respectively.

Placental scars were found in 16 reproductive tracts from animals which ranged from two to seven years in age. No placental scars were found in any females aged one year old; (n=5). The mean number of dark placental scars present per reproductive tract was 9.5 (sd=7.8, n=16). The largest number of placental scars was found in a reproductive tract from a female aged six years caught in January 1981. In the right uterus 21 dark scars were counted while only four dark scars were counted in the left uterus. No grey scars were present. Grey placental scars made up only 12% of the total number of placental scars recorded.

Life table analysis

In order to summarize the information on mortality, separate life tables of the kl_x series (Caughley 1977) were constructed for each sex using the data from 1980. Calculation of the life table statistics followed the methods of Caughley (1977) where; survivorship (l_x) is the probability at birth that an animal will survive to age x; mortality (d_x) is the probability

Table 12. Life tables for male and female arctic foxes trapped during November to April 1980.

Females

Age at birth pulse (Years)	Observed age frequency	Smoothed age frequency	l_x	d_x	q_x	L_x	e_x	P_x	F_x
0	197	274.0[a]	1.000	0.909	0.909	0.546	0.76	0.143	0.000
1	25	25.0	0.091	0.027	0.296	0.078	2.40	0.692	1.966
2	19	17.6	0.064	0.020	0.312	0.054	2.19	0.667	1.966
3	12	12.1	0.044	0.015	0.339	0.036	1.95	0.667	1.966
4	8	8.0	0.029	0.010	0.350	0.024	1.72	0.667	1.966
5	5	5.2	0.019	0.007	0.346	0.016	1.37	0.625	1.966
6	2	3.4	0.012	0.004	0.323	0.010	0.83	0.000	1.966
7	2	2.3	0.008						
8	3	1.5							
9	1	1.0							

Males

Age at birth pulse (Years)	Observed age frequency	Smoothed age frequency	l_x	d_x	q_x	L_x	e_x
0	120	146.2[a]	1.000	0.897	0.897	0.552	0.78
1	15	15.0	0.103	0.080	0.780	0.063	2.18
2	22	3.3	0.023	0.000	0.000	0.023	7.04
3	11	3.3	0.023	0.000	0.000	0.023	6.04
4	5	3.3	0.023	0.001	0.030	0.022	5.04
5	7	3.2	0.022	0.000	0.000	0.022	4.27
6	1	3.2	0.022	0.000	0.000	0.022	3.27
7	1	3.2	0.022	0.002	0.062	0.021	2.27
8	1	3.0	0.020	0.004	0.233	0.018	1.45
9	2	2.3	0.016	0.010	0.652	0.011	0.69
10	1	0.8	0.006				

[a] = adjusted age frequency (m_x=3.60)

that an animal will die during the age interval x to x+1; mortality rate (q_x) is the proportion of animals alive at age x that die before age x+1; L_x is the mean survival between ages x and x+1 and life expectancy (e_x) is the mean age at death of the cohort members (table 12). Smoothed age frequencies were generated by converting observed age frequencies to probits and regressing these probits on age raised to the *i*th power (Caughley 1977). The resulting regressions were: $Probit=14.58-13.10x^{0.1}$ for females and $Probit=0.78-1.01x^{11.9}$ for males. Age frequency of juveniles in the life table was adjusted by multiplying the smoothed age frequencies for the 1980 adult age classes by age specific fecundity (m_x). Because the sample size of adult females was small, the reproductive data were pooled. Fecundity was then calculated by dividing the total number of placental scars by two times the number of adult females harvested in 1981. This gave a value of $m_x=3.60$. Mortality rates for both sexes during their first year were similar, although female mortality rates were slightly higher. In two year old animals, male mortality rates are much higher than female mortality rates. From ages three to six years female mortality is much higher than male mortality.

The 1981 harvest was the highest recorded in Holman since 1974 (table 15). The age structure of the population contained an extremely high proportion of juveniles (table 9). To determine what factors may have been acting on the population age structure to produce the age structure observed in the 1981 harvest, a deterministic population model (Leslie 1945, 1948) was constructed

Table 13. Leslie projection matrix (M), smoothed 1980 age distribution (vector x), 1981 age distribution (vector a), and predicted age vectors from the matrix model simulations.

$$
M = \begin{array}{ccccccc}
0.000 & 1.966 & 1.966 & 1.966 & 1.966 & 1.966 & 1.966 \\
0.143 & & & & & & \\
 & 0.692 & & & & & \\
 & & 0.667 & & & & \\
 & & & 0.667 & & & \\
 & & & & 0.667 & & \\
 & & & & & 0.625 & \\
 & & & & & & 0.000
\end{array}
\qquad
x = \begin{array}{c}
274.0 \\ 25.0 \\ 17.6 \\ 12.1 \\ 8.0 \\ 5.2 \\ 3.4
\end{array}
$$

Age (Years)	1981 age frequency (%) N=395	Predicted age frequency (%) F =1.966	Predicted age frequency (%) F =26.000	Predicted age frequency (%) F =1.966, P /12.000	Predicted age frequency (%) F =5.000, P /5.000
0	95.6	62.2	95.6	95.2	95.6
1	0.7	17.6	2.0	2.2	1.9
2	0.7	7.7	0.9	1.0	0.9
3	a= 0.6	b= 5.2	c= 0.6	d= 0.7	e= 0.6
4	0.6	3.6	0.4	0.5	0.4
5	0.6	2.4	0.3	0.3	0.3
6	0.6	1.4	0.2	0.2	0.2

from the 1980 female life table (table 13). The model consists of a projection matrix containing female age specific fecundity rates (F_x) in the first row. Elements in the subdiagonal contained age specific survival rates (P_x) while the remaining matrix elements had a value of 0. When the projection matrix was multiplied by a column vector containing the smoothed age frequency distribution at time t, the model produced a column vector which predicted the age frequency distribution at time t+1.

The age specific survivorship term (P_x) is the probability that a female aged x to x+1 at time t would survive to the age class x+1 to x+2 at time t+1 (Leslie 1945, 1948). From the life table $P = L_{x+1}/L_x$. Age specific fecundity (F_x) is defined as the number of daughters born during the time interval t to t+1, per female aged x to x+1 at time t, who will be alive in the group 0 to 1 at time t+1 (Leslie 1945, 1948). From the life table F_x is approximated by $F_x = L_0 m_x$.

Values for age specific survivorship (P_x) and fecundity (F_x) are derived from the smoothed 1980 age frequency distribution and presented in table 12. Both the 1980 and 1981 age distribution vectors and the results of difference simulations using the projection matrix based on the 1980 data are shown in table 13. Using the age vector from the 1980 harvest the first run of the model predicted a population consisting of 62.2% juveniles (vector b, table 13). This underestimated the proportion of juveniles observed in the 1981 harvest by 33.4% and overestimated

Table 14. Spearman correlation (R) between indices of physical condition of arctic foxes and reproductive m
An asterisk denotes significance at p<0.05.

		JUVENILES				ADULTS		
		Ovary diameter (mm)	Uterus width (mm)	Number of follicles	Follicle size (mm)	Ovary diameter (mm)	Uterus width (mm)	Number of follicles
Body weight index (kg/cm)	R=	0.492*	0.172	0.586*	0.302*	0.486	-0.086	0.350
	N=	104	71	110	61	6	6	10
Body weight (kg)	R=	0.565*	0.137	0.573	0.281*	0.064	-0.207	0.321
	N=	127	82	135	70	11	10	15
Subjective score	R=	0.411*	0.064	0.470*	0.313*	-0.343	-0.648	0.218
	N=	145	94	155	80	11	10	15
Posterior girth (cm)	R=	0.454*	0.050	0.550*	0.241*	0.036	-0.543	0.551
	N=	117	81	124	70	7	6	11

Fo

lation (R) between indices of physical condition of arctic foxes and reproductive measurements.
notes significance at p<0.05.

	JUVENILES			ADULTS			
er	Uterus width (mm)	Number of follicles	Follicle size (mm)	Ovary diameter (mm)	Uterus width (mm)	Number of follicles	Follicle size (mm)
	0.172 71	0.586* 110	0.302* 61	0.486 6	-0.086 6	0.350 10	0.714 6
	0.137 82	0.573 135	0.281* 70	0.064 11	-0.207 10	0.321 15	0.495 10
	0.064 94	0.470* 155	0.313* 80	-0.343 11	-0.648 10	0.218 15	-0.107 10
	0.050 81	0.550* 124	0.241* 70	0.036 7	-0.543 6	0.551 ~~11~~	0.143 6

the proportion of adults in the harvest by a corresponding amount. In order to increase the proportion of juveniles to correspond to my 1981 harvest data, the F_x term was increased. The value of F_x producing the age vector (vector c, table 13) which agreed best with the observed 1981 age vector, had a value of 26.0. The proportion of juveniles in the predicted age vector was 95.6%, which equalled the proportion observed in the 1981 harvest exactly. This approach is not thought to be realistic. If L_0 had been increased to the unlikely value of 1.0 then a m_x value of $m_x=26.0$ would be required. This is unreasonably large considering it represents only the female segment of the population. Examination of the effect of change in the survivorship values was investigated next. Survivorship was reduced equally across all age classes. When P_x was divided by 12.0 the predicted age vector consisted of 95.2% juveniles which was very close to the observed proportion of juveniles in the 1981 harvest (vector d, table 13). This approach also appeared to be unrealistic. During 1980-81 there was no indication from the Inuit trappers or in our own work that a large mortality of arctic fox was occurring. When both fecundity and survivorship were altered together, an age vector consisting of 95.6% juveniles was produced when $F_x=5.0$ and $P_x/5.0$ (vector e, table 13). At $F_x=5.0$, m_x would equal 9.158 if $L_0=0.546$. An increase to $L_0=0.85$ would require a m_x value of 5.882 to produce $F_x=5.0$.

Table 15. Index of abundance of ringed seal birth lairs in Prince Albert Sound, Northwest Territories with corresponding annual rates of fox predation on ringed seal pups. The annual harvest statistics for the village of Holman are shown for the years 1972 to 1982.

Year	Number of pelts traded[1]	Number of birth lairs	Successful predation rate %	Source
1972	2215	45	8.9	Smith 1976a
1973	703	38	39.5	Smith 1976a
1974	3892	32	34.4	Smith 1976a
1975	1923	4	0.0	Smith 1976a
1976	356	2	50.0	Smith unpubl.
1977	1436	7	22.0	Smith unpubl.
1978	2740	--	--	
1979	596	--	--	
1980	1887	--	--	
1981	3803	8	25.0	This study
1982	3174	--	--	

[1]Government of the Northwest Territories fur and game statistics unpublished.

Although these values for m_x and L_0 are high they might be realistic under favourable conditions.

Relationship between condition and reproductive status

The association between physical condition and reproduction was examined using Spearman correlation analysis. Significant correlations were found between the physical condition indices and the reproductive measurements in juveniles only (table 14). In adults, significant negative correlation was found only between the subjective score method and uterine width (table 14).

Predation of ringed seal pups

Table 15 lists successful predation rates of the arctic fox on ringed seal pups. Predation rates of foxes on seal pups show wide fluctuation from a low of 0% in 1975 to a high of 50% in 1976. No significant correlation was found between predation rates of foxes on seal pups and the fox harvest during the following year. However a Chi-square test of independence showed that fox harvests were not independent of fox predation rates on seal pups during the previous year (χ^2=71.0, df=6, $p<0.05$).

Discussion

The variation observed in both the age structure and sex ratio of the fox catches from individual trappers, points to the importance of obtaining large samples from as many traplines as possible in studies of arctic foxes taken from a large geographical region.

The changes in the lumped age frequency distributions of annual arctic fox harvests found in this study are similar to those reported in previous studies (Smirnov 1967; Macpherson 1969). During years of high arctic fox harvests, over 85% of the trapped animals are aged 0+, supporting the contention of a biased harvest of juveniles (Smirnov 1967; Bradley et al. 1981). Overrepresentation of juvenile foxes in the fall harvest is believed to result from their poorly developed hunting skills and trap naivety (Smirnov 1967). As the winter progresses Bradley et al. (1981) suggest that the increasing proportion of adults in the harvest results from increased hunger. We do not believe this to be the case. In some years the physical condition of arctic fox is much better in animals trapped in March than foxes trapped in November. Therefore the trap susceptibility of adults has not increased simply as a result of increased hunger.

Instead, trap susceptibility of the arctic fox may result from variations in the patterns of seasonal movements by different segments of the population. Little information is available on this subject. The general direction of movement is from the land towards the coast in the fall and then back onto the land in the spring (Chesemore 1968a). Fine (1980) found that juvenile male arctic foxes maintained larger home ranges than do females and suggested that males dispersed first. This could explain the very large proportion of juveniles with a preponderance of males seen in the fall harvests of 1980-81. In the 1979-80 harvest the greater number of adults in the harvest suggests either lower production of juveniles, increased adult dispersal or both. The tendency of males to move earlier than females is shown by the male: female sex ratio of 6:1 in the November harvest of that year. If conditions such as reduced lemming availability occurred during the latter part of the summer then juveniles may have been forced to move to the coast before the trapping season opened. This would account for the equal representation of juveniles of both sexes in the November harvest. Increased movement by adults resulting in an increasing proportion of adults being caught beginning in January may be related to an increase in sexual activity (Storm, Andrews, Phillips, Bishop, Siniff and Tester 1976). Spermatogenesis in arctic fox begins in January (Sokolov 1957) while oestrous occurs between March and May (Boitzov 1937; Dementyeff 1951).

In both samples containing large numbers of adult animals the mean ages of males were greater than the mean ages of females. Storm et al. (1976) in their spring catches of red fox, Vulpes vulpes, kits at the den, found that males outnumbered females although foetal sex ratios were 1:1. They suggested that female mortality at birth or during the first few days of life was higher than male mortality. In the arctic fox, males were found to be in much better condition than females from November to March. Males are larger which may allow them to outcompete females by maintaining a greater home range (Fine 1980) and by physical dominance. Also the poorer condition of females may result from the energetic costs of reproduction. Poorer condition of females would suggest increased susceptibility to trapping, but this effect may be masked by the greater tendency of males to wander.

Arctic fox have a very high reproductive potential. Two reproductive tracts in this study had over 20 placental scars present. Macpherson (1969) found one reproductive tract with 21 placental scars present while Lavrov (1932) reported one litter of 22 young and Gmelin (1760, cited by Boitzov 1937) observed a litter of 25 young. Previously reported mean litter sizes based on placental scar counts range from 8.85 to 12.9 with a total sample mean of 10.58 (sd=3.08, n=118) (Macpherson 1969); however, he did not differentiate between different types of placental scars. The mean litter size in this study based only on dark placental scars was 9.49 (sd=7.81, n=16). If both dark and gray scars are included in the sample, mean litter size per female increased to 10.75.

Reproduction by female arctic foxes in their first year is affected by their physical condition. Maturation of the follicles and the number of maturing follicles could be delayed in female foxes in poor condition or it may be halted altogether. Captive juvenile blue fox normally ovulate at least one week later than adults or they may not ovulate at all (Johnson 1946). He also found that female foxes kept extremely fat, regularly had 10-14 kits, while thin females had only five or six kits or none at all.

Arctic fox pups are born in late May to early June in the U.S.S.R. (Lavrov 1932) and early June in Alaska and Canada (Fine 1980; Speller 1972). Assuming a gestation period of 52 days (Venge 1959), mating occurs between the end of March to mid-April, which corresponds to the peak in numbers and size of follicles and the appearance of corpora lutea in this study. The period of mating in foxes also corresponds to the period during which the birth of ringed seal pups occurs in the Holman area (Smith 1976b). Seal pups are an alternative source of food for the arctic fox and present a large return per unit effort especially during years of lemming scarcity (Smith 1976a). The incidence of seal remains in fox stomachs has been found to increase in foxes collected at Resolute, N.W.T. during years of lemming scarcity (Macpherson 1969), although in that paper it is uncertain whether this represented increased predation of seal pups or increased scavenging of bear kills. It is interesting to note in the study by Macpherson (1969) that seal remains were not found in the stomachs of foxes collected from Baker Lake or

Eskimo Point, two communities located on the west side of Hudson Bay. In these areas, the incidence of caribou remains in fox stomachs increased during years of lemming scarcity (Macpherson 1969). Predation of seal pups by foxes would help to maintain or improve physical condition to levels necessary for successful reproduction to occur. Based on limited data, years during which fox predation of ringed seal pups is high appear to be followed by relatively large harvest of foxes. However, if an increase in lemming numbers fails to occur later in the spring or summer, other factors act to reduce reproductive success. These include intra-uterine mortality, abandonment of the kits after birth (Speller 1972), or mortality resulting from intraspecific aggression (Macpherson 1969).

The mortality rate of adult females when compared to that of adult males is higher. I suggest that increased mortality of female arctic foxes occurs as a result of the increase in the energy requirements of reproducing female foxes during years when reproductive success is high. This hypothesis when tested using the Leslie population model appeared to explain the sudden change in the age structure of the harvest observed between 1980 and 1981. The large fox harvest in Holman in 1981, the lower level of physical condition observed in females during that fall and the observed differences between the age frequency distributions of the two sexes also support this contention. The construction of a kl composite life table assumes that our samples were obtained from a closed population with a stationary age distribution (Caughley 1977). It is unlikely when dealing with arctic fox populations that these assumptions are correct. Extensive movement of large numbers of arctic foxes has been documented in Candda (Wrigley and Hatch 1976), although not in the area surrounding the Beaufort Sea. However, long distance movements by individual foxes are known to occur between Alaska, Banks Island, Victoria Island and the Coppermine area on the Canadian mainland (Urquhart 1973; Eberhardt and Hanson 1978). The movement of large numbers of juveniles into the study area would also account for the sudden increase in the proportion of juveniles observed in the harvests between 1980 and 1981.

Implications for Management

Arctic fox populations are tied very closely to changes in the abundance of their primary source of food, the lemming (Macpherson 1969; Speller 1972). It appears from my results that under certain conditions arctic foxes adopt a strategy of maximizing juvenile production at the possible cost of increased adult female mortality. Indications of a relationship between reproductive success and good physiological condition of juvenile foxes points to the importance of a reliable food source during the late winter early spring months. In the Amundsen Gulf region food resources such as seal pups appear to be consistently utilized. This contrasts with the findings of others (Macpherson 1969) that foxes under certain conditions feed extensively on caribou remains. However, the fox's utilization of the sea ice habitat and its possible feeding on ringed seal pups was not a specific aim of Macpherson's (1969) study. In order to examine if foxes feed on seal pups along the Hudson Bay coast, studies similar to this one would be required.

The arctic fox's apparent willingness to travel over long distances in short periods of time (Urquhart 1973; Eberhardt and Hanson 1978) and its varied feeding habits (Macpherson 1969, Chesemore 1978b) suggest that it is a very opportunistic animal moving back and forth between the sea ice and the land depending on the availability of local food resources.

The dependence of many modern day Inuit on long haired fur as a large part of their cash revenue emphasizes the importance of a flexible management plan for dealing with this resource.

Apart from the unpredictability of the fur market, arctic fox harvests which vary so greatly in numbers from year to year make this a rather uncertain resource on which the Inuit must earn a living.

Management strategies aimed at maximizing catches in good years and preserving breeding stock in poor years probably make the greatest sense both economically and from the biological point of view.

If it were possible to effectively monitor the age structure and physiological condition of foxes on an annual basis, schemes involving shortening or extending trapping seasons might be effective in increasing economic yields and preserving the breeding stock. In years of high fox abundance maximum trapping effort extending into late May or until a decrease in fur quality was observed, would be appropriate. This could serve to reduce fox numbers, thus increasing the food available to the remaining foxes and could result in higher recruitment. In poor years when fox numbers are low, the trapping season could be cut short, thus preserving a larger number of foxes. These would be in good condition because of less competition for food and the net result of preserving them as breeding stock would be increased recruitment. Increased trapping effort in high abundance years and reduced effort in years of low fox numbers also is reasonable in terms of cost per unit effort. This is in fact what often occurs, but frequently the spring catch in poor years forms a significant part of the total harvest.

Monitoring of the fox populations should concentrate on the two critical periods in the fox life cycle, fall and spring. In the fall, the winter fur has not finished growing. Females are recovering from the demands of reproduction and availability of food is limited because the sea ice has not formed, restricting their access to new areas. Examination of physical condition and the recording of a juvenile: adult ratio at this time would provide an indication of the reproductive success during the summer and also the ability of the population to survive during the fall. This would provide an opportunity to predict the success and effects of the harvest of the coming season.

Several practical schemes might be used to increase the monetary returns from fox trapping. Some of these such as the creation of outpost trapping camps, the establishment of fuel caches using boat transportation and the cooperation among trappers in checking their traplines are already being attempted. Establishment of food caches of surplus marine mammal carcasses, especially in fox denning areas, could also serve to decrease dispersion away from trapping areas in the fall and increase yields. This same strategy during the spring months in years of low fox abundance might also serve to improve the condition of foxes and thus increase production.

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