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**POPULATION TRENDS, AGE STRUCTURE, AND REPRODUCTIVE
CHARACTERISTICS OF FEMALE LYNX IN ALASKA, 1961 THROUGH 1973**

University of Alaska

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POPULATION TRENDS, AGE STRUCTURE, AND REPRODUCTIVE
CHARACTERISTICS OF FEMALE LYNX IN ALASKA, 1961 THROUGH 1973

A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By
Robin Mary O'Connor, B.S.
Fairbanks, Alaska
December 1984

POPULATION TRENDS, AGE STRUCTURE, AND REPRODUCTIVE
CHARACTERISTICS OF FEMALE LYNX IN ALASKA, 1961 THROUGH 1973

RECOMMENDED:

John Blyh
Ed H. Follen
Samuel J. Harbo

Chairman, Advisory Committee

Robert B. Weeden

Program Head, Wildlife and Fisheries

APPROVED:

W. S. Ruz

Director of Graduate Programs

17 Dec 1984

Date

ABSTRACT

Data from 3,130 female Alaska lynx carcasses were examined to determine if lynx age structure and reproductive rates varied during two peaks and one low in the lynx and snowshoe hare populations (1961-62 through 1972-73). Between periods of hare abundance and scarcity, declines in both lynx ovulation and implantation caused a decline in overall productivity from 2.8 to 0.2 recent placental scars (RPS) per yearling, respectively, and from 3.7 to 1.4 RPS per adult. Decreased reproduction contributed to declines in the proportions of kits and yearlings in the collection and to the subsequent decline in the lynx population; regional differences in these relationships are discussed. Peaks in hare populations, lynx reproductive rates, and proportions of kits in the collection occurred before peaks in the lynx population and harvest, thus were more timely predictors of lynx population declines. Natural oscillations in recruitment are important to consider when evaluating lynx management strategies.

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INTRODUCTION

Prior to 1970, there was little demand for information on lynx (Lynx [Felis] canadensis) ecology - lynx did not eat economically important prey or compete with hunters, they were not seen very often, and fur prices were relatively low. Demand for lynx pelts has increased since the early 1970's, primarily due to the endangered and threatened status of many felids traditionally preferred by the fur industry and due to changes in fashions. Correspondingly, the average pelt price for lynx increased eightfold from 1970-71 (\$35) to 1982-83 (\$263) (Appendix 1). Alaska's estimated 1982-83 lynx harvest was 5,652 pelts with a value of nearly \$1.5 million (Appendix 2) (Melchior 1984). Based on these raw pelt values, lynx contributed more to Alaska's 1982-83 estimated \$6 million fur harvest than did any other furbearer except marten (Martes americana).

The economic importance of lynx has increased the concern and demand for data on lynx ecology. The inclusion since 1977 of lynx in Appendix II of the Convention on International Trade of Endangered Species (CITES) requires signatory states to justify their management program before exporting pelts. Although CITES has been a catalyst for lynx research, we still lack information on many aspects of lynx ecology pertinent to management. For example, concern has been expressed that continued intense trapping pressure when the population is low may reduce lynx populations to dangerously low levels and prevent the subsequent peak in lynx numbers from reaching levels as high as those observed during previous cycles (Berrie 1973, Brand and Keith 1979, Todd 1983). Critics of this view argue that low success by

trappers in years of low lynx numbers will result in a self-regulating situation by reducing the trapping incentive and pressure during those years (Burris 1971). Inadequate population data limit our ability to evaluate the effects of harvests. Although I do not discuss the effects of trapping on lynx populations in this thesis, the trapping controversy is one of the primary issues I hope my data can help resolve.

To improve both the management and understanding of lynx populations, it is necessary to determine what factors limit lynx productivity. Research on lynx productivity in Alberta has been extensive and includes studies by van Zyll de Jong (1963), Nellis et al. (1972), Brand et al. (1976), and Brand and Keith (1979). Lynx productivity has also been studied in Newfoundland (Saunders 1961, 1964), on Cape Breton Island (Parker et al. 1983), and in Ontario (Stewart 1973).

A long-term study of Alaska lynx populations begun in 1961 provided data for my research. During the winters from November 1961 through March 1971 and from November 1972 through March 1973, the Alaska Department of Fish and Game (ADF&G) purchased approximately 6,000 lynx carcasses from trappers to assess the annual productivity of lynx, to relate production of young to population trends, and to study the relationship of lynx abundance to the density of snowshoe hares (Lepus americanus). To my knowledge, this constitutes the largest collection of lynx carcasses in the world and the first collection to span a complete population cycle. ADF&G has also sent questionnaires to trappers since 1965 to monitor fluctuations in lynx, snowshoe hares,

and other small game populations.

Portions of ADF&G's lynx carcass data have been analyzed previously. Nava (1970) studied the reproductive biology of Alaska lynx collected during the winter of 1964-65. Berrie (1973) reported results from his analyses of the 1964-65 through 1969-70 collection of carcasses, including the lynx age structure and the mean number of placental scars (mPS) in adult lynx. The more recent need for management information, partly due to the inclusion of lynx on Appendix II of CITES, resulted in a decision by ADF&G in 1980 to examine additional sections of the accumulated lynx data.

This thesis consists of my analyses of the interrelationships between snowshoe hare population trends, lynx population trends, lynx age structure, and lynx reproduction (age of puberty, numbers of corpora lutea [CL] and recent placental scars [RPS]). I used data from 3,130 of the female lynx carcasses that ADF&G collected from three regions of Alaska (Yukon, Tanana, and Copper Basins) (Figure 1) during a complete population cycle. "Cycle" in this paper is used to denote periodic, regular fluctuations with approximately 8-11 years between successive peaks.

My primary objectives were to determine if a pattern of change in female reproduction existed during the 10-year cycle of lynx and to examine the relationship between lynx reproduction and snowshoe hare abundance. The first two sections of the thesis (Snowshoe Hare and Lynx Population Trends, Age Structure of the Female Lynx Carcass Collection) provided the data necessary for examining the primary objectives in the third section (Reproductive Characteristics of Female

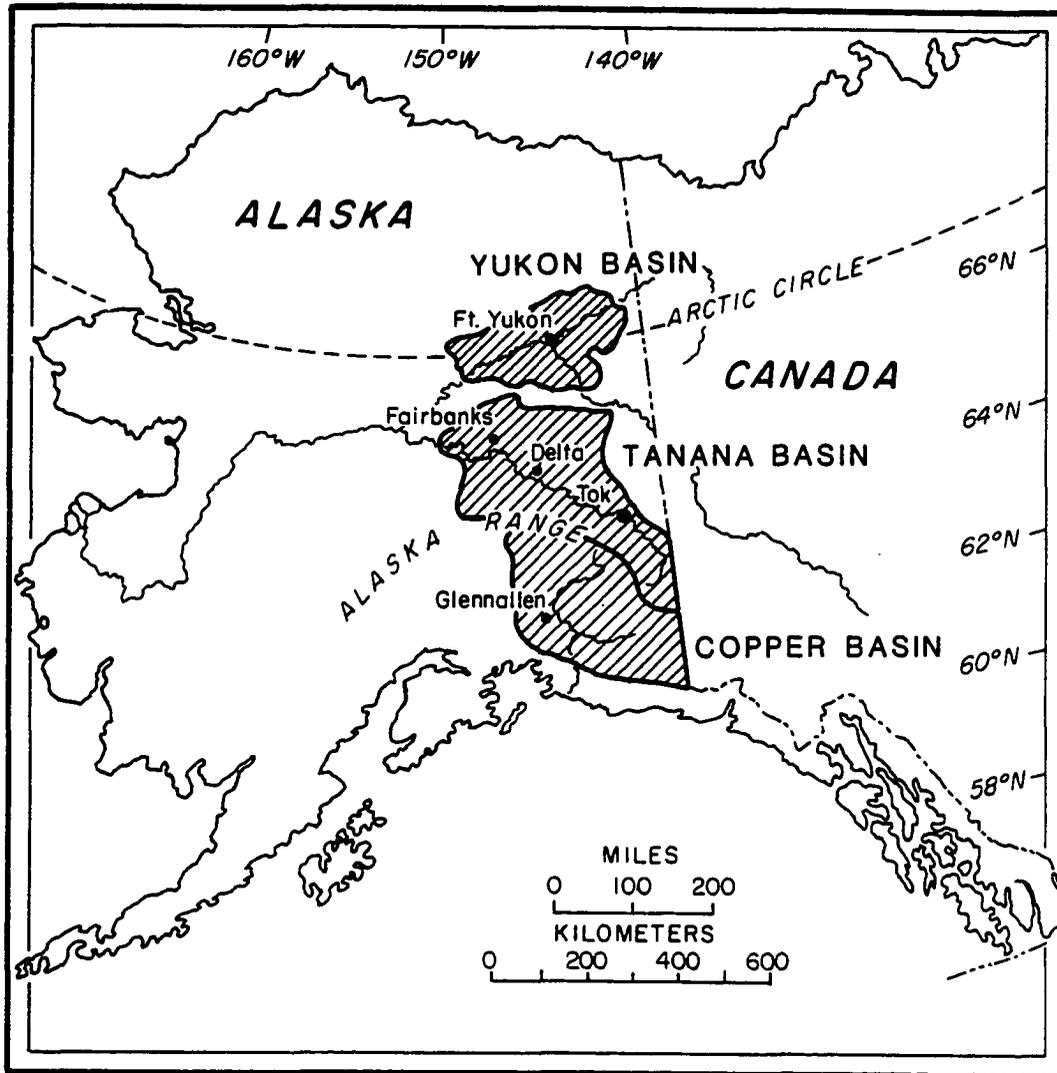


Figure 1. Three regions of Alaska (Yukon, Tanana, and Copper Basins) from which trapper questionnaires and lynx carcasses were examined.

Lynx). My preliminary results were presented at the International Cat Symposium in 1982 (O'Connor, in press). A flow chart illustrating the chronology of research on ADF&G's lynx carcass collection is presented in Appendix 3.

SNOWSHOE HARE AND LYNX POPULATION TRENDS

The cyclic nature of lynx abundance and its correspondence with changes in abundance of snowshoe hare, the lynx's major prey, has been well documented (Elton and Nicholson 1942, Keith 1963, Brand et al. 1976). Lynx populations increase and decrease within 1 to 2 years of similar changes in hare numbers (Buckley 1954, Brand et al. 1976, Brand and Keith 1979). The dynamics and regularity of these cycles have long intrigued biologists and have been discussed in detail by many authors including Keith (1963, 1974), Fox (1978), Finerty (1980), and Wolff (1980). Regional asynchrony in fluctuations of lynx and hare populations have been reported in Alaska (Buckley 1954, Nava 1970, Burris 1971) and Canada (Stewart 1973, Brand and Keith 1979, Todd 1983).

I analyzed data from ADF&G's collection of lynx carcasses with respect to hare and lynx population cycles in the three regions of Alaska. Hare and lynx population data pertaining to the period when lynx carcasses were collected were obtained from literature, ADF&G unpublished data, ADF&G trapper questionnaires, and reports of lynx pelts exported from Alaska. The objectives of my analyses of hare and lynx populations were:

1. To compare lynx population data from trapper questionnaires with lynx pelt export numbers.
2. To identify annual changes in snowshoe hare and lynx abundance in Alaska from the winters of 1961-62 through 1972-73.
3. To determine if regional differences existed in the timing of

snowshoe hare and lynx population cycles within Alaska.

4. To examine the temporal relationship between snowshoe hare and lynx population cycles.

METHODS

Throughout this thesis, results of data collected during the winter are denoted with a hyphenation of the 2 years that the winter season adjoined. For example, data collected from November 1964 through March 1965 is referred to as "1964-65".

Annual snowshoe hare abundance was assessed from comments by Trapp (1962), Nava (1970), and Ernest (1974) and from results of ADF&G trapper questionnaires (1965-66 through 1975-76). Annual lynx abundance was assessed from comments by Nava (1970), results of trapper questionnaires (1965-66 through 1975-76), and the number of lynx pelts exported from Alaska (1961-62 through 1975-76).

ADF&G Trapper Questionnaires

Since 1965-66, ADF&G has mailed questionnaires annually to trappers throughout Alaska at the end of each winter to monitor the abundance of snowshoe hares and lynx. Trappers are asked to rate the hare and lynx populations in their area as abundant, intermediate, or scarce. I tallied the questionnaire responses from 1965-66 through 1975-76 by area (Yukon Basin, Fairbanks, Delta, Tok, and Copper Basin). I included questionnaires from several winters (1973-74 through 1975-76) after the lynx carcass collection period to help identify long-term annual and regional patterns in population changes. Original trapper questionnaires from 1969-70 were not available so I used

Berrie's (1971) summary of the responses from that winter. The boundaries Berrie chose for his areas may have been different than my boundaries, though, so my 1969-70 indices may be slightly different than if I had tallied the original responses.

I calculated a Hare Abundance Index (HAI) and a Lynx Abundance Index (LAI) for the five areas of Alaska using trapper questionnaire data with methods described by Brand and Keith (1979, p.828):

Abundance values of 1, 2, and 3 were assigned to the responses of scarce, average, and abundant, respectively. The following equation was then used to calculate the hare abundance index (I):

$$I = [(\sum_{i=1}^n R_i - n)/2n] \times 100$$

where R_i is the numerical value assigned to the i th trapper response, and n is the number of trappers responding from a given region. This index thus expresses the cumulative response value of trappers in a given region as a percentage of the range of possible values. For example, if all trappers reported hares scarce, the index would be zero; if all reported hares abundant, it would be 100.

Brand and Keith calculated a linear relationship ($r = 0.97$, d.f. = 10) between the questionnaire indices and estimates of hare densities from hare studies in the area. This relationship did not hold for densities greater than 400 hares/100 ha of hare habitat because indices were already 100% and could not increase with increasing hare densities. I classified the abundance indices with the same criteria Brand and Keith used for their hare abundance indices; hares or lynx were classified as "scarce" when indices were 0-19%, "intermediate" when indices were 20-50%, and "abundant" when indices were >50%. In Brand and Keith's study, these categories represented hare densities of approximately 0-100, 100-250, and >250 hares/100 ha of habitat, respectively.

I tested for annual and regional asynchrony in the trapper questionnaire responses with Kruskal-Wallis (K-W) and K-W Pairwise Comparison tests ($P < 0.05$) (Conover 1980).

Lynx Pelt Exports

Since 1910, the Territory, and later the State, of Alaska has required that all furs exported from Alaska be reported. To estimate the number of lynx pelts exported from Alaska during and after the lynx carcass collection period, I summed the annual number of lynx pelts exported by fur dealers, trappers, and for personal use. These data were available from ADF&G computer printouts for each year since 1966-67. I used Courtright's (1968) record of the number of lynx pelts exported from Alaska for the years 1961-62 through 1965-66. Records of the regional distribution of pelt exports were not available.

RESULTS

Population Trends Cited in Unpublished Literature

Hare populations in Interior Alaska increased from 1959 to 1961 (Trapp 1962) and peaked north of the Alaska Range in 1962-63 and south of the range in 1963-64 (Nava 1970, Ernest 1974). In 1964-65, very few hares occurred in any of the areas from which ADF&G received lynx carcasses (Nava 1970).

Data on lynx population levels from 1961-62 through 1965-66 were somewhat lacking. Nava (1970) reported, however, that lynx harvest increased 14% from 1963-64 to 1964-65 according to questionnaires he sent to 98 trappers in the areas from which ADF&G collected lynx carcasses. He noted that lynx were very scarce north of the Alaska

Range in 1965-66 and most of the lynx carcasses ADF&G collected were from the Glennallen area. Nava also reported that the lynx population and harvest were very low in the winter of 1966-67 and remained low through his thesis publication date (May 1970).

Population Indices from Trapper Questionnaires

The number of trappers from my three study areas that responded to questionnaires between 1965-66 and 1975-76 ranged from 44 to 93 annually for hare abundance questions and from 39 to 93 annually for lynx abundance questions (Appendices 4, 5). Hare and lynx population levels in Fairbanks, Delta, and Tok were not significantly different from each other during any year ($P > 0.05$) (Appendix 6). I pooled data from these three areas and refer to the pooled set as the Tanana Basin data.

Responses to trapper questionnaires indicated that hare and lynx populations varied between some years (Appendices 7, 8) and between some regions (Appendix 9) throughout the sampling period. In each region, hares were scarce in 1965-66, were abundant for four consecutive winters in the late 1960's to early 1970's, and were scarce in 1974-75 and 1975-76 (Figure 2, Appendix 10). However, the timing of hare and lynx population peaks and the amplitude of the peaks were not the same in all regions; regional differences existed for hare population levels in 7 of the 11 winters examined and also for lynx population levels in 7 of the 11 winters ($P < 0.05$), although these 7 winters were not the same for hares and lynx. Hare and lynx populations in the Yukon Basin were different from both the Tanana and Copper Basin populations in most of these 7 winters.

In the Yukon Basin, hares were scarce in 1965-66 and abundant from

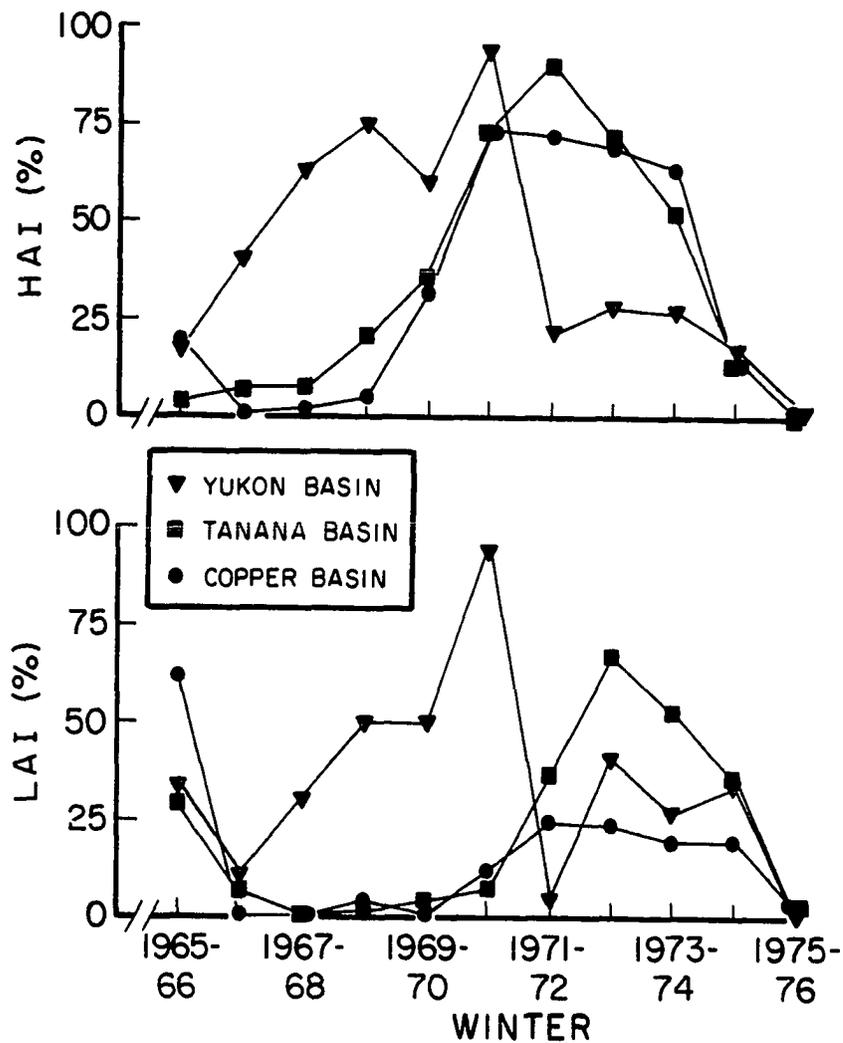


Figure 2. Snowshoe Hare Abundance Indices (HAI) and Lynx Abundance Indices (LAI) for three regions of Alaska, 1965-66 through 1975-76. Indices were calculated from trapper questionnaire responses with methods by Brand and Keith (1979). (Indices of 0-19% = scarce, 20-50% = intermediate, and 51-100% = abundant).

1967-68 through 1970-71. Lynx were scarce in 1966-67 and abundant from 1968-69 through 1970-71 (Appendix 11). Hare and lynx populations peaked in 1970-71, rapidly declined in 1971-72, and remained at intermediate or scarce levels through 1975-76.

In the Tanana Basin, hares were scarce from 1965-66 through 1967-68, increased to a peak in 1971-72, decreased (but were still abundant) for 2 years after the peak, and were scarce in 1974-75 and 1975-76. Lynx were scarce from 1966-67 through 1970-71, peaked in 1972-73, then declined to scarce levels by 1975-76.

In the Copper Basin, hares were scarce from 1965-66 through 1968-69 and abundant from 1970-71 through 1973-74. The hare population "plateaued" at abundant levels from 1970-71 through 1973-74 before rapidly declining in 1974-75. Lynx populations were abundant in 1965-66, scarce from 1966-67 through 1970-71, and plateaued at intermediate and scarce levels from 1971-72 through 1974-75 with the "peak" in 1971-72.

Lynx Pelt Exports

The number of lynx pelts reported exported from Alaska increased from 1,107 pelts in 1961-62 to a "broad peak" of 4,700 pelts in 1963-64 to 5,134 pelts in 1965-66 (Figure 3, Appendix 1). Pelt export numbers were relatively low from 1966-67 through 1970-71 then rapidly increased to a peak of 7,902 pelts in 1973-74. After this peak, the lynx pelt exports rapidly declined to 1,738 pelts by 1977-78.

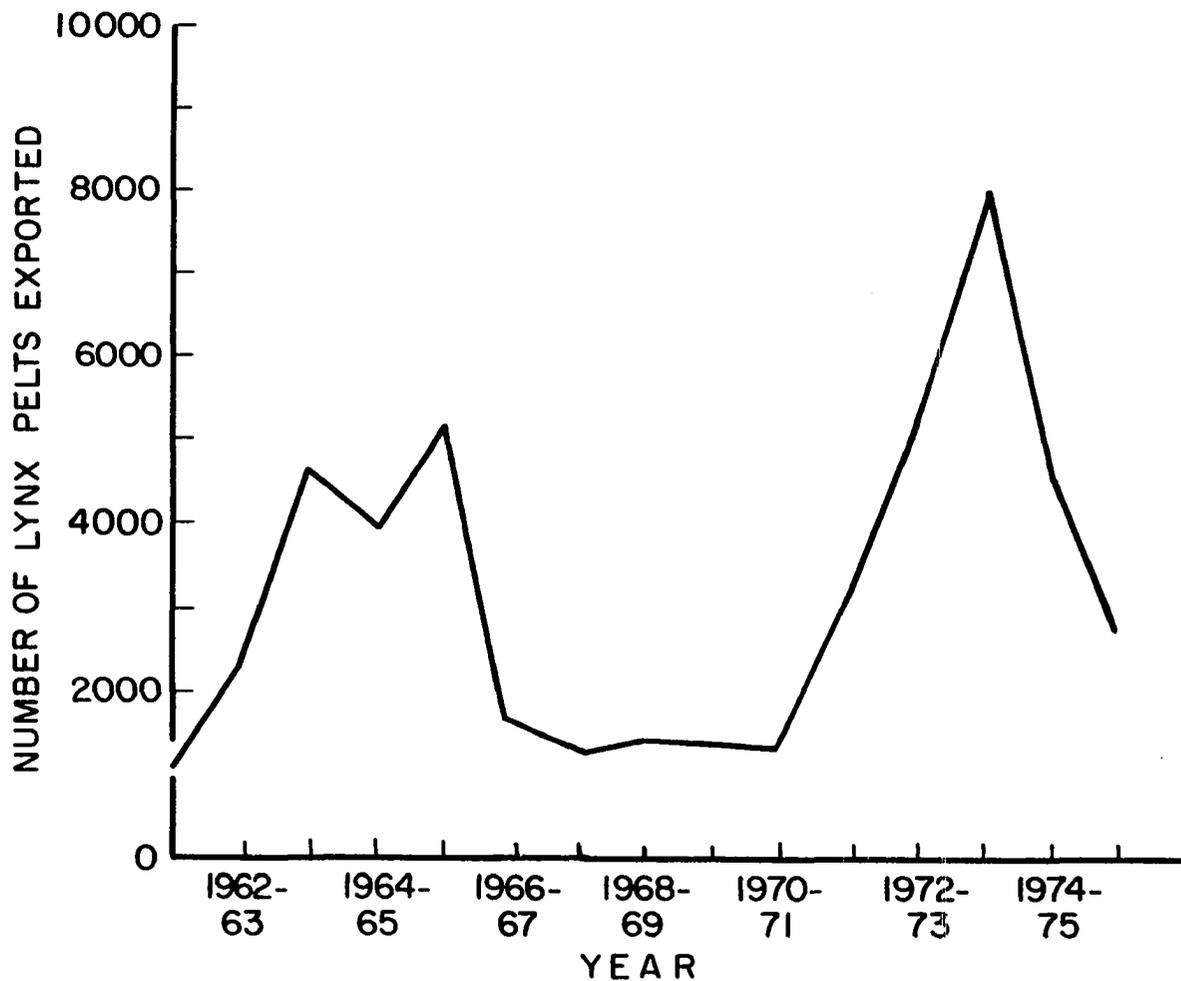


Figure 3. Number of lynx pelts exported from Alaska, 1961-62 through 1975-76 (numbers from 1961-62 through 1965-66 are from Courtright [1968]; numbers from 1966-67 through 1975-76 are a sum of fur dealer, trapper, and personal use exports [ADF&G unpubl.]).

DISCUSSION

Comparison of Lynx Population Indices

Trends in lynx populations have been described using: (1) indices of lynx abundance from trapper questionnaires (Brand and Keith 1979, this study) and (2) estimates of lynx harvest (number of lynx trapped as reported in trapper questionnaires, number of pelts sold or exported) (Elton and Nicholson 1942, Keith 1963, Buckley 1954, Brand and Keith 1979). My study indicates that agreement between estimates of harvest and indices of population size was sometimes lacking. From 1966-67 through 1970-71, the numbers of lynx pelts exported from Alaska were relatively low, as were the Tanana and Copper Basin LAIs (Figure 4). The Yukon Basin LAIs, however, indicated intermediate and abundant lynx populations during that time, which does not agree with the export trends. In addition, the 1973-74 peak in pelt exports lagged 2-3 winters behind the peaks in the regional LAIs. A steep decline in exports occurred in 1974-75 but the number exported was still relatively high (only 12% fewer pelts than the peak in exports during the previous cycle) even though 1974-75 was 2-4 winters after peak LAIs. Therefore, in my study, statewide export data did not always appear to simply reflect an "average" of data from several regions asynchronous in the timing of their lynx population peaks. However, I compared statewide pelt exports with LAIs from only three regions of Alaska. A different relationship between pelt exports and LAIs could occur if other regions of the state contributed significantly to the statewide export and if peak populations in those regions were not synchronous with my three regions.

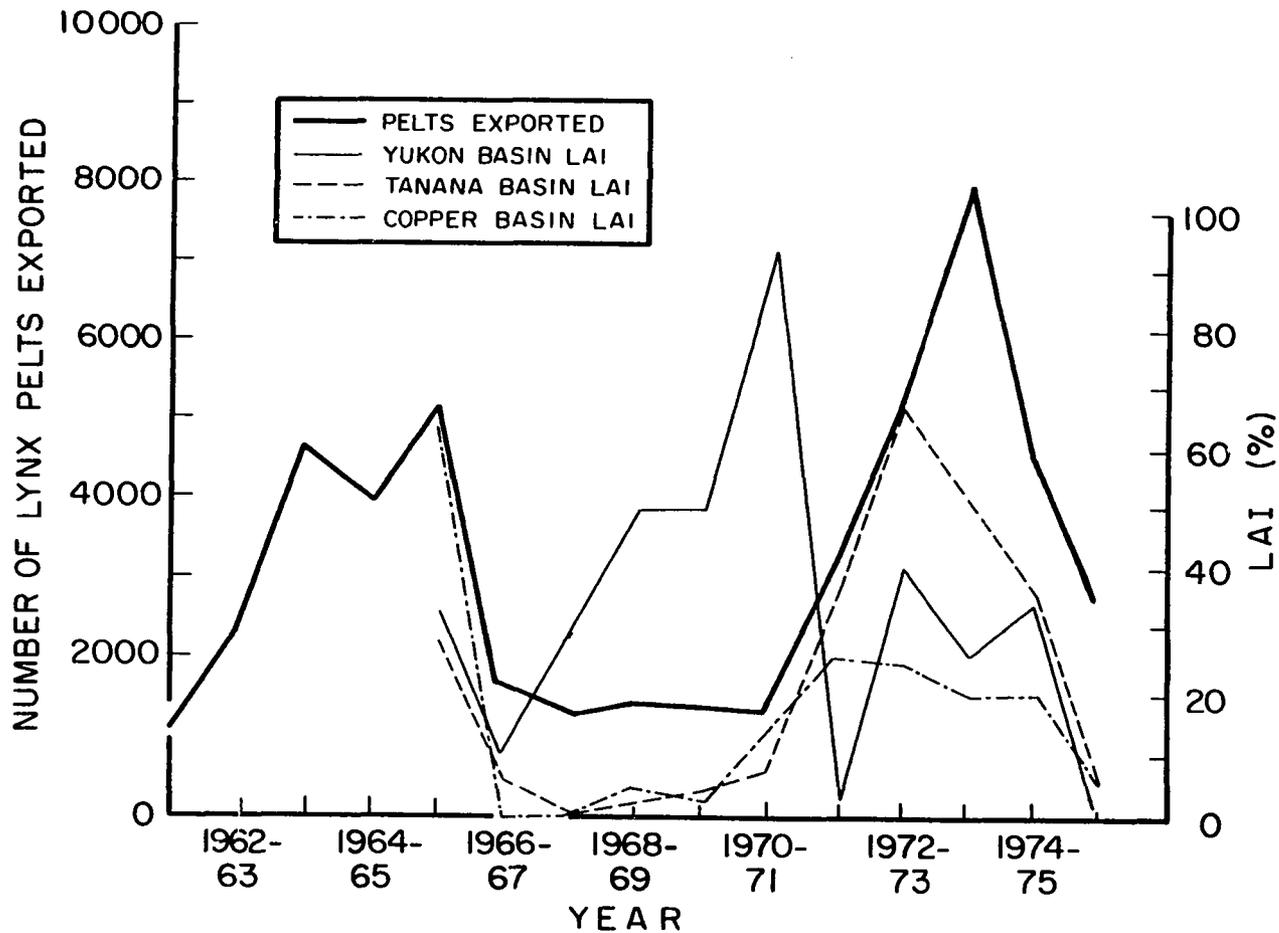


Figure 4. Number of lynx pelts exported from Alaska (1961-62 through 1975-76) and Lynx Abundance Indices (LAI) for three regions of Alaska (1965-66 through 1975-76) (numbers from 1961-62 through 1965-66 are from Courtright [1968]; numbers from 1966-67 through 1975-76 are a sum of fur dealer, trapper and personal use exports [ADF&G unpubl.]).

I found no evidence to suggest that LAIs were inaccurate and I believe that LAIs provide a more accurate index of lynx population trends than do statewide pelt exports. Export figures may be influenced by pelt prices, trapping intensity, availability of fur animals, alternate sources of income, and weather (Buckley 1954, Courtright 1968, Brand and Keith 1979). Although Stewart (1973) found no correlation between Ontario lynx harvest and pelt price ($P > 0.05$) he did acknowledge the increased trapping incentive when pelt prices were high. Brand and Keith (1979) concluded that the number of lynx pelts sold in Alberta accurately reflected the timing of a peak and two lows in the lynx population (estimated from snow-tracking). Courtright (1968) stated that the number of lynx pelts exported from Alaska may not accurately reflect the actual number of lynx in the state, but he concluded that the exports should be indicative of long-term population trends. I believe that the number of lynx pelts exported is probably influenced more by factors other than population density than are trapper questionnaire responses. Other data also suggests that the questionnaire indices accurately reflected population levels. Trappers in the Copper Basin noted that the amplitude of the Copper Basin lynx population peak was much lower in the 1970's than during the 1960's (C. Gardner, pers. commun.). In addition, results from hare tagging studies near Central and Fairbanks, Alaska (Ernest 1974) agreed with the Tanana HAI in denoting peak hare densities in 1971-72; estimated hare densities in the tagging study were 604 hares/km². Wolff (1980) estimated that hare densities in Fairbanks declined 50-fold to 12 hares/km² by 1974-75. These reports agree with the population trends suggested by the HAIs and

LAI's, thus, I used questionnaire indices rather than export data to indicate population trends.

Agreement between estimates of lynx harvest also was sometimes lacking. Nava (1970) calculated a 14% increase in the lynx harvest from 1963-64 to 1964-65 (based on his own trapper questionnaires) but the number of pelts exported from Alaska decreased during that time. Nava's questionnaire responses could not be compared with the number of pelts exported from the same regions because regional export data were not available. Courtright (1968) discussed the problems associated with using harvest records as indices of harvest or population size. Caution should be exercised when comparing harvest results calculated from different indices.

Currently, the lynx harvest in Alaska can be monitored more closely than in historical times by examining "sealing" documents. Since 1977-78, trappers have been required by law to have a locking tag attached to their lynx pelts ("sealed") by an ADF&G representative who also records harvest date, location, and pelt measurements. A comparison of the lynx population trends indicated by sealing records, export data, and trapper questionnaires would help assess the reliability of each as an index to lynx populations. However, the additional influence of high pelt prices since the early 1970's may result in a different relationship between harvest and actual population size than occurred during the lynx carcass collection of the 1960's.

Regional Differences

In Alberta, regional differences in trapper questionnaire responses reflected actual differences in hare densities between regions

(determined by trapping studies) (J. R. Cary, pers. commun.). Regional differences in ADF&G questionnaire responses also probably reflect actual variability in the timing or amplitude of hare and lynx cycles among these regions.

In my study, regional peaks in hare populations (HAI) differed by up to 2 years, as did peaks in lynx populations (LAI). Buckley (1954) and ADF&G unpublished data also noted differences of 1-2 years in regional peaks in Alaska hare and lynx populations. Burris (1971) stated that the broad 2-4 year peak in lynx pelt exports probably reflects consecutive population peaks in different areas of Alaska. Todd (1983) stated that in Alberta regional peaks in lynx populations differed by 1-2 years, possibly due to the differences in trapping intensity and the ingress of lynx from other regions.

The timing of the Yukon Basin hare and lynx cycles seemed to be advanced with respect to the Tanana and Copper Basin cycles. Although each region had four consecutive winters of abundant hares, the Yukon Basin hares were abundant from 1967-68 through 1970-71 and the Tanana and Copper Basin hares were abundant from 1970-71 through 1973-74. In addition, the Yukon Basin lynx populations were at intermediate or abundant levels during four winters when lynx were scarce in the other two regions.

During the early 1970's, hare and lynx populations in the Copper Basin peaked one winter prior to populations in the Tanana Basin. This conflicts with previous reports that peaks in hare abundance in the Interior preceded peaks in south-central Alaska by 1-2 years (Buckley 1954) and, similarly, that cycles north of the Alaska Range preceded

cycles south of the range by 1 year (Nava 1970). The Copper Basin indices showed a "plateau" in peak hare and lynx populations rather than the well-defined peak seen in the other regions. Trappers in the Copper Basin thought this plateau was probably an artifact of asynchrony in the timing of peak populations in areas within the Copper Basin region (C. Gardner, pers. commun.). Copper Basin cycles were similar to the Tanana Basin cycles primarily in the timing of increases (but not necessarily the peaks) or decreases and in the amplitude of the hare cycles.

Regional differences in population cycles may result in part from regional differences in abundance of high quality hare habitat. Certain areas may support large numbers of hares for several years after the population decline is well underway in the surrounding areas (ADF&G unpubl.). Keith (1963) reported this situation for hares in Alberta and suggested such areas represented highly favorable hare habitat. "Dense spruce or willow-alder thickets play an important role in snowshoe hare cycles in that they provide protective cover from predators during a population crash. Snowshoe hare, which are thus able to avoid local extinction by seeking these refuges, provide the stock for subsequent population increase (Wolff 1980)." Thus, hare populations in these "pockets" may be able to increase more rapidly when conditions improve again. Because lynx depend heavily on hares for food during all phases of the cycle (Brand et al. 1976), regional differences in hare abundance may result in regional differences in lynx abundance. The Yukon Basin is generally regarded as some of Alaska's best lynx habitat, perhaps due to the short fire cycle which produces a high proportion of successional habitat, thus providing good habitat for hares (Stephenson 1984).

Brand and Keith (1979) suggested that regional differences in the lynx cycles might require management programs to be implemented on a regional, rather than state- or province-wide, basis (Todd 1983). Todd (1983) made regional management recommendations after reviewing Brand and Keith's data and current information. Although my data also indicate that regional differences exist, I suggest that the importance of lynx movements be evaluated before considering such a management strategy. Recent evidence from radio-collared lynx indicates that lynx can travel long distances in a relatively short time; one adult female from Kluane Lake (Yukon Territory) was trapped approximately 720 km (450 mi) from the location she was collared 10 months earlier; two other lynx from the same study were trapped approximately 240 km (150 mi) from their collaring locations (Ward 1983). The effectiveness of regional management programs would be influenced by large numbers of lynx moving into or out of those regions.

Temporal Relationship between Hare and Lynx Populations

In my study, lynx population trends usually appeared to change in response to changes in hare abundance. The temporal relationship between hare and lynx populations within each region can be illustrated by examining trends in the two populations with respect to the timing of: (1) increases and decreases in population levels, (2) years of abundance and scarcity, and (3) population peaks. In most cases, lynx populations increased only after increases in the previous winter's hare population. Decreases in the lynx population usually occurred concurrent with, or the winter after, decreases in the hare population. In eight of nine cases, an abundance or scarcity of lynx occurred the

first winter after hares became abundant or scarce, respectively (Table 1). The one exception was in the Tanana Basin; lynx became abundant in 1972, which was two winters after an abundance of hares. In the Copper Basin, lynx were actually intermediate/scarce during the highest point of the lynx cycle in that region but this also occurred the first winter after hares became abundant. Peak hare and lynx populations occurred during the same winter in the Yukon Basin but peak hare populations preceded peak lynx populations by one winter in the Tanana and Copper Basins. Thus, although the temporal relationships between hare and lynx cycles were not always consistent, the lynx populations did appear to fluctuate in response to hare abundance.

In other studies, numerical responses of lynx populations also followed within 1-2 years of similar changes in hare populations, however peak lynx harvest did not consistently precede or follow peak hare populations. Brand and Keith (1979) concluded that lynx populations and fur harvests reached a cyclic peak 1-2 years after cyclic peaks of snowshoe hares and that the predictability of this demographic event allows the use of these data as an index to the status of lynx and is useful for management decisions. Todd (1983) disagreed with Brand and Keith's conclusion because in the early 1980's the peak lynx fur harvest occurred the same winter as, or preceded by 1 year, the peak hare population in four of eight zones in Alberta. Gilpin (1973) also noted that the lynx fur harvest cycle may sometimes precede the hare cycle. Gilpin suggested that trappers might be a major pressure on the population and that the lynx cycle might reflect changes in trapping strategy rather than changes in population densities of lynx. This

Table 1. Winters^a of abundant and scarce snowshoe hare and lynx population levels in three regions of Alaska, 1965-66 through 1975-76.

Population level ^b	Region					
	Yukon Basin		Tanana Basin		Copper Basin	
	Hares	Lynx	Hares	Lynx	Hares	Lynx
Abundant						1965
	1967					
	1968	1968				
	1969	1969				
	1970	1970	1970		1970	
			1971		1971	1971
			1972	1972	1972	1972
			1973	1973	1973	1973
						1974 } ^c
Scarce						
	1965		1965		1965	
		1966	1966	1966	1966	1966
			1967	1967	1967	1967
				1968	1968	1968
				1969		1969
				1970		1970
		1971				
	1974		1974		1974	
	1975	1975	1975	1975	1975	1975

^a Winters are abbreviated, for example: 1967 = winter of 1967-68.

^b According to indices calculated from trapper questionnaires (Appendices 10, 11).

^c Lynx abundance rated intermediate or scarce according to my criteria (see Methods) but these years represent the highest levels of lynx population for that cycle in the Copper Basin.

suggestion of Gilpin's was challenged by Finerty (1980) who noted that Gilpin compared the hare cycle of eastern Canada with the lynx cycle of western Canada. Finerty stated that the appropriate comparison suggests that the phase relationship between lynx and hare pelts is what would be expected for a predator-follows-prey situation. In my study, the lynx population (based on LAIs) did not cycle in synchrony with the lynx fur harvest (based on pelt exports); the regional peak lynx populations preceded peak exports by up to 3 years. Therefore, Brand and Keith's conclusion regarding the predictability of the temporal relationships between hare and lynx cycles, and between the lynx population and fur harvest, may not be applicable to all cycles.

The lack of buffer prey species in northern environments may force obligate predators such as lynx, great horned owls (Bubo virginianus), and goshawks (Accipiter gentilis) to fluctuate with the hare cycle (Wolff 1980). In Alberta, even during a hare scarcity 65% of the biomass in the lynx diet was hares (Brand and Keith 1979). Brand et al. (1976) reported that during periods of hare scarcity, the dietary shift from hares to alternative prey did not compensate completely for the low hare population and that the consumption rates were perhaps 20% below the normal maintenance level for a wild lynx. This dependence probably results in a high mortality of young lynx during periods of hare scarcity and contributes significantly to the close correspondence between hare and lynx cycles.

AGE STRUCTURE OF THE FEMALE LYNX CARCASS COLLECTION

Several studies indicate that the age structure of lynx populations fluctuates during the lynx cycle, probably in response to changing levels of the snowshoe hare population (Berrie 1973, Brand and Keith 1979, Parker et al. 1983). The age structure of the lynx carcass collection was of interest to me for two reasons. First, I wanted to evaluate female lynx reproductive characteristics with respect to yearling and adult age-classes. Second, the growth or decline of a population is influenced by its age structure because reproductive and mortality rates vary by age. Age structure data combined with data on reproductive rates can provide valuable information for understanding the population dynamics of lynx.

The objectives of this section were:

1. To determine if the age structure of the female lynx carcass collection differed between years or between regions.
2. To examine the age structure of the female lynx carcass collection with respect to hare and lynx population levels.

METHODS

Age determinations based on legbone ossification and incremental lines in canine tooth cementum had been recorded for most of the lynx carcasses collected by ADF&G prior to 1972-73. In some cases, the ossification and cementum ages were different. I used several age determination techniques (incremental lines in canine tooth cementum, legbone ossification, and skull morphology) in combination to arrive at one age that resolved these differences and to age classify the 1972-73

lynx.

Laboratory Techniques

The following is a summary of the techniques used to prepare lynx carcasses for age determination (Berrie 1970, 1973). The skull, a radius, and an ulna were removed from the lynx carcasses and cleaned by boiling. An upper canine was removed from the skull, stored in 1-5% formalin, and later decalcified in nitric acid (915 ml H₂O; 10 ml 100% formalin; 75 ml conc. HNO₂) and rinsed. The tooth was longitudinally sectioned into sections 18 microns thick on a cryostat. These sections were mounted on a glass slide, stained with Paragon multiple stain, and examined under a microscope to count incremental lines in the tooth cementum. Small lynx teeth that obviously were from kits were not sectioned.

Age Determination

Prior to my study, Berrie (1970) classified lynx as kits (0-12 months), subadults (referred to here as yearlings) (13-24 months), or adults (25+ months) with criteria based on incremental lines in canine tooth cementum and the degree of ossification in the epiphyses of the radius and ulna. He assumed that the first incremental line in cementum was deposited during the lynx's second winter, with an additional line deposited annually thereafter (Klevesal and Kleinenberg 1969, Nava 1970). Berrie grouped radii and ulnas into age-classes based on Nava's (1970) criteria that kits had unossified epiphyseal sutures, yearlings had partially ossified epiphyses but with a definite line of demarcation, and adults had ossified epiphyses. Ages determined from these cementum and ossification criteria did not always

agree; discrepancies most frequently occurred in the yearling and 2-year old age-classes.

Before I could proceed with my analysis of the age structure of the lynx collection, I had to: (1) resolve discrepancies between cementum and ossification ages of approximately 600 lynx carcasses, (2) check the consistency of my age classification with Berrie's for the lynx carcasses without discrepancies, and (3) classify the 1972-73 lynx carcasses into kit, yearling, or adult age-classes.

Because my primary thesis objective was to examine changes in female lynx reproduction, I excluded data from female lynx with incomplete reproductive histories (see section on Reproductive Characteristics of Female Lynx), and from all male lynx. Then I re-examined legbones and reread tooth sections to resolve the discrepancies between cementum and ossification ages that were assigned to individual lynx. Noting the trapping date and assuming a June 1 birthdate, I used three criteria to assign lynx to one of the three age-classes: (1) counts of incremental lines in tooth cementum (Nellis et al. 1972, Grue and Jensen 1979, Brand and Keith 1979), (2) the degree of ossification in the radius and ulna using van Zyll de Jong's (1963) criteria (Table 2) which are more detailed than Nava's, and (3) closure of the apical foramen in the canine tooth root during the second year of life (Saunders 1964, van Zyll de Jong 1963). For the first criterion, I assumed, as did Berrie, that the first incremental line in the tooth was deposited during the second winter of life, with an additional line deposited annually thereafter. However, I did not count "secondary" incremental lines; such lines do not continue around

Table 2. Criteria for age classification of lynx radii and ulnas by ossification stage^a. Modified from van Zyll de Jong (1963).

Month of collection	Age		
	Kit (0-12 months)	Yearling (13-24 months)	Adult (25+ months)
November	1111	2151	5353 ^b
		4151	5555
December	1111	4151	5353 ^b
		5151	5555
January	1111	4151	5555
	1151 ^b	5151	
February	1111	4151	5555
		5151	
		5252	
March	2151	5252	5555
		5353	

^a Ossification stages: 1 = unossified, 3 = evidence of suture, 5 = ossified; 2 and 4 denote intermediate between two stages. Order of bones: proximal ulna, distal ulna, proximal radius, distal radius.

^b Suggested by my data.

the root apex and are probably deposited during the lynx's first winter (Grue and Jensen 1979). When discrepancies in age classification still existed, I examined morphological features of the skull such as the shape of the temporal and lambdoidal ridges, the development of the sagittal crest, and tooth replacement, for distinct features of an age-class (Saunders 1964). Animals still with unresolved discrepancies were excluded from my analyses.

To determine if it was necessary to check the age classification of approximately 3,700 lynx or only to check those with discrepancies (to determine the consistency between my age classification and Berrie's), I selected a systematic sample of 5% (153 lynx) of each of the 3 age-classes (32 kits, 58 yearlings, 63 adults) from the lynx specimens that had no age discrepancies and that I had not examined. I assigned an age to those lynx based on the skull, tooth section, and/or legbones of these individuals. Tooth sections from 12 of the 153 lynx were missing but noted by Berrie as "0" for the number of cementum lines instead of the missing data code; 10 of these 12 lynx were kits and probably had no teeth sectioned. The other two lynx plus an additional four lynx had insufficient data for me to place them confidently into one age-class. The data available, however, did not disagree with Berrie's classification so they were included in the originally estimated age-class. I disagreed with Berrie's age classification in only one case; a lynx collected in February was classified as a yearling by Berrie but the skull and legbones clearly indicated it was a kit. I decided there was sufficient agreement between Berrie's classification and mine to deem it unnecessary to

re-check the specimens without discrepancies.

I age-classified the 1972-73 female lynx using cementum annuli, legbone ossification, and skull morphology with the same criteria I used to classify lynx with discrepancies.

I tested for differences between years and between regions in the age structure of the lynx carcasses with K-W, K-W Pairwise Comparison, and Mann-Whitney tests ($P < 0.05$) (Conover 1980).

RESULTS

I included data from 3,130 female lynx carcasses in my age structure analysis. The age structure of lynx from Fairbanks, Delta, and Tok were not significantly different from each other during any year ($P > 0.05$). I pooled data from these three areas and refer to the pooled set as the Tanana Basin data. Lynx carcasses were collected from 1961-62 through 1972-73 from three regions of Alaska: Yukon Basin (362 carcasses), Tanana Basin (1,588 carcasses), and Copper Basin (1,180 carcasses).

Annual Changes

The age structure of the female lynx carcass collection within each region changed significantly during the collection period (Figure 5; Appendices 12, 13). In all regions, the age structure of lynx collected in 1963-64, 1964-65, and 1970-71 differed significantly from the age structure of lynx collected in 1965-66, 1966-67, and 1967-68. The age structure shifted from predominantly young lynx (>50% kits plus yearlings) from 1961-62 through 1964-65 in all regions to predominantly adult lynx (>70%) from 1965-66 through 1967-68 in the Yukon and Tanana

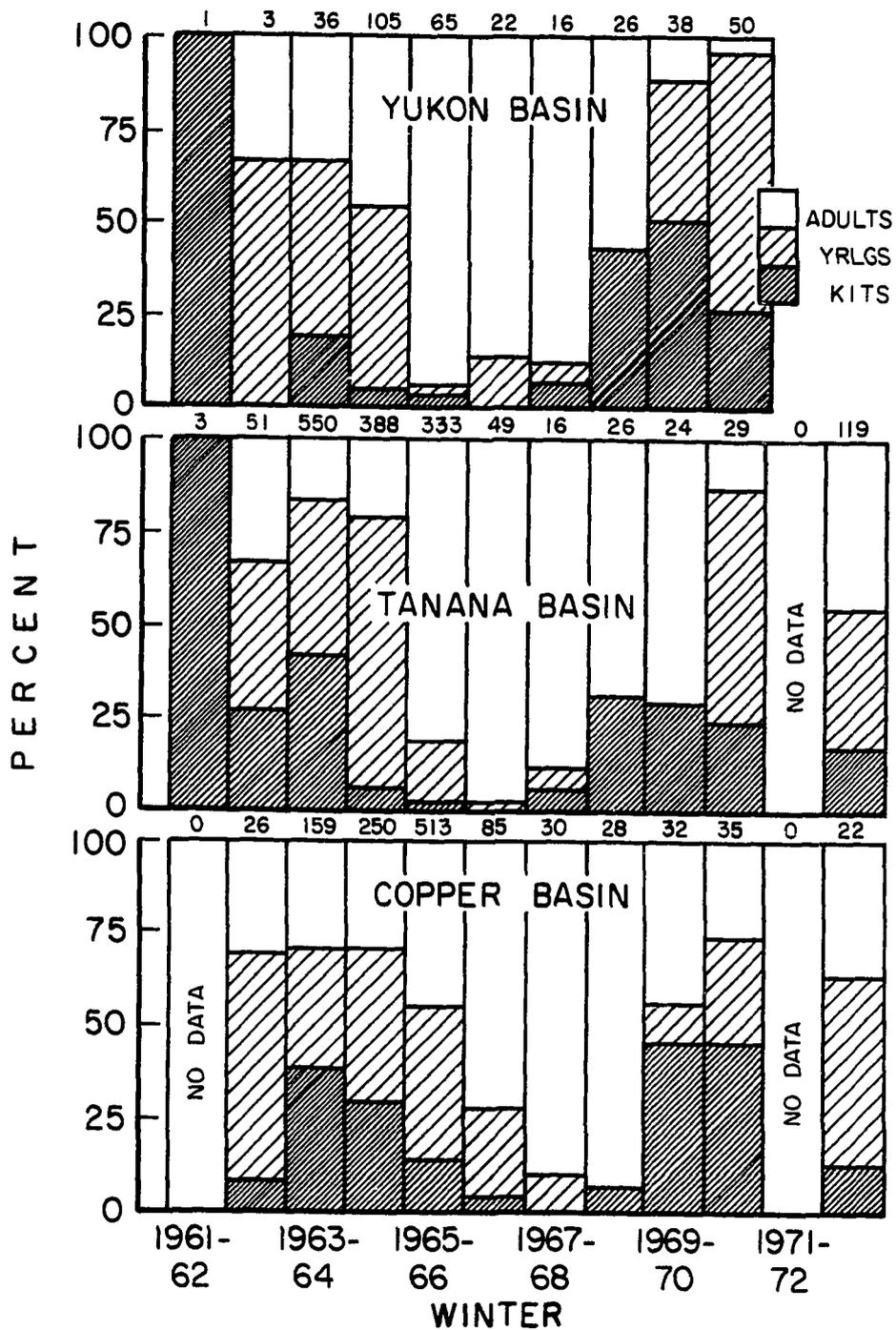


Figure 5. Age distribution of 3,130 female lynx carcasses collected from three regions of Alaska, 1961-62 through 1972-73 (kits = 0-12 months, yearlings = 13-24 months, and adults = 25+ months). Annual sample sizes are noted above the figure for each region.

Basins and from 1966-67 through 1968-69 in the Copper Basin. In 1970-71 and 1972-73, the proportions of young lynx in my sample again exceeded 50% in the regions from which I had data. Changes in the proportion of kits in annual collections were similar to those for kits and yearlings combined. In each region, no kits were collected during one winter in the mid-1960's and no yearlings were collected in 1968-69. The proportion of kits in the collection from the Tanana Basin did not differ from 1968-69 through 1972-73 ($P > 0.25$).

Regional Differences

Significant regional differences in age distribution occurred in 6 of the 10 winters in which lynx carcasses were collected (1961-62 data excluded because of small sample sizes) (Appendix 14). In 1963-64 and 1964-65, the collection from the Tanana Basin had a higher proportion of kits or yearlings than did the collections from the Yukon or Copper Basins. In 1965-66 and 1966-67, the collections from the Copper Basin had higher proportions of kits and yearlings than did the Yukon and/or the Tanana Basins. In 1968-69, the Copper Basin collection had a lower proportion of kits than did the Yukon or Tanana Basin collections.

Changes in the age structure of the yearly samples of lynx from north of the Alaska Range appeared to precede by 1 year similar changes in the samples collected south of the Range (Copper Basin). For instance, the largest decrease in the proportion of young lynx (kits plus yearlings) was in 1965-66 in the Yukon and Tanana Basins but in 1966-67 in the Copper Basin (Figure 5). The three winters with the lowest proportions of young lynx were 1965-66 through 1967-68 in the Yukon and Tanana Basins but 1966-67 through 1968-69 in the Copper

Basin. No kits were collected in the Yukon and Tanana Basins in 1966-67 nor in the Copper Basin in 1967-68. The largest increase in the proportion of kits in the collection was in 1968-69 in the Yukon and Tanana Basins but in 1969-70 in the Copper Basin.

Lynx Age Structure in Relation to Hare Populations

In Alberta, lynx numbers did not change over winter during the population declines in hares and lynx (Brand et al. 1976); the disappearance of kits and adults probably occurred between spring and winter (Brand and Keith 1979). Therefore, to examine the relationship of lynx age structure to hare abundance in my study I pooled age data according to the previous winter's hare population. For example, I pooled age data from all lynx that were collected during the first winter after a winter of hare abundance.

A complete reversal in the ratio of young lynx (kits plus yearlings) to adult lynx occurred between years of hare abundance and scarcity. Of 1,091 lynx collected during the first winters following winters of hare abundance, 76% were young lynx and 24% were adults (Table 3). Conversely, of 288 lynx collected during the first winters following winters of hare scarcity, 22% were young lynx and 78% were adults. The proportion of young lynx collected during the first winters after winters of hare abundance did not differ significantly from the proportion of adult lynx collected during the first winters after winters of hare scarcity ($P > 0.75$).

Changes in the lynx age structure within each region also seemed to correspond to changes in hare population levels. During the 7 years that trapper questionnaires coincided with the carcass collection

Table 3. Age distribution of female lynx carcasses in relation to the previous winter's snowshoe hare population level. Data from three regions of Alaska.

Lynx age ^a	Previous winter's hare population ^b			
	Abundant		Scarce	
	n	%	n	%
Kits	378	34.6	29	10.1
Yearlings	453	41.5	33	11.4
Adults	<u>260</u>	23.8	<u>226</u>	78.5
Total	1091		288	

^a kits = 0-12 months, yearlings = 13-24 months, adults = 25+ months.

^b According to Hare Abundance Indices (HAI). Prior to the use of HAIs, years designated as having peak hare populations were also considered to have hare populations that would have been classified as abundant.

period (1965-66 through 1972-73), the two winters with the lowest proportions of young lynx collected were the first winters following the lowest HAIs in each region. Young lynx predominated (> 50%) during seven of the eight region-winters (one winter in one region = one region-winter) which immediately followed winters of hare abundance. In the Yukon Basin, changes in the proportion of kits collected paralleled changes in the previous winter's hare population. The proportion of kits in the collection decreased from 19% of 36 lynx during the first winter following a peak hare population, to 0% of 22 lynx during the first winter following a scarcity of hares three years later. The proportion of kits then increased to a peak of 50% of 38 lynx during the winter following another peak hare population. After a small decrease in the hare population during the following winter, only 26% of the 50 lynx collected were kits.

The relationship between lynx age structure and hare population levels was not consistent among regions. In the Tanana and Copper Basins, the proportion of young lynx tended to increase and decrease with similar changes in size of the previous winter's hare population, but the relationship was not as well-defined as in the Yukon Basin. In the Tanana and Copper Basins, the highest proportion of kits were not always collected the first winter following the most abundant hare populations. In the Tanana Basin, the proportion of young lynx (especially yearlings) was lower in 1972-73 than in 1970-71, even though the hares were more abundant during 1971-72 than 1969-70. In the Copper Basin, 47% of the 32 lynx collected in 1969-70 were kits even though hares were scarce during the previous winter, however hares

were at intermediate levels and increasing during 1969-70. Prior to the availability of data from trapper questionnaires, the highest proportion of kits in all regions was collected in 1963-64, concurrent with or the first winter after hare population peaks.

Lynx Age Structure in Relation to Lynx Populations

The highest proportion of kits was collected one winter prior to the peak LAI in the Yukon Basin, four winters prior to the peak LAI in the Tanana Basin (although there were no differences [$P > 0.05$] in the proportion of kits during these four winters), and possibly up to two winters prior to the "peak" LAI in the Copper Basin. The absence of carcass data prevented me from determining whether the proportion of kits increased or decreased in 1971-72. All three regions had a peak in the proportion of kits in 1963 even though lynx populations reportedly peaked in the Copper Basin 1 year after populations peaked north of the Alaska Range.

DISCUSSION

Annual changes in the age structure of lynx carcass collections were noted in this study as well as in Alberta and Cape Breton Island. In Alberta, the representation of kits in a collection was $\leq 3\%$ during 3 years of hare scarcity (Brand and Keith (1979). Similarly, in my study each region had a total of 3-4 winters in which $< 8\%$ of the lynx collected were kits.

Lynx Age Structure in Relation to Hare Populations

Annual changes and regional differences in the age structure of

the lynx collection appeared to correspond with changes in the snowshoe hare population. This pattern also emerged when I pooled age data according to the previous winter's hare population.

The proportion of lynx kits in carcass collections varied with hare abundance in other studies, as well. Nellis et al. (1972) stated that the number of lynx kits that survived their first winter was directly related to the number of hares. Brand and Keith (1979) noted a decline in the proportion of kits in trapped samples from 31% of 52 lynx during the winter following an abundance of hares to <1% of 518 during two winters following a scarcity of hares. The number of kits that Brand and Keith collected from regions with high hare populations was 70% higher than in collections from regions with low hare populations. They stated that data from Manitoba also showed a decrease in the proportion of kits trapped during a hare decline (40% in 1971-72 to 2% in 1973-74) (W. H. Koonz, pers. commun. to Brand and Keith 1979) and they concluded that the occurrence of kits in the winter population, therefore, appeared directly related to hare abundance. On Cape Breton Island, the representation of lynx kits in the harvest declined ($\underline{P} < 0.05$) from 29% to 9% to 2% (sample sizes of 42, 57, and 55 lynx, respectively) during 3 years of declining hare populations (Parker et al. 1983). These declining proportions were similar to the declining proportion of kits in the three regions in my study during several successive years of a hare decline (19% to 5% to 3% in the Yukon Basin, 41% to 6% to 2% to 0% in the Tanana Basin, and 30% to 14% to 4% to 0% in the Copper Basin). On Cape Breton Island, the proportion of kits plus yearlings declined ($\underline{P} < 0.005$) from 81% to

76% to 41% during the 3-year period of declining hare populations. However, the decline in the proportion of young lynx in the collection probably can be attributed to a declining proportion of kits because the proportion of yearlings collected during that time did not change significantly ($P > 0.05$).

Decreased recruitment of lynx to winter populations when hares are scarce probably results from increased mortality, especially of young lynx, and decreased lynx reproduction. Nellis et al. (1972, p.328) postulated that "There is some minimum density of hares below which a female lynx is not capable of successfully rearing kittens. Mortality of kittens (perhaps directly, or indirectly through starvation) between birth and December was probably the primary reason for no recruitment in the 3 years of lowest numbers of hares." Brand and Keith (1979) also concluded that postnatal mortality of kits, ranging from 65-95%, was the primary cause of lowered recruitment of winter populations. My results (see section on Reproductive Characteristics of Female Lynx) and Brand and Keith's results suggest that female lynx reproductive rates also fluctuate in relation to hare populations and may be an important component of changes in recruitment.

Lynx Age Structure in Relation to Lynx Populations

High populations are often assumed to have abundant young-of-the-year. In my study, the highest proportion of kits were collected several winters prior to peak lynx populations, not during peak lynx populations. The temporal relationship between peak proportions of kits and peak lynx populations was difficult to determine for the Tanana and Copper Basins because of the lack of a

well-defined peak in the proportion of kits in the Tanana Basin and because of the absence of carcass data from 1971-72. However, it appears that in the Yukon and Tanana Basins, and possibly in the Copper Basin, the highest proportions of kits in the collection did not occur during the highest population levels. Although I did not have data on when the lynx population peaked during the early 1960's, the highest proportion of kits in the collected in each region occurred in 1963-64.

In Alberta, Brand and Keith (1979) stated that the status of lynx populations is predictable because "(1) lynx populations and fur harvests reach cyclic peaks 1-2 years after cyclic peaks in snowshoe hares, and (2) recruitment of kits to winter populations decreases dramatically 2 years after the peak in the lynx fur harvest and remains near zero for the next 3 to 4 years." They concluded that these population characteristics provide a simple index for lynx population status and are useful in making management decisions. My results conflict with Brand and Keith's in several ways. As I discussed in the section on Snowshoe Hare and Lynx Population Trends, in one region of Alaska (Yukon Basin) the lynx population peaked the same year as the hare population, not 1-2 years later as in the other two regions and in Brand and Keith's study. In addition, the lynx populations in each region peaked 1-3 years before the highest number of pelts were exported from Alaska, not during the same year as in Brand and Keith's study. In my study, the recruitment of kits could not be compared to the fur harvest for each region because the regional distribution of harvest data was not available. However, in both the 1960's and early 1970's, the recruitment of kits in each region declined for several

years before the peak in the statewide lynx harvest (pelt exports), not 2 years after as in Brand and Keith's study. Similarly, the highest proportions of kits in the collections during the late 1960's occurred 1-4 years before the peak lynx population (though it was difficult to determine when the peak numbers of kits were collected in the Tanana and Copper Basins). The disparity between Brand and Keith's and my results suggests to me that these temporal relationships may not be predictable for all cycles or regions.

Considerations in Interpreting Age Structure Data

Many criteria for determining the ages of carcasses of the genus Lynx have been explored including counts of incremental lines in tooth cementum (Nava 1970; Crowe 1972, 1975; Nellis et al. 1972; Stewart 1973; Berrie 1973; Brand and Keith 1979; Grue and Jensen 1979; Kvam 1979), the degree of ossification in the legbones (Saunders 1964, van Zyll de Jong 1963, Conley 1968, Nava 1970), skull morphology (Saunders 1964, Conley 1968), eyelens weight (Conley 1968, Nava 1970, Stewart 1973), canine root growth (Saunders 1964), and body size (Saunders 1964). Cementum annuli are currently thought to be the most reliable estimators of age in lynx and bobcats (McCord and Cardoza 1982).

Due to the importance of assessing changes in the age structure as population levels change, the accuracy of the different age determination criteria used is of concern. If a criterion's accuracy varies during different phases of the lynx cycle, errors in classification could mask meaningful changes in the age distribution. Several factors may influence the reliability of certain age determination criteria. Lynx nutrition and levels of stress change

dramatically during the 10-year population cycle, possibly influencing skull morphology, the rate of bone ossification, or deposition of incremental lines in tooth cementum. Saunders (1964) stated that the emaciated condition of some lynx probably held back the development of the animal so muscle growth had not progressed normally to effect the narrowing of the temporal ridge and extension of the lambdoidal ridge. The fusion of the epiphyses in black-tailed deer (Odocoileus hemionus columbianus) was delayed in animals fed a low-level nutrition diet (Lewell and Cowan 1963). However, in a study of white-tailed deer (O. virginianus), age appeared to be the over-riding determinant of epiphyseal fusion and other factors such as nutrition had secondary roles (Purdue 1983). The most desirable techniques for determining ages are those that are consistent, regardless of nutrition or stress. I combined data from several techniques to help prevent inconsistency in age determination of carcasses collected during different phases of the population cycle.

Several studies suggest that the age structure of trapped samples of the genus Lynx is not representative of the age structure of the population. Bailey (1974) stated that bobcat kits were more easily trapped than were adults, thus kits were over-represented in trapped samples. Parker et al. (1983) suggested that (1) as adult female lynx are removed from the population through the winter, more kits become orphaned and are very susceptible to being trapped, (2) the proportion of kits in trapped samples is dependent upon the availability of snowshoe hares; when hares are scarce, kit mortality prior to the trapping season is high, thus, the proportion of kits in the population

and in trapped samples is low. When hares are abundant, kit mortality prior to the trapping season is low, thus, the proportion of kits in population and trapped samples is high, and (3) yearlings are the most prone to being trapped because it is the first winter in which they must hunt for themselves. Brand and Keith (1979) found some disparity between the age structure of lynx in field surveys and in trapped samples. They concluded that because the mother provides food for the lynx kits throughout most of the winter, kits were under-represented in the trapped samples. J. R. Cary (pers. commun.) said that lynx are so easy to trap that a higher age-specific trapability in some age-classes would not occur. The inherent problems in assessing the actual age structure of a lynx population make it difficult to evaluate how well the age structure of a trapped sample represents the age structure of the population. Even if age-classes are not trapped in proportion to their representation in the population, the changes in the proportions of young lynx trapped during the 10-year cycle can indicate changes in recruitment if the trapping selectivity pattern remains unchanged. The question of whether hare abundance causes changes in trapping selectivity remains unanswered.

REPRODUCTIVE CHARACTERISTICS OF FEMALE LYNX

Lynx population cycles are a function of changes in reproductive, mortality, and immigration/emigration rates. The degree to which each of these factors influences the cycles is not well understood.

Mortality and immigration/emigration are difficult and expensive characteristics to assess in lynx populations because of the generally solitary, secretive nature of these animals. Reproductive performance can be more readily evaluated because of the availability of reproductive tracts from harvested/trapped animals.

Knowledge of the reproductive biology of lynx is useful for management of the species. The population dynamics of this cyclic species can be better understood by determining which factors influence lynx reproduction, how that influence is manifested (cessation of ovulation and/or implantation, intra-uterine mortality), and how to monitor changes in lynx productivity. The reproductive biology of North American lynx has been studied in Newfoundland (Saunders 1961), Cape Breton Island (Parker et al. 1983), Ontario (Stewart 1973), Alberta (Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979), western Canada (van Zyll de Jong 1963), and Alaska (Berrie 1970, 1973; Nava 1970). Many of these studies suggest that the reproductive success of lynx is closely associated with abundance of snowshoe hares but none of the studies had data from an entire population cycle. ADF&G's lynx carcass collection, however, did span an entire population cycle, thus enabled me to examine annual and regional changes in relation to hare abundance.

ADF&G has records of the number of CL and placental scars (PS) in

the reproductive tracts of lynx carcasses collected from 1961-62 through 1972-73. Using these data, my objectives were:

1. To determine if annual and/or regional variations exist in female lynx reproduction.
2. To determine whether ovulation and/or implantation in lynx fluctuated during a 10-year population cycle of lynx.
3. To examine the relationship between lynx reproduction and hare populations trends.
4. To compare reproductive rates in yearling and adult lynx.
5. To examine the relationship between lynx reproduction and lynx population trends.

DEFINITIONS OF ACRONYMS

Throughout this chapter, I use several acronyms for the reproductive characteristics that were examined. Although these acronyms are defined in the text, I have summarized them below for easy reference:

CL = corpora lutea. Refers to corpora from recent and previous breeding seasons.

mCL = mean number of CL per female with CL.

PS = placental scars. May include both faded and dark scars.

mPS = mean number of PS.

RPS = recent placental scars. Excludes PS judged to be from previous or unsuccessful pregnancies.

mRPS = mean number of RPS per female with RPS.

METHODS

Reproductive performance of female lynx was assessed from lynx

carcasses by macroscopic counts of the number of CL in the ovaries and the number of RPS in the uteri. Reproductive tracts were removed from the carcasses, placed in freezer bags with water, and frozen. At a later date, they were thawed and both uterine horns slit open and examined against a background light source to count all PS (dark and light) (Berrie 1970). Diagramatic sketches of the uteri noting the location and color of PS were drawn on the necropsy sheets for specimens collected in all years except 1968-69 and 1969-70. Ovaries were stored in 10% formalin for approximately 2 months to harden and were then sectioned with a razor blade to count CL (Berrie 1970).

Most lynx commence breeding activity in late March and early April (Nava 1970), parturition occurs approximately 63-70 days later (Saunders 1961), and the kits remain with the mother until the following breeding season. Breeding seasons, unlike winter trapping seasons, are denoted in this thesis by non-hyphenated years. For example, reproductive information from a female collected during the winter of 1963-64 reflects her reproductive performance through spring 1963 and is referred to as 1963 data. "Yearling" reproduction in this study refers to females which ovulated at approximately 10 months and gave birth on approximately their first birthday; these lynx were trapped as yearlings. When I refer to reproduction during a certain hare or lynx population level, "during" refers to the population levels of the winter immediately preceding the reproductive season specified.

Duke (1949) and Crowe (1975) provided evidence that the CL in bobcats (Lynx [Felis] rufus) do not degenerate histologically into

corpora albicantia but can persist for more than 1 year. Brand and Keith (1979) suggested a similar situation for lynx; therefore, this discussion will refer to both recent CL and corpora from previous cycles (formerly called corpora albicantia [van Zyll de Jong 1963, Nava 1970, Stewart 1973]) as CL.

Reproductive tracts had been discarded before I began my research, so I used the data recorded on the necropsy sheets for my reproductive analyses. Sketches of the uteri indicate that many adult lynx, and some yearlings, had several shades of PS. I assumed that the lightest shades were from pregnancies which terminated prior to parturition or from pregnancies in previous years. Because I wanted a measure of the number of young born during the most recent spring, I counted only PS judged to be from successful pregnancies and from the most recent breeding season. I made that subjective decision based on the darkness and spacing of the PS relative to other PS. I excluded data from lynx carcasses trapped between 16 March and 30 June for two reasons: (1) to avoid combining data from females that had bred during that year's breeding season with data from members of the same cohort that had not and (2) because estrus and pregnancy can influence the intensity of older PS in red foxes (Vulpes vulpes) (Englund 1970, Lindström 1982), thus may influence the intensity of PS in lynx as well. If a necropsy sheet did not indicate the month of collection, I assumed that the lynx was not collected between 16 March and 30 June because <10% of the carcasses with known collection dates were taken during that period. Only carcasses with data from either both ovaries or both uterine horns were included in my sample. The sum of the number of CL in both

ovaries and the sum of the number of RPS in both uterine horns were used for my analyses.

K-W, K-W Pairwise Comparison, and Mann-Whitney tests ($P < 0.05$) were conducted using the BMDP3S program (Dixon et al. 1981) to identify annual and regional variability in lynx reproduction. Chi-square contingency tables were used to compare proportions of breeders.

RESULTS

I included data from 2,323 yearling and adult female lynx carcasses in my analysis of lynx reproduction; 2,290 lynx had data on ovulation and 2,076 had data on implantation. Yearling reproductive data were scarce from 1966 through 1969 and were not available from each region during those years. Fairbanks, Delta, and Tok did not have significantly different values ($P < 0.05$) for the mean number of CL per female with CL (mCL) or the mean number of RPS per female with RPS (mRPS) during any year so I pooled data from these areas and refer to the pooled set as the Tanana Basin data.

Annual Changes

Lynx ovulation fluctuated during the lynx carcass collection period with fluctuations particularly evident in the yearling age-class. Although regional sample sizes were very small in some years, in each region the proportions of yearlings with CL decreased from >97% in 1962 and 1963, to <12% in 1966, then increased again to >80% in 1969, 1970, and 1972 (Figure 6, Appendices 15-17). In contrast, each year at least 90% of the adults had CL; the lowest proportions occurred in 1966. Annual differences in the proportion of

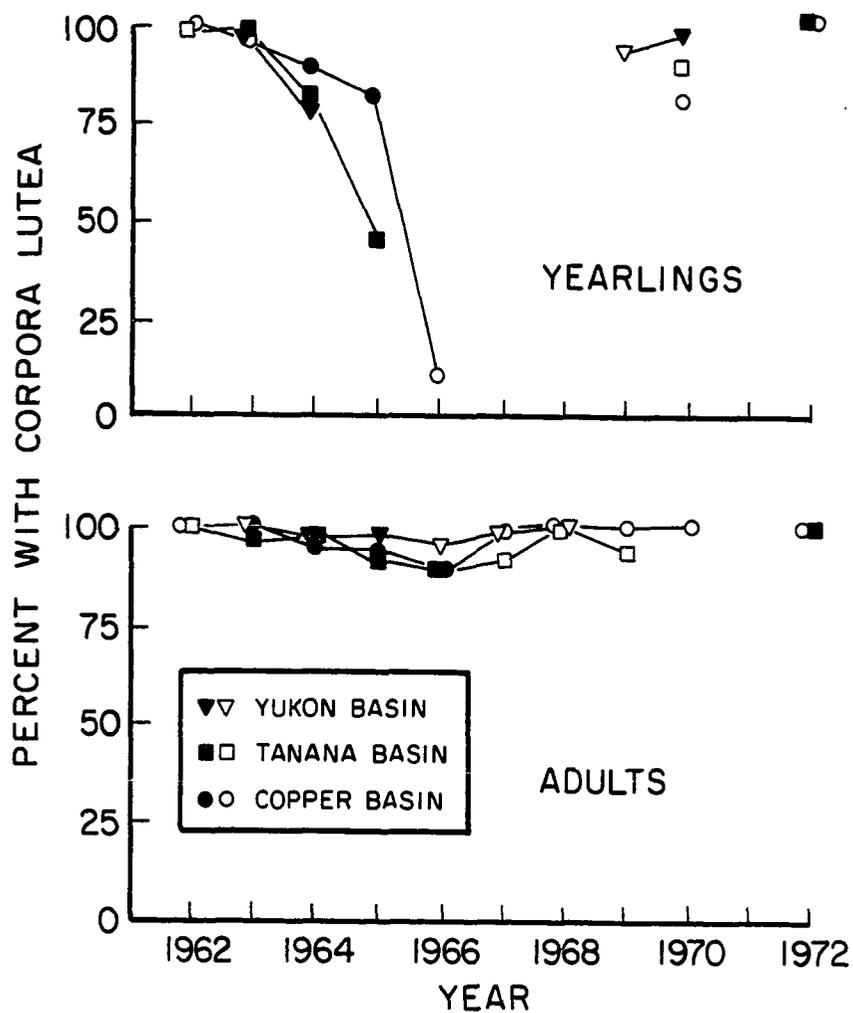


Figure 6. Percentage of yearling and adult lynx with corpora lutea, 1962 through 1972. Data from carcasses collected in three regions of Alaska. Open symbols denote sample sizes 8-25 and solid symbols denote sample sizes >25.

adults ovulating could not accurately be assessed because CL in lynx can persist for several years and my method of counting could not distinguish CL from different years. The yearling mCLs peaked in 1963, were lowest in mid-1960's, were relatively high in 1970, and decreased in 1972 (Figure 7, Appendix 18). Adults had a pattern of change in mCL similar to yearlings, with the exception that in the Yukon Basin the adult mCL did not peak in 1963 but had a low plateau from 1963 through 1965 (Figure 8, Appendix 19). During the 1963 peak in ovulation, the yearling mCL ranged from 5.6 ± 0.80 ($n = 16$) (Yukon Basin) to 6.3 ± 0.27 ($n = 27$) (Tanana Basin) and the adult mCL ranged from 9.5 ± 2.05 ($n = 11$) (Yukon Basin) to 17.9 ± 2.64 ($n = 43$) (Copper Basin). Regions with significant differences in mCL between years are listed in Appendices 20 and 21.

The successful implantation of fertilized ova in lynx also fluctuated during the carcass collection period. In 1963, 56-83% of the ovulating yearlings in each region had RPS (Figure 9). These proportions decreased through 1965 (except in the Yukon Basin where the yearling sample size was 1). The few yearling data collected after 1967 indicated that the proportion of ovulating yearlings with RPS increased in 1970 then decreased in 1972. The proportions of ovulating adults with RPS decreased from 87-93% in 1963 to lows of 33% in 1966 in the Yukon Basin, 26% in 1966 in the Tanana Basin, and 8% in 1967 in the Copper Basin. In all 3 regions, the mRPS differed between some years in adult lynx ($P < 0.05$) (Figure 10, Appendices 22, 23) but not in yearlings (Figure 11, Appendix 24). In general, the adult mRPS in all regions decreased from 1962 or 1963 through 1967 then increased through

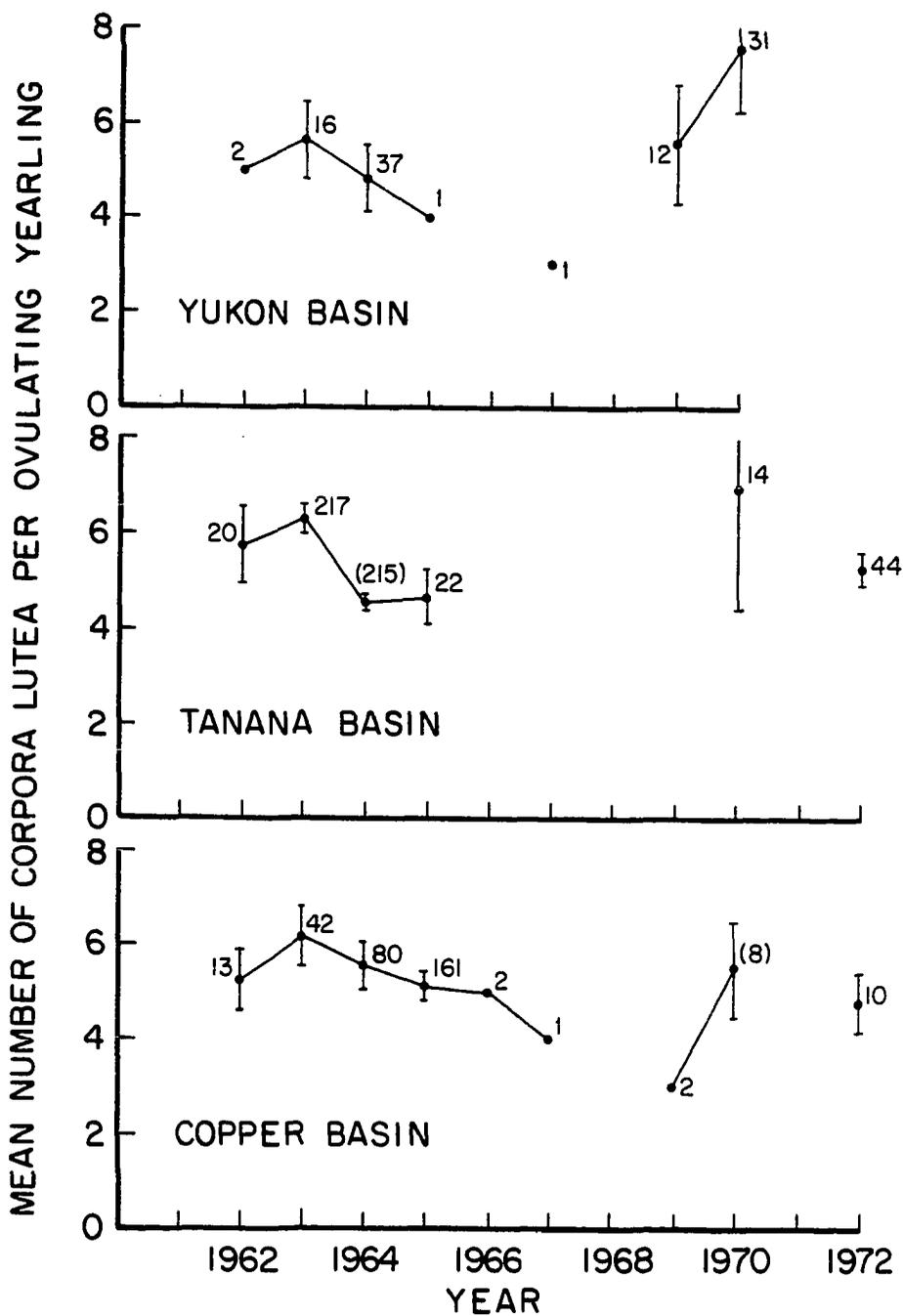


Figure 7. Mean number of corpora lutea per ovulating yearling lynx in three regions of Alaska, 1962 through 1972. 95% CI and sample sizes are noted. Parentheses denote samples with means significantly different than those in the previous year (Kruskal-Wallis Pairwise Comparison, $p < 0.05$).

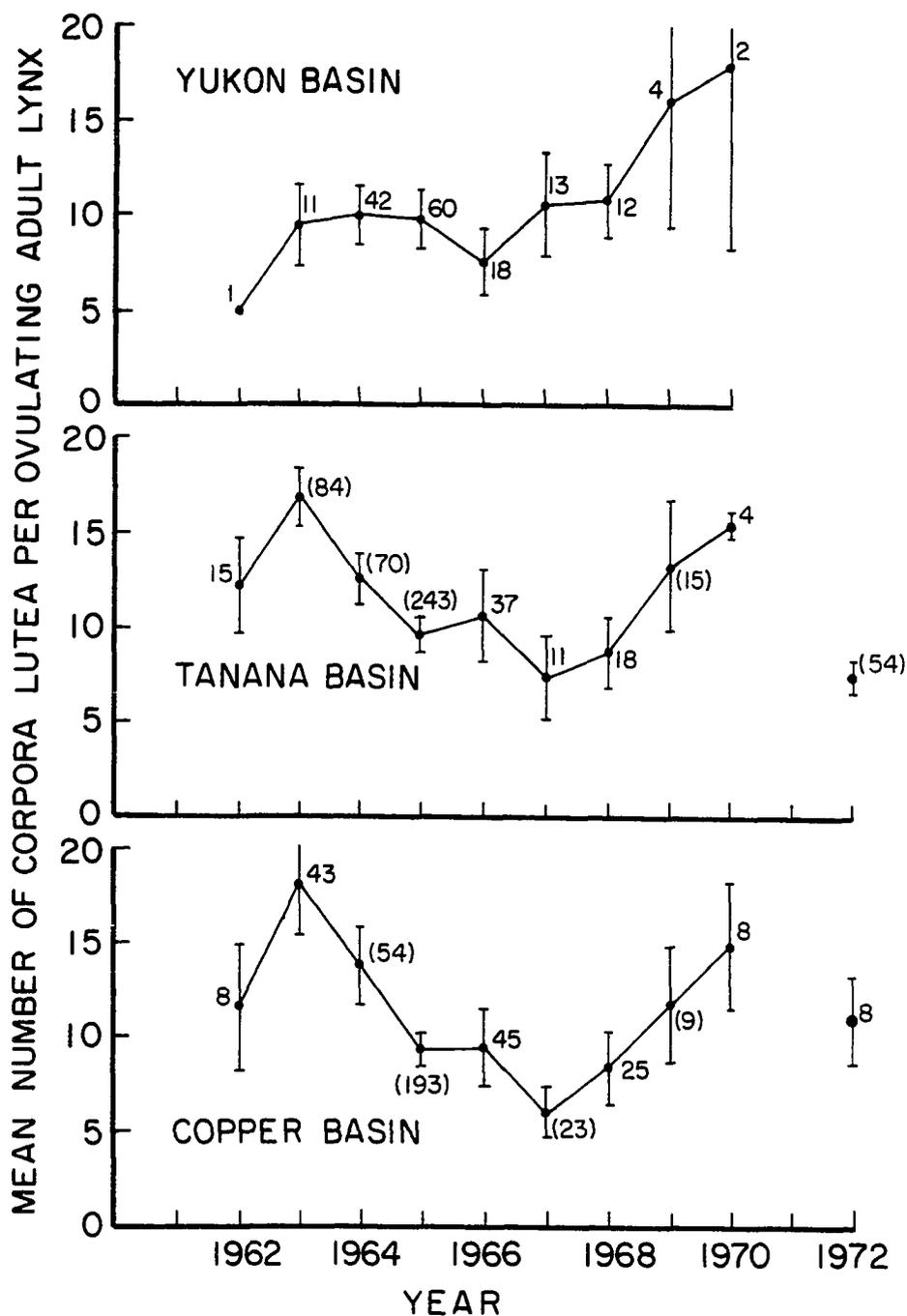


Figure 8. Mean number of corpora lutea per ovulating adult lynx in three regions of Alaska, 1962 through 1972. 95% CI and sample sizes are noted. Parentheses denote samples with means significantly different than those in the previous year (Kruskal-Wallis Pairwise Comparison, $p < 0.05$).

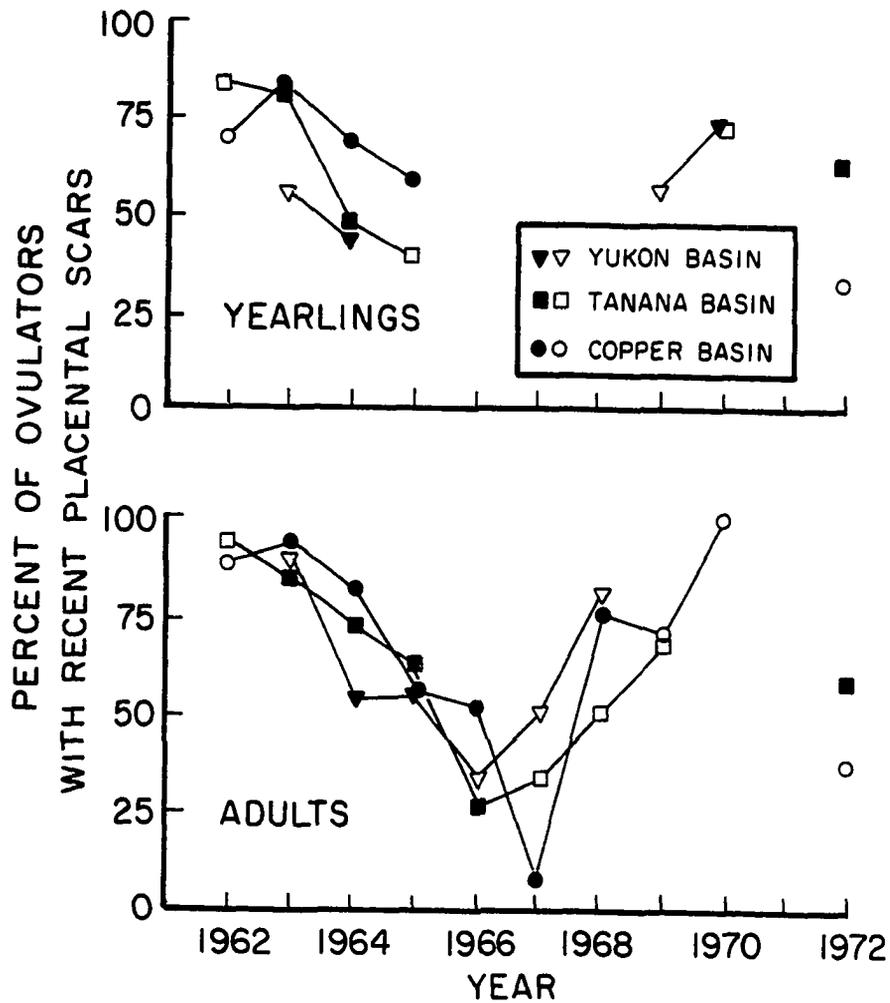


Figure 9. Percentage of ovulating yearling and adult lynx with recent placental scars, 1962 through 1972. Open symbols denote sample sizes 8-25 and solid symbols denote sample sizes >25.

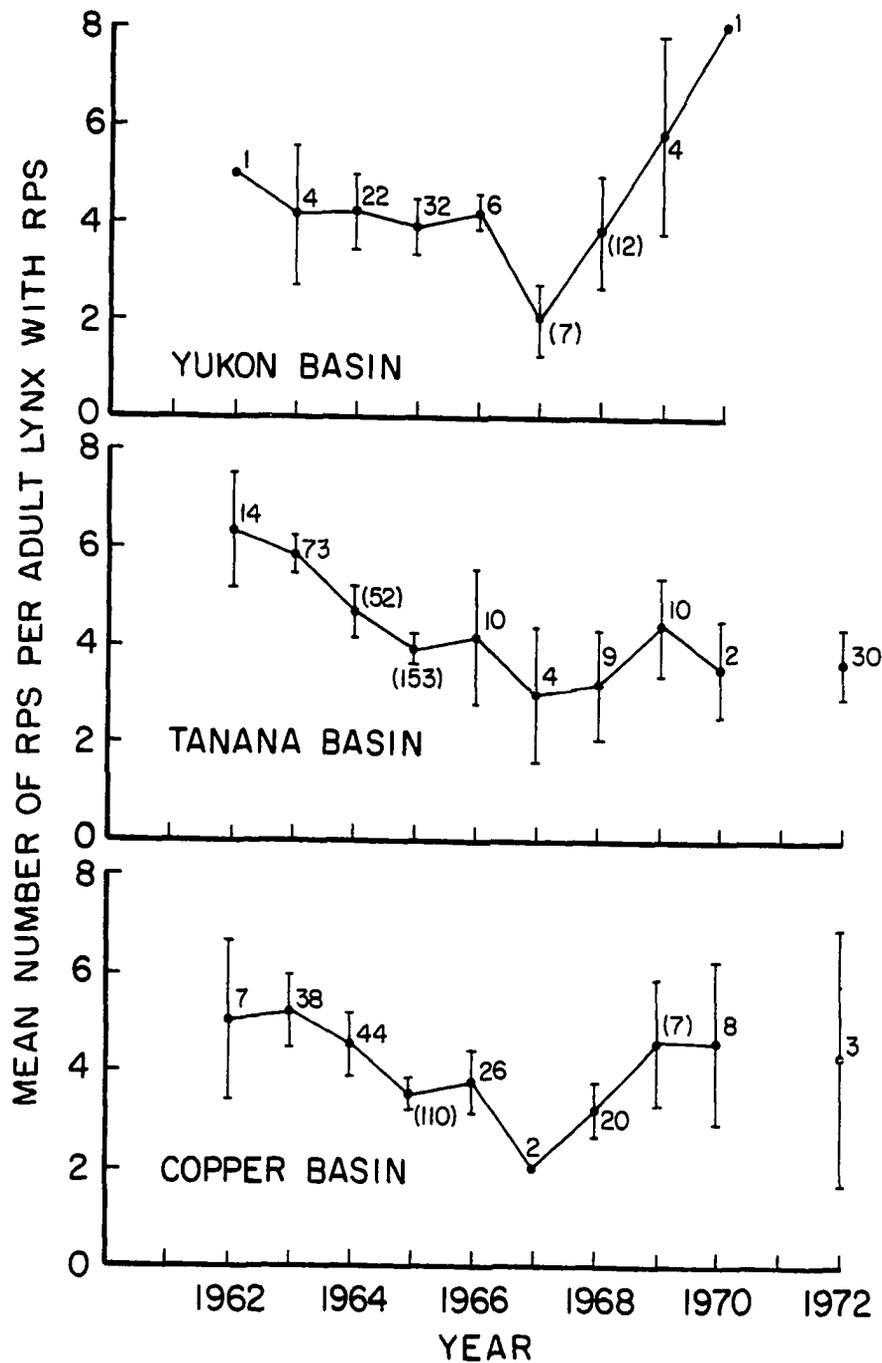


Figure 10. Mean number of recent placental scars (RPS) per adult lynx with RPS, 1962 through 1972. Data from carcasses collected in three regions of Alaska. 95% CI and sample sizes are noted. Parentheses denote samples with means significantly different than those in the previous year (Kruskal-Wallis Pairwise Comparison, $P < 0.05$).

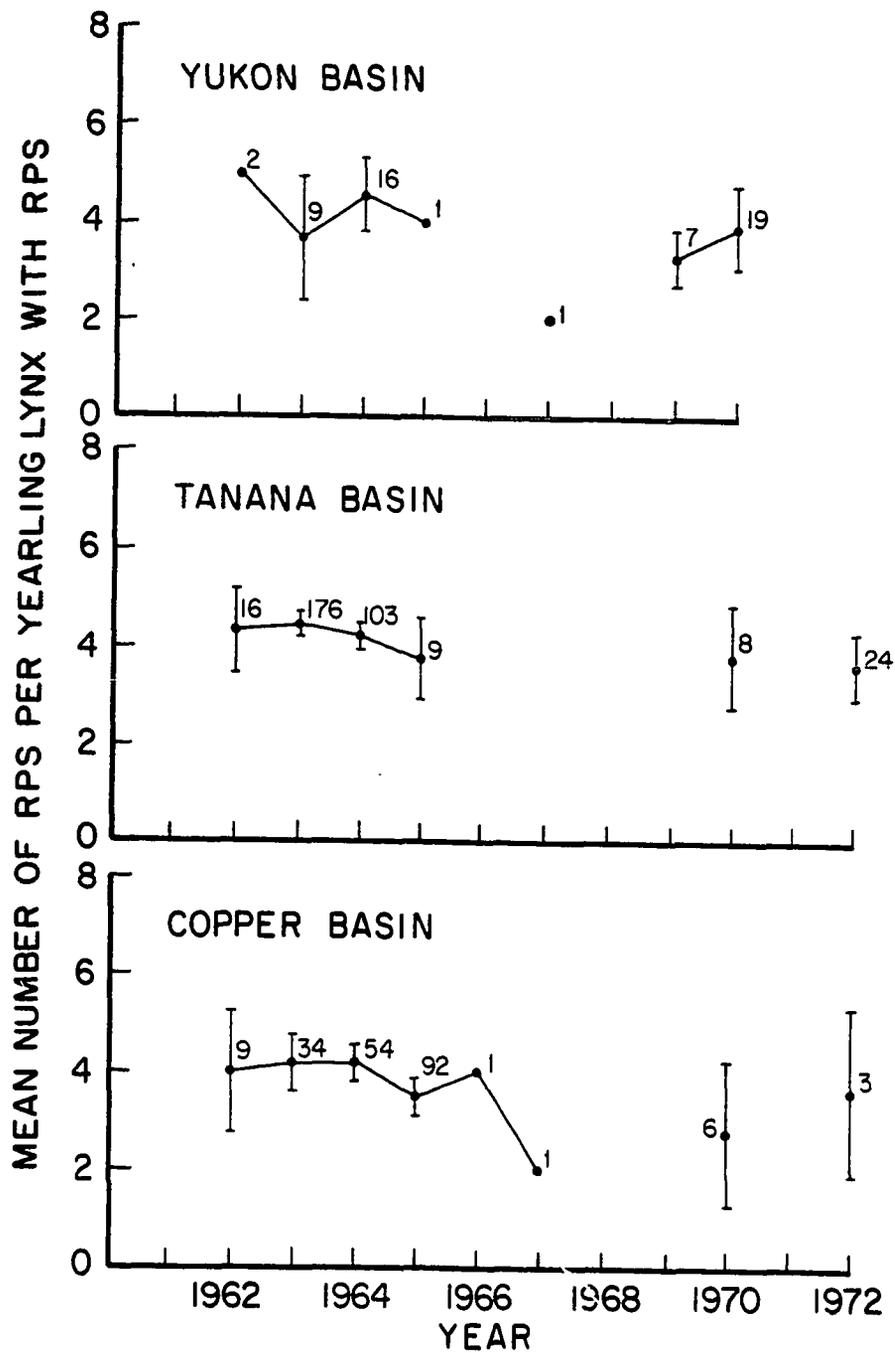


Figure 11. Mean number of recent placental scars (RPS) per yearling lynx with RPS, 1962 through 1972. Data from carcasses collected in three regions of Alaska. 95% CI and sample sizes are noted.

1969. In the Yukon Basin, the only significant annual differences in the adult mRPS were between 1967 and all other years (except 1962 when the sample size was 1). In the Tanana Basin, the adult mRPS in 1962 and 1963 were significantly higher than the mRPS from all other years (except 1970 when the sample size was 2). No differences were detected in the adult mRPS in the Tanana Basin from 1965 to 1972. In the Copper Basin, the adult mRPS in 1962, 1963, and 1964 were significantly higher than in 1965, 1967, and 1968 but were not significantly different from the mRPS in 1969, 1970, and 1972. When sample sizes were >1 , the yearling mRPS ranged from 2.8 to 5.0 and the adult mRPS ranged from 2.0 to 6.3.

Implantation values in 1968 and 1969 may be slightly inflated because I could not eliminate faded scars during those years due to the absence of drawings of the uteri.

Regional Differences

During at least 1 year, regional differences were detected in the proportion of yearlings with CL, the yearling and adult mCLs, and the proportion of ovulating yearlings and adults with RPS ($P < 0.05$) (Appendix 25). Copper Basin lynx had significantly different reproductive values from Yukon and/or Tanana Basins lynx in all cases when regional differences were detected. In some years, the Copper and Tanana Basin lynx had significantly different reproductive values from the Yukon Basin lynx, however the Tanana Basin lynx never had significantly different values from both the Yukon and Copper Basin lynx during the same year. When differences in reproduction were detected, the Copper Basin lynx had higher values than the Yukon and/or

Tanana Basin lynx from 1964 through 1966, lower values than the Yukon Basin lynx in 1967 and 1969, and higher values than the Tanana Basin lynx in 1972. No regional differences were detected in the proportions of adult lynx with CL, the yearling mRPS, or the adult mRPS.

Lynx Reproduction in Relation to Hare Populations

The relationship between lynx reproduction and hare abundance was evident when I compared: (1) reproductive data pooled from all regions and years having an abundance of hares to reproductive data pooled from all regions and years having a scarcity of hares, (2) annual changes in lynx reproduction within each region to annual changes in hare populations, and (3) regional differences in lynx reproduction to regional differences in hare populations.

When lynx reproductive data were pooled according to the previous winter's hare population, all measures of lynx reproduction were higher when hares were abundant than when hares were scarce. Between years of hare abundance and scarcity, a dramatic decline (97% to 18%) occurred in the proportion of yearlings with CL. Significant declines were also noted in the proportions of adults with CL, the yearling and adult mCL, the proportion of yearling and adult ovulators with RPS, and the adult mRPS (Table 4, 5). Although the yearling mRPS also declined when hares were scarce, this difference was not significant, perhaps due to the small sample size (2 yearlings) when hares were scarce.

A similar relationship between lynx reproduction and hare abundance was evident when I compared annual changes in lynx reproduction and hare populations within each region. However, the absence of trapper questionnaires prior to 1965-66 and the absence of

Table 4. Ovulation in yearling(Y) and adult(A) lynx in relation to snowshoe hare populations. Reproductive data from carcasses collected in three regions of Alaska. Sample sizes noted in parentheses.

	Lynx age	Hare population level ^a		Significance level from tests for differences in reproduction between different hare popns.
		Abundant	Scarce	
% with CL ^b	Y	97.2 (422)	18.5 (27)	$\underline{P} < < (0.001$
	A	98.7 (232)	94.4 (197)	$0.01 < \underline{P} < 0.025$
Significance level ^c from tests for differences in reproduction between age-classes		$0.10 < \underline{P} < 0.25$	$\underline{P} < 0.001$	} ^c
Mean number of CL ^d ± 95% CI	Y	6.0 ± 0.21 (410)	4.0 ± 0.78 (5)	$0.005 < \underline{P} < 0.01$
	A	13.0 ± 0.91 (229)	8.7 ± 0.81 (186)	$\underline{P} < 0.0005$
Significance level ^e from tests for differences in reproduction between age-classes		$\underline{P} < 0.0005$	$0.005 < \underline{P} < 0.01$	} ^e

^a According to Hare Abundance Indices. Prior to the use of HAJs, years designated as having peak hare populations were also considered to have hare populations that would have been classified as abundant.

^b CL = corpora lutea; includes CL from recent and previous ovulations.

^c χ^2 Contingency Table, 1 df.

^d per ovulating female.

^e Mann-Whitney, 1-tailed.

Table 5. Presence of recent placental scars (RPS) in yearling(Y) and adult(A) lynx in relation to snowshoe hare populations. Reproductive data from carcasses collected from three regions of Alaska. Sample sizes noted in parentheses.

	Lynx age	Hare population level ^a		Significance level from tests for differences in reproduction between different hare popns.
		Abundant	Scarce	
% ovulators with RPS	Y	72.3 (404)	28.6 (7)	0.01 < P < 0.025 } b
	A	76.9 (229)	42.6 (197)	
Significance level ^b from tests for differences in reproduction between age-classes		0.10 < <u>P</u> < 0.25	(sample too small)	
Mean number of RPS ^c ± 95% CI	Y	4.2 ± 0.18 (292)	3.0 ± 1.96 (2)	0.10 < <u>P</u> < 0.25 } d
	A	4.9 ± 0.31 (176)	3.6 ± 0.33 (85)	
Significance level ^d from tests for differences in reproduction between age-classes		<u>P</u> < 0.005	<u>P</u> > 0.25	

^a see footnote in Table 4.

^b χ^2 Contingency Table, 1df.

^c per female with RPS.

^d Mann-Whitney, 1-tailed.

lynx carcass data in 1971-72 and after 1972-73, made it difficult to determine the exact temporal relationship between annual lynx reproduction and hare abundance. In each region, more than 89% of the yearling lynx ovulated during abundant hare populations. The lowest proportions of yearlings with CL occurred during scarce and intermediate hare populations although sample sizes of lynx were sometimes small during years of hare scarcity. The lowest proportions of adults with CL occurred in 1966 during a hare scarcity in all regions. The highest yearling and adult mCLs occurred during the spring preceding or during the most abundant levels of hares; the lowest mCLs occurred during years of hare scarcity. The proportions of yearling and adult lynx with RPS usually were highest during the spring preceding the peak hare population and lowest during the "crash" of the hare population. In the Tanana Basin, the adult mRPS significantly decreased during the decline in hare abundance from 1963 through 1965.

Trends in lynx reproduction in each region, however, did not always correspond to similar trends in hare populations. In the Tanana Basin, there was no difference ($P > 0.05$) in the adult mRPS from 1965 through 1972 during the hare scarcity and subsequent increase of the hare population; perhaps the lack of significance was due to small sample sizes. In addition, I did not detect a difference between years in the yearling mRPS in any region, even though hare populations were fluctuating. In some cases, increases or decreases in lynx reproduction occurred prior to similar changes in the hare population.

Regional differences in lynx reproduction usually reflected differences in the hare populations within those regions. In 1964, the

yearling mCL, the adult mCL, and the proportion of ovulating adults with RPS were higher ($P < 0.05$) in the Copper Basin than in the Yukon Basin and likely corresponded to the later peak in hare abundance in the Copper Basin. In 1965, the proportion of ovulating yearlings was higher ($P < 0.05$) in the Copper Basin than in the Tanana Basin and also likely corresponded to the later peak in hare populations south of the Alaska Range. The 1967 adult mCL, the 1967 proportion of adults with RPS, and the 1969 yearling mCL were lower ($P < 0.05$) in the Copper Basin than in the Yukon Basin and likewise corresponded to the less abundant hare populations in the Copper Basin. In 1972, however, the adult mCL was higher ($P < 0.05$) in the Copper Basin than in the Tanana Basin even though HAIs were higher in the latter region.

Age-class differences in reproduction seemed to be related to hare abundance. When hares were abundant, yearling and adult lynx had similar proportions of ovulators and similar proportions of implantors, but the yearlings had lower mCL and mRPS than did the adults (Tables 4, 5). When hares were scarce, yearlings had lower values than did adults for all measures of reproduction, although the sample size of yearlings with RPS was too small to allow a test for the significance of the lower proportion of yearlings with RPS. Small sample sizes also probably caused the lack of a significant difference in mRPS between yearlings and adults.

Lynx Reproduction in Relation to Lynx Populations

I compared lynx reproduction from 1965 through 1972 to the following winter's index of lynx population size (LAI) to determine if changes in reproduction resulted in immediate changes in population

trends. Most increases and decreases in lynx reproduction were followed by similar changes in the following winter's lynx population. The most notable exception was in the Tanana Basin where reproduction peaked in 1970 (or possibly 1971, although no data were available then), however the lynx population peaked in 1972-73. Thus, reproduction peaked several years before the lynx population peaked. In the Yukon and Tanana Basins, the proportion of adults with RPS was lowest during the spring preceding the first winter with a scarcity of lynx (indicated by LAIs). In the Copper Basin, the proportion of adults with RPS was lowest during the spring following the first winter with a scarcity of hares.

DISCUSSION

Lynx reproduction from 1962 through 1972 fluctuated in an apparently cyclic manner and corresponded closely with changes in snowshoe hare populations. Changes in female reproduction during the 10-year cycle resembled patterns suggested by reproductive rates from short-term studies. Increases in lynx reproduction during an abundance of hares suggests that reproduction is strongly influenced by nutrition. Reproductive rates also varied according to the age of the female and the reproductive variable being considered.

Lynx Reproduction in Relation to Hare Populations

I examined the relationship between lynx reproduction and hare abundance by pooling reproductive data according to the preceding winter's hare population. For example, I pooled reproductive data from all females collected during the spring following a winter of hare

abundance. In general, lynx reproductive rates were higher when hares were abundant than when hares were scarce. Similar results were evident from annual and regional changes in lynx reproduction but were not as well-defined as with the pooled data. The following discussion refers to my pooled data.

The age of puberty in lynx is likely influenced by snowshoe hare population levels. In my study, the proportion of yearlings ovulating declined from 97% of 422 yearlings to 18% of 27 yearlings between periods of hare abundance and scarcity, respectively ($P < 0.001$) (Table 4). No other lynx studies in North America have had sufficient sample sizes to test for differences in the age of puberty with fluctuating hare population levels. However, results from other studies support my conclusion. In Alberta, 15 of 16 (94%) yearling lynx examined in 1962 and 1963 (the springs prior to and during a hare peak) had ovulated (van Zyll de Jong 1963), and 61% of the 143 yearling lynx examined in 1972 and 1973 in regions with abundant hare populations during the subsequent cycle had ovulated (Brand and Keith 1979). In a Newfoundland study done when hares were scarce, lynx did not ovulate as yearlings (Saunders 1961).

The influence of hare abundance on adult lynx ovulation was more difficult to determine. In my study, in Alberta (van Zyll de Jong 1963), and in Ontario (Stewart 1973), more than 90% of all adult female lynx examined had CL, however a high proportion of adults with CL does not necessarily indicate that a high proportion of adults ovulated during the most recent breeding season. Lynx can retain CL for several years (Nellis et al. 1972, Brand and Keith 1979) and my method of

counting did not distinguish CL of different years. Thus, the probability of detecting annual differences in adult ovulation was reduced. In my study the proportion of adults with CL only decreased from 99% of 232 adults to 94% of 197 adults between years of hare abundance and scarcity but this difference was significant ($0.01 < p < 0.025$). This decline in the proportion of adults with CL could result from a lower proportion of yearling lynx ovulating when hares are scarce; such non-breeding yearlings then enter the adult age class with no prior CL. Brand et al. (1976) did not find a significant difference in the proportion of adults with CL between areas of hare abundance and scarcity. Nellis et al. (1972) reported that female lynx (ages unspecified) in Alberta conceived regardless of hare densities; 15 of 17 (88%) of the female lynx they collected during a "trough" in the hare cycle (1964-65 through 1966-67) had recent CL. A decrease in the mCL during periods of hare scarcity was noted in my study and in Alberta (Brand and Keith 1979).

A higher proportion of yearling and adult ovulators had evidence of a recent successful pregnancy (presence of RPS) when hares were abundant than when hares were scarce. In my study, the proportion of ovulating lynx with RPS decreased from 72% of 404 yearlings to 28% of 7 yearlings and from 77% of 228 adults to 43% of 197 adults ($p < 0.001$) between years of hare abundance and scarcity, respectively. Similarly, the proportion of adult lynx with PS declined from 73% of 78 adults to 33% of 100 adults ($p < 0.001$) in Alberta (Brand and Keith 1979) and from 75% of 4 adults to 64% of 14 adults on Cape Breton Island (Parker et al. 1983) during declines in the hare populations in those areas.

The mean number of blastocysts implanted (= mRPS) in yearling and adult lynx was higher when hares were abundant (4.2 and 4.9, respectively) than when hares were scarce (3.0 and 3.6, respectively), although for yearlings this difference was not significant, perhaps due to small sample sizes. Similarly, in Alberta the adult mPS decreased from 4.6 to 3.4 between years of hare abundance and scarcity, however none of the nine yearlings collected when hares were intermediate or scarce had PS (Brand and Keith 1979). On Cape Breton Island, the mPS in yearling and adult lynx did not decrease with the decreasing hare population, but the sample sizes of lynx were very small during the lowest hare population (Parker et al. 1983).

Changes in reproductive rates in the Copper Basin lynx appeared to sometimes lag behind changes in the Tanana and/or Yukon Basin lynx, perhaps due to differences in the hare cycles between those regions. However, trends in lynx reproduction were quite similar among all regions in my study despite apparent variations in the hare populations within those regions. Perhaps the variability in hare abundance among years was much greater than among regions.

Age Class Differences in Lynx Reproduction

Some measures of yearling and adult lynx reproduction were similar when hares were abundant but all measures of yearling reproduction were much lower than those for adults when hares were scarce. When hares were abundant there were no differences in the proportions of adults and yearlings ovulating or in the proportion of adults and yearlings with RPS. Unlike my results, during an abundance of hares in Alberta the proportion of ovulators with PS was lower in yearlings than in

adults ($P < 0.001$) (Brand and Keith 1979). The discrepancy between my results and Brand and Keith's may result because I included only PS judged to be from successful implantations in the most recent breeding season.

Observed differences in yearling and adult ovulation do not necessarily reflect actual differences in the most recent season's ovulation between the two age-classes. Evidence that CL can accumulate for several years is provided by the rising trend in the mCL with age in lynx (Brand and Keith 1979) and in their close relative, the bobcat (Crowe 1975). Crowe suggested that CL may even persist throughout the life of an individual. In contrast, observed differences in yearling and adult implantation should reflect age-class differences in implantation during the most recent breeding season. In my study, the mRPS was higher in adult lynx than in yearlings during periods of both hare abundance and scarcity.

Influence of Nutrition on Reproduction

North American lynx depend on snowshoe hares as a primary food source during all phases of the cycle (Brand et al. 1976), thus, as hare abundance rises and declines so does the carrying capacity for lynx. Lynx in Alberta responded to changes in hare populations both functionally (changes in diet) and numerically, however, the shift to alternative prey as the hare population declined did not completely compensate for the decrease in biomass of hares killed per lynx; the mean daily consumption rate of individual lynx decreased 37%, perhaps 20% below that required to maintain body weight (Brand et al. 1976).

When hares are scarce, under-nutrition in lynx likely influences reproductive success and kit survival.

Nutrition influences many stages of reproduction in wild animals (Sadleir 1969), therefore it is not surprising that a variable reproductive rate occurs in an animal whose primary prey fluctuates so dramatically in abundance within an 8-11 year period. Nutrition may influence lynx productivity through changes in the energy and hormonal balance of the individual. Dietary changes and decreased consumption rates in lynx can cause a negative energy balance during periods of hare scarcity (Brand and Keith 1979). There is evidence that a negative energy balance can lead to reproductive failure by influencing estrus, the fertilizability of ova or ease of conception, embryonic survival, prenatal losses, and birth rate (Ratray 1977). Reproductive failure may result from the adverse effects of under-nutrition on the synthesis and release of gonadotropins in the pituitary and also the response of target organs to gonadotropins or gonadal hormones (Ratray 1977).

In my study, trends in lynx reproduction usually correlated well with trends in the previous winter's hare population, thus indicating a short response-time in these reproductive changes. At other times the trends differed by 1-2 years. This variability likely reflects the additional influence of other factors such as snow conditions, weather, lynx population size, densities of other predators, stress, and availability of alternate prey; all may act in concert with nutrition to influence lynx reproduction. The subjective nature of the trapper questionnaire responses and the normal variability in wild populations

may account for some of the variability in the temporal relationships observed.

Effects of Reproductive Changes on Lynx Populations

Because mortality can occur during many phases of the reproductive cycle, the proportion of females with CL, the mCL, the proportion of ovulators with RPS, and the mRPS produce estimates of litter size that decrease in size. The most accurate measurement of recruitment would be to observe kits in the wild. Some phases of the reproductive cycle have higher rates of mortality than others. In my study, for example, yearling ovulation appeared to be influenced by hare abundance more than was implantation.

The cumulative effect of mortality during different phases of the reproductive cycle can result in drastic declines in recruitment. I used the results presented in Tables 4 and 5 in the following formula to calculate the change in the total number of implantations (RPS) in a female lynx population when hares were abundant versus scarce:

$$(\text{number of females}) \times (\% \text{ with CL}) \times (\% \text{ of ovulators with RPS}) \times (\text{mRPS}) = \text{total number of RPS}$$

A hypothetical population of 1,000 yearling female lynx would produce 2,752 RPS (2.8 RPS/yearling) when hares were abundant. The same population would produce only 159 RPS (0.2 RPS/yearling) when hares were scarce, merely 6% of the number produced when hares were abundant. Adult lynx productivity would decrease less; 3,719 RPS (3.7 RPS/adult) when hares were abundant versus 1,448 (1.4 RPS/adult) when hares were

scarce. These declines in prenatal productivity during periods of hare scarcity are probably accompanied by increasing rates of postnatal mortality; Brand and Keith (1979) documented changes in lynx reproductive rates during changes in hare abundance but they concluded that post-natal mortality of kits before winter removed 65-95% of the kits born during a lynx population decline and appeared to be the primary factor limiting recruitment. Thus, drastic declines in the lynx population likely result from decreased numbers of breeding yearlings, decreased reproductive rates in yearlings and adults, and high rates of mortality in kits that are born.

In my study, during most years increases and decreases in lynx reproduction were followed by similar changes in the following winter's lynx population. However, correspondence between changes in lynx reproduction and changes in the following winter's LAI was sometimes lacking. Although reproduction directly influences population growth, the mortality of kits can determine the degree to which increases in reproduction result in increases in the population. A time-lag may occur between increases in reproduction and increases in population size, depending on the current population size and mortality rate. For example, lynx reproductive rates may increase but unless kits survive no recruits would be added to the population, thus, the population could show a net decrease. In addition, absolute numbers of lynx during a population peak may be high enough to produce an additional few years of net gain in population size even though reproductive rates have been declining during those few years.

Lynx reproduction measured by examining female lynx reproductive tracts, therefore, does not appear to be a reliable "predictor" of the following winter's lynx population. The additional influence of age structure and mortality and immigration/emigration rates on lynx abundance also need to be considered to predict the status of the following winter's lynx population more reliably. Similarly, it is important to remember that the lynx population can increase even though the reproductive rates are decreasing.

Considerations in Comparing Data From Different Studies

Caution is necessary when interpreting my results on lynx reproduction with respect to results from other studies. Comparability of results from different studies may vary depending on terminology, dates of data collection, and methods of processing reproductive tracts.

The terminology used to describe lynx reproduction is not always consistent. "Corpora lutea" refers to luteal bodies of recent and previous cycles in some studies (van Zyll de Jong 1963, Brand and Keith 1979, this study), refers only to luteal bodies of the most recent cycle in other studies (Nava 1970, Saunders 1961), and is undefined in still others. Mean numbers of CL are calculated from ovulating females in some studies (van Zyll de Jong, Brand and Keith 1979, this study), and from all females in other studies (Nava 1970, O'Connor, in press). In still other studies, the methods of calculation are undefined. Similar discrepancies exist for counts of PS. Proportions of females with PS are calculated from all females in some studies and from ovulating females in other studies. Mean numbers of PS are calculated

from females with PS in some studies (Brand and Keith 1979, Parker et al. 1983, this study), and from all females in other studies (O'Connor, in press); in other studies, the methods of calculation are undefined. Also, most authors have not specified whether they included in their PS counts those PS of a lighter shade than others and possibly from a previous or unsuccessful pregnancy.

Sometimes researchers included reproductive data from females collected during the breeding season in the calculation of that cohort's reproductive rate (Saunders 1961) and, therefore, combined data from members of the same cohort which may have participated in different numbers of breeding seasons. In addition, the condition of estrus or pregnancy might influence the intensity of PS and this could affect the PS counts (see next subheading).

Finally, the results I have presented differ somewhat from results noted by Nava (1970) and Berrie (1973), even though we used data from many of the same lynx carcasses. These differences probably exist because I excluded females with age discrepancies, females collected between 16 March and 30 June (excluded from reproductive analysis only), and PS judged to be from previous cycles or unsuccessful pregnancies. I believe that these exclusions were important for calculating the best estimate of lynx reproductive rates from the most recent breeding season.

Reliability of Using Placental Scars to Estimate Litter Size

PS counts are often used to estimate litter size in carnivores. PS of varying intensity/darkness are commonly present in individual uteri; thus, the examiner must decide which PS represent full-term

young and should be included to calculate mean litter sizes or breeding frequency. Frequently, the only evidence of intrauterine mortality is a faded PS because the fetuses are often resorbed or aborted. In my sample, some individual yearling lynx had both dark and faded PS. These PS obviously originated from the same (and only) litter. Therefore, I assumed that these light PS resulted from embryonic loss and I did not include them in my counts of RPS. Several factors may influence the intensity of PS and should be considered when comparing reproductive data from different studies and when calculating reproductive statistics.

Estrus and pregnancy cause fading of PS in red foxes (Englund 1970, Lindström 1981) and prairie voles (Microtus ochrogaster) (Martin et al. 1976). Although the effects of the reproductive season on the intensity of lynx PS has not been researched, I excluded reproductive data from females collected during the breeding season to prevent estrus or pregnancy from influencing PS counts.

The decision regarding which PS represent successful implantations from the most recent season must be decided so that the results do not vary with the date the animal was collected. This was only attained in red foxes if estrus and pregnant females were excluded (Englund 1970, Lindström 1981) and if PS of lighter shades were included as the number of months post-partum progressed (Lindström 1981). Although Nellis et al. (1972) stated that PS rapidly regress in lynx, Nava (1970) found no difference in the mean number of PS in yearlings taken early and late in the season and concluded that PS do not fade to the point of being overlooked during the collection period (November to March).

Methods of processing female lynx reproductive tracts may also influence PS counts. PS were visible in uteri that were examined fresh or after being frozen (Nava 1970, Parker et al. 1983, this study). PS were faint or indistinct in most lynx reproductive tracts that had been "cleared" (Nellis et al. 1972), stored in 10% formalin (Saunders 1961, van Zyll de Jong 1963), or stored in 30% alcohol (Stewart 1973). A notable exception is that Brand and Keith (1979) stored their lynx reproductive tracts in 10% formalin and PS were still visible. Clearing and fixing has been shown to influence the transparency and contrast of uterine tissue in prairie voles (Martin et al. 1976). I found no evidence to suggest that clearing or fixing lynx reproductive tracts improved the readability of PS.

Factors that influence PS coloration can cause inconsistencies in the interpretation of reproductive data because of the difficulty in trying to assess which PS represent full-term young. I recommend that researchers standardize their method of evaluating and recording PS counts in a manner similar to that used by Lindström (1981). Lindström classified red fox PS into 6 shade categories following Englund (1970); shade 1 being barely detectable and shade 6 being completely black. Because red fox PS fade with time, Lindström included increasingly lighter shades in his calculation of mPS as the time postpartum progressed. This approach enhances the comparability of reproductive data from different studies and reduces the subjective decisions of the investigator with respect to what to include as a RPS. A standardized method of evaluating PS intensity would also facilitate re-evaluation

of the data as information becomes available defining factors that influence PS intensity.

SUMMARY AND CONCLUSIONS

Female lynx carcasses were collected from Alaska trappers during the winters of 1961-62 through 1970-71 and 1972-73. To my knowledge, this is the first collection of lynx carcasses to span a complete population cycle and is the largest collection of which I am aware. My study analyzed the patterns of change in the age structure and reproductive characteristics of female lynx using data from 3,130 of these carcasses. The relationships of snowshoe hare population trends to lynx population trends, age structure, and reproduction are discussed.

Data on Alaska snowshoe hare and lynx population trends were available from literature, from abundance indices calculated with the results of trapper questionnaires, and from reports of lynx pelt exports. Agreement was lacking between peak LAIs from the three regions I examined and peaks in the number of lynx pelts exported from Alaska; LAIs are probably a more accurate index of lynx populations than are exports or harvest records because of the possible influence of trapping intensity and pelt prices on exports and harvest. In general, hare and lynx populations peaked in the early 1960's, were scarce in the mid-1960's, and peaked again in the early 1970's. Although previous reports from unpublished literature indicate that hare populations north of the Alaska Range peak 1 year prior to populations south of the Range, the abundance indices for my three regions did not completely support the same conclusion. In the late 1960's/early 1970's, cycles in the Yukon Basin were advanced by up to 2 years with respect to cycles in the Tanana and Copper Basins but the

Copper Basin cycles actually peaked 1 year prior to Tanana Basin cycles. The temporal relationship of the hare and lynx cycles was not the same in each region; however, in eight of nine region-winters, lynx populations became abundant (or were at their highest level) or became scarce 1 year after hares reached similar levels.

The age structure of the lynx population was studied with data from 3,130 female lynx carcasses. Lynx were classified as kits, yearlings, or adults based on incremental lines in tooth cementum, the degree of ossification in the radius and ulna, canine root growth, and/or skull morphology. Significant differences in the age structure occurred between some winters in all regions and between regions in 6 of 10 winters. Age structure changes north of the Alaska Range appeared to precede by one winter changes south of the Range. Predominantly young lynx (76% kits plus yearlings) were collected during the first winters following winters of hare abundance and predominantly adult lynx (78%) were collected during the first winters following winters of hare scarcity. In my study, the highest proportions of kits were collected one to possibly four winters prior to peak lynx populations, not 2 years after a peak population as noted by Brand and Keith (1979). Because the results of my study conflict with Brand and Keith's (1979), I suggest that the temporal relationship among peaks in the proportion of kits collected, the lynx population, and the lynx harvest are not always predictable. Research is necessary to determine whether criteria used for age classification are influenced by the fluctuating levels of nutrition experienced by lynx during the 10-year cycle. Several researchers have suggested that

trapped samples of lynx do not accurately represent the age structure of the actual population but I had no data to support or refute this claim.

Patterns of change in female lynx reproduction were examined by studying numbers of CL and RPS in 2,323 yearling and adult lynx carcasses collected during 10 winters. Changes in reproductive rates were most clearly and unambiguously detected in yearling lynx because of their exposure to only one breeding season. In each region, I detected significant differences between some years in the proportions of yearlings and adults with CL, the mCL for yearlings and adults, the proportions of yearlings and adults with RPS, and the adult mRPS. Reproductive rates usually peaked in 1962 or 1963, were lowest in 1966 or 1967, were high in 1970, and decreased in 1972. Mean numbers of CL were highest in the spring preceding or during the hare population peak and were lowest during periods of hare scarcity, thus suggesting a short response-time in these reproductive changes. When reproductive data were pooled according to similar levels in the previous winter's hare population, all measures of lynx reproduction were higher when hares were abundant than when hares were scarce, although the difference in mRPS for yearlings was not significant. This study is the first to document significant changes in the proportion of yearlings ovulating during different hare population levels, however results from other studies suggest a similar relationship. When hares were abundant, most (97%) yearlings ovulated and most (72%) yearlings with CL also had RPS but when hares were scarce, very few (18%) yearlings ovulated and only 29% of the ovulators had RPS. Adult lynx

were more productive than were yearlings, especially when hares were scarce. During periods of hare scarcity, the cumulative effect of decreased reproduction at many stages of the reproductive cycle can contribute to drastic declines in recruitment. Between periods of hare abundance and scarcity, the cumulative effect of declines in ovulation and implantation resulted in an overall decrease in productivity from 2.8 RPS/yearling to 0.2 RPS/yearling and from 3.7 RPS/adult to 1.4 RPS/adult. Nutrition is likely the primary factor causing decreased reproductive rates during periods of hare scarcity because lynx depend heavily on hares for food at all phases of the cycle. Changes in reproductive rates did not always result in similar changes in the following winter's LAIs, thus, lynx reproductive rates alone are not reliable predictors of the following winter's lynx population. Peaks in reproduction occurred 1-3 springs prior to peaks in the lynx population. This time-lag is likely due to the additional influences of postnatal mortality and absolute numbers of lynx on population growth. Results from different studies of lynx reproduction may vary depending on the terminology used, dates carcasses were collected, and methods of processing reproductive tracts. Suggestions for eliminating this problem are discussed.

Historically, lynx and snowshoe hares in North America have cycled in close correspondence. Lynx are highly specialized to prey on snowshoe hares, thus as hare abundance rises and declines so does the carrying capacity for lynx. Variable reproductive rates are likely to be highly adaptive in an animal whose primary prey fluctuates so

dramatically during an 8-11 year period. The effects of human exploitation (trapping) of lynx must be understood in terms of these natural oscillations. In recent years, concern has been expressed that lynx populations may be in danger of over-exploitation. The degree to which trapping influences lynx population cycles is not well understood but Berrie (1973) and Brand and Keith (1979) suggested that lynx populations are probably most severely impacted by intense trapping pressure during the period of declining or low numbers of lynx.

Because of the secretive nature of lynx, the different phases of the lynx population cycle are identified primarily through indirect assessments of their status. Useful predictors of lynx population declines would be data on the age structure and reproductive activity of the lynx populations and the status of the hare population. Population declines are detected after they occur by examining records of harvest and pelt exports. This study suggests, however, that at that point lynx reproduction may already have declined for several years and it may be relatively late for an effective response by the manager. The degree to which changes in productivity influence lynx recruitment cannot be known until the additional influence of mortality and movements on lynx populations are understood. In Alberta, lynx reproductive rates declined during scarce hare populations but Brand and Keith (1979) concluded that kit mortality between birth and winter was the primary factor limiting recruitment. The effects of trapping on lynx populations can be better evaluated if knowledge of the reproductive characteristics are combined with data on mortality and movements.

Long-term studies are especially important for understanding the ecology of cyclic species because factors influencing the population may vary during the span of the cycle. Hornocker and Bailey (in press) emphasized the need for a long-term approach to research. They drew an analogy between short-term research and a "stopped video tape"; 2-3 year studies yield accurate information regarding the current situation for a population but provide little insight into the long-term population dynamics. This thesis provides an account of a complete 10-year cycle in hare and lynx population trends, lynx age structure, and lynx reproduction; the variability in each is evident.

Appendix 1. Estimated number of pelts exported, average pelt price, and number of pelts sealed for Alaska lynx, 1961-62 through 1982-83.

Winter	Number of pelts exported ^a	Average pelt price (\$) ^b	Number of pelts sealed ^c
1961-62	1107	16	
62-63	2312	13	
63-64	4700	10	
64-65	3957	22	
65-66	5134	35	
66-67	1615	35	
67-68	1240	24	
68-69	1386	47	
69-70	1360	35	
70-71	1277	35	
71-72	2853	50	
72-73	4520	100	
73-74	7902	125	
74-75	4500	150	
75-76	2676	175	
76-77	1847	200	
77-78	1738	250	2014
78-79	2387	366	2416
79-80	1849	255	2743
80-81	2483	235	3285
81-82	3984	276	5221
82-83	3222	263	5652

^a Numbers of pelts exported 1961-62 through 1965-66 are from Courtright (1968); numbers from 1966-67 through 1982-83 are a sum of fur dealer, trapper, and personal use exports (ADF&G unpubl.).

^b Pelt prices from 1961-62 through 1976-77 are from Skoog (1978); prices from 1977-78 through 1982-83 are means of the average pelt price paid for Alaska and Canada lynx in the January, February, and May Seattle Fur Exchange auctions.

^c Since 1977-78, the State of Alaska has required that all lynx pelts in the state must be sealed (have a locking metal tag attached by an ADF&G representative).

Appendix 2. Alaska's 1982-83 fur exports, harvest, and estimated raw pelt values (from Melchior 1984).

Species	Reported Exports	Estimated Harvest	Average ^a Pelt Price(\$)	Estimated Value(\$)
Beaver	3,331	6,654 ^b	25.42	169,145
Coyote	NA	150 ^c	27.46	4,119
Lynx	3,222	5,652 ^b	263.07	1,486,871
Marten	16,379	30,481 ^d	56.61	1,725,529
Mink	7,711	14,350 ^d	31.19	447,577
Muskrat	6,193	11,525 ^d	2.80	32,270
River Otter	869	1,591 ^b	39.10	62,208
Red Fox ^e	3,238	6,026 ^d	51.66	311,303
Red Squirrel	201	374 ^d	1.48	554
Weasel (Ermine)	240	447 ^d	5.00	2,235
White fox (Arctic)	646	1,202 ^d	25.55	30,711
Wolf	NA	818 ^b	180.38	147,551
Wolverine	NA	767 ^b	203.00	155,701
Totals	42,030+	80,037		\$4,575,774

^a Most pelt prices from mid-winter average prices paid for Alaskan goods at the Seattle Fur Exchange. The exceptions are beaver and muskrat (May sale) and red squirrel and weasel prices are from Ontario Trappers Association sales.

^b Number sealed.

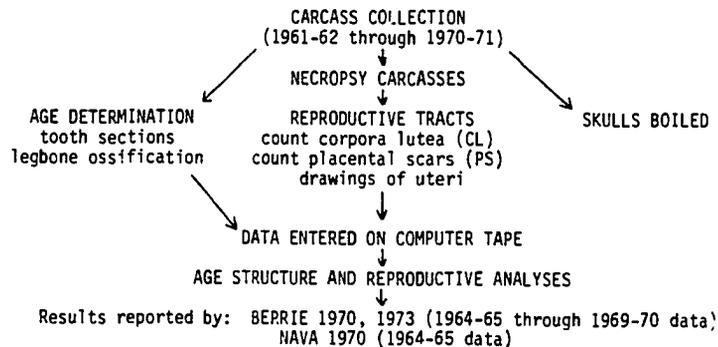
^c Lacking export data for coyotes, this is an educated guess.

^d Estimates = 1.861 x reported exports (1.861 = mean number sealed divided by number exported for beaver, lynx, and otter).

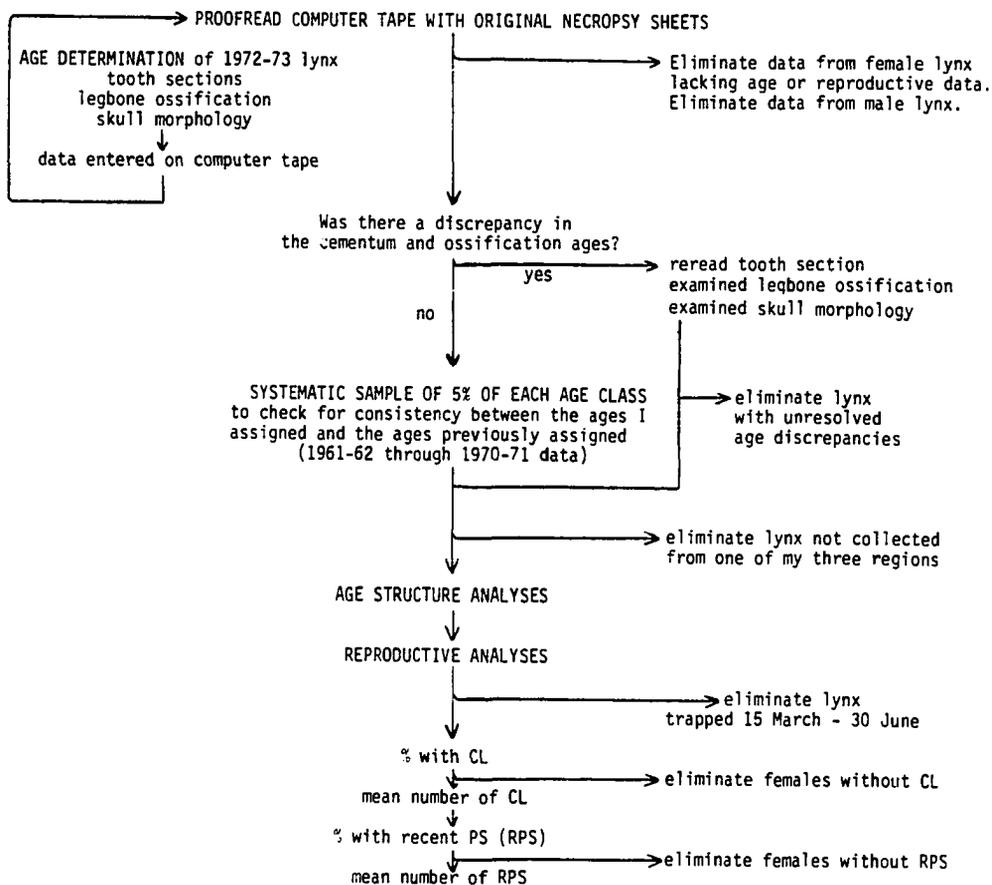
^e Includes blacks, cross, and silvers.

Appendix 3. Chronology of research on the Alaska Department of Fish and Game's 1961 through 1973 lynx carcass collection that is pertinent to this thesis.

ADF&G, Berrie, Nava:



O'Connor:



Appendix 4. Trapper questionnaire responses regarding snowshoe hare population levels for three regions (five areas) of Alaska, 1965-66 through 1975-76.

Winter	Hare population level	Region						Total number of responses
		Tanana Basin			Tanana totals	Yukon Basin	Copper Basin	
		Fairbanks	Delta	Tok				
1965-66	Abundant	0	0	0	0	0	1	93
	Intermediate	4	2	0	6	2	5	
	Scarce	37	14	11	62	4	13	
1966-67	Abundant	1	0	0	1	1	0	47
	Intermediate	1	1	0	2	2	0	
	Scarce	16	7	4	27	2	12	
1967-68	Abundant	0	0	0	0	4	0	72
	Intermediate	4	0	2	6	2	1	
	Scarce	19	9	8	36	2	21	
1968-69	Abundant	0	0	0	0	3	0	57
	Intermediate	6	5	2	13	3	2	
	Scarce	10	5	4	19	0	17	
1969-70 ^a	Abundant	2	1	1	4	2	2	53
	Intermediate	6	1	3	10	2	10	
	Scarce	5	5	2	12	1	10	
1970-71	Abundant	6	3	4	13	7	14	53
	Intermediate	9	1	2	12	1	5	
	Scarce	0	1	0	1	0	0	
1971-72	Abundant	19	3	3	25	2	8	60
	Intermediate	1	2	1	4	2	7	

Appendix 4. (Continued)

Winter	Hare population level	Region					Total Number of Responses	
		Tanana Basin			Tanana totals	Yukon Basin		Copper Basin
		Fairbanks	Delta	Tok				
1972-73	Scarce	1	0	0	1	10	1	51
	Abundant	11	1	1	13	0	9	
	Intermediate	6	3	2	11	5	4	
1973-74	Scarce	0	1	1	2	4	3	81
	Abundant	7	3	2	12	2	7	
	Intermediate	26.5	4	3	33.5	2	5	
1974-75	Scarce	7.5	1	1	9.5	7	3	47
	Abundant	0	0	0	0	0	0	
	Intermediate	7	2	0	9	3	1	
1975-76	Scarce	17	5	3	25	6	3	44
	Abundant	0	0	0	0	0	0	
	Intermediate	1	0	0	1	1	0	
	Scarce	23	9	2	34	4	4	

^a Original trapper questionnaires not found; summarized results were from Berrie (1971).

Appendix 5. Trapper questionnaire responses regarding lynx population levels for three regions (five areas) of Alaska, 1965-66 to 1975-76.

Winter	Lynx population level	Region					Total number of responses	
		Tanana Basin			Tanana totals	Yukon Basin		Copper Basin
		Fairbanks	Delta	Tok				
1965-66	Abundant	2	2	0	4	0	8.5	93
	Intermediate	20	7	4.5	31.5	4	6.5	
	Scarce	19	7	6.5	32.5	2	4	
1966-67	Abundant	0	0	1	1	0	0	48
	Intermediate	0	2	0	2	1	0	
	Scarce	18	6	4	28	4	12	
1967-68	Abundant	0	0	0	0	0	0	72
	Intermediate	1	0	0	1	5	0	
	Scarce	22	9	10	41	3	22	
1968-69	Abundant	0	0	0	0	1	0	52
	Intermediate	1	0	0	1	4	1	
	Scarce	15	10	6	31	1	13	
1969-70 ^a	Abundant	0	0	0	0	2	0	52
	Intermediate	1	1	0	2	1	1	
	Scarce	12	6	6	24	2	20	
1970-71	Abundant	0	0	0	0	7	0	53
	Intermediate	2	1	1	4	1	5	
	Scarce	12	4	5	21	0	15	
1971-72	Abundant	3	0	0	3	3	0	57
	Intermediate	9	4	1	14	5	8	

Appendix 5. (Continued)

Winter	Lynx population level	Region						Total number of responses
		Tanana Basin			Tanana totals	Yukon Basin	Copper Basin	
		Fairbanks	Delta	Tok				
1972-73	Scarce	7	0	3	10	6	8	53
	Abundant	8	2	2	12	0	2	
	Intermediate	5	2	2	9	5	5	
1973-74	Scarce	3	1	0	4	4	12	80
	Abundant	12	5	2	19	3	0.5	
	Intermediate	12	2	3	17	1	5.5	
1974-75	Scarce	13	1	1	15	9	10	55
	Abundant	3	1	0	4	1	1	
	Intermediate	13	5	2.5	20.5	5	0	
1975-76	Scarce	10	4	1.5	15.5	4	4	39
	Abundant	0	0	0	0	0	0	
	Intermediate	1	2	0.5	3.5	0	0.5	
	Scarce	19	6	1.5	26.5	5	3.5	

^a Original trapper questionnaires not found; summarized results were from Berrie (1971).

Appendix 6. Differences^a in snowshoe hare population levels and lynx population levels among five areas^b of Alaska, 1965-66 through 1975-76. Data from trapper questionnaires.

Winter	Hare population level	Lynx population level
1965-66	--	C > FDT
1966-67	FDTC < Y	--
1967-68	FDTC < Y	--
1968-69	FDTC < Y C < D	FDTC < Y
1969-70	--	FDTC < Y
1970-71	--	FDTC < Y
1971-72	FDTC > Y F > C	--
1972-73	FC > Y	FDT > C FT > Y
1973-74	--	FDT > C D > Y
1974-75	--	--
1975-76	--	--

^a Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
'--' denotes $P > 0.05$.

^b F = Fairbanks, D = Delta, T = Tok, C = Copper Basin, Y = Yukon Basin.

Appendix 7. Regions with differences^a between winters in snowshoe hare population levels as reflected by trapper questionnaires from three regions^b of Alaska, 1965-66 through 1974-75.

Winter	Winter								
	1966-67	1967-68	1968-69	1969-70	1970-71	1971-72	1972-73	1973-74	1974-75 ^c
1965-66	C	YC	YT	YT	YTC	TC	TC	TC	T
1966-67		--	T	TC	YTC	TC	TC	TC	--
1967-68			T	TC	TC	YTC	TC	YTC	Y
1968-69				TC	TC	YTC	YTC	YTC	Y
1969-70					TC	YTC	TC	TC	YT
1970-71						Y	Y	YTC	YTC
1971-72							T	T	TC
1972-73								T	TC
1973-74									TC

^a Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
 '--' denotes $P \geq 0.05$.

^b Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^c Sample size from Copper Basin < 5.

Appendix 8. Regions with winter to winter differences^a in lynx population levels as reflected by trapper questionnaires from three regions^b of Alaska, 1965-66 through 1974-75.

Winter	Winter								
	1966- 67	1967- 68	1968- 69	1969- 70	1970- 71	1971- 72	1972- 73	1973- 74	1974- 75
1965-66	TC	TC	TC	TC	YTC	C	TC	TC	C
1966-67		--	Y	--	Y	TC	TC	TC	T
1967-68			--	--	YC	TC	TC	TC	T
1968-69				--	Y	TC	TC	TC	T
1969-70					Y	TC	TC	TC	T
1970-71						YT	YT	YT	YT
1971-72							T	--	--
1972-73								--	T
1973-74									T

^a Kruskal-Wallis Pairwise Comparison ($\underline{P} < 0.05$);
'--' denotes $\underline{P} \geq 0.05$.

^b Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

Appendix 9. Regional^a differences^b in snowshoe hare population levels and in lynx population levels in Alaska as reflected by trapper questionnaires, 1965-66 through 1975-76.

Winter	Hare population level	Lynx population level
1965-66	T < C	T < C
1966-67	Y > TC	--
1967-68	Y > TC	Y > TC
1968-69	Y > TC	Y > TC
1969-70	--	Y > TC
1970-71	--	Y > TC
1971-72	Y < C < T	--
1972-73	Y < CT	YC < T
1973-74	Y < CT	YC < T
1974-75	-- ^c	--
1975-76	-- ^c	-- ^c

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($\underline{p} < 0.05$);
 '--' denotes $\underline{p} \geq 0.05$.

^c Sample size from Copper Basin <5.

Appendix 10. Snowshoe Hare Abundance Indices (%)^a for three regions (five areas) of Alaska, 1965-66 through 1975-76. Calculated from trapper questionnaires using methods of Brand and Keith (1979).

Winter	Region					
	Tanana Basin			Tanana Basin	Yukon Basin	Copper Basin
	Fairbanks	Delta	Tok			
1965-66	5	6	0	4	17	18
1966-67	8	6	0	7	40	0
1967-68	9	0	10	7	63	2
1968-69	19	25	17	20	75	5
1969-70	39	21	42	35	60	32
1970-71	70	70	83	73	94	74
1971-72	95	80	88	90	21	72
1972-73	65	50	50	71	28	69
1973-74	49	63	58	52	27	63
1974-75	15	14	0	13	17	13 ^b
1975-76	2	0	0	1	10	0 ^b

^a Indices of 0-19% = scarce, 20-50% = intermediate, and 51-100% = abundant population levels.

^b Number of questionnaires <5.

Appendix 11. Lynx Abundance Indices (%)^a for three regions (five areas) of Alaska, 1965-66 to 1975-76. Calculated from trapper questionnaires using methods of Brand and Keith (1979).

Winter	Region					
	Tanana Basin			Tanana Basin	Yukon Basin	Copper Basin
	Fairbanks	Delta	Tok			
1965-66	55	34	20	29	33	62
1966-67	0	13	20	7	10	0
1967-68	2	0	0	1	31	0
1968-69	3	0	0	2	50	4
1969-70	4	7	0	4	50	2
1970-71	7	10	8	8	94	13
1971-72	39	50	13	37	4	25
1972-73	66	60	75	68	41	24
1973-74	49	75	58	54	27	20
1974-75	37	35	31	36	35	20
1975-76	3	13	13	6	0	6 ^b

^a Indices of 0-19% = scarce, 20-50% = intermediate, and 51-100% = abundant population levels.

^b Number of questionnaires <5.

Appendix 12. Age distribution of female lynx carasses collected from three regions of Alaska, 1961-62 through 1972-73.

Winter	Age ^a	Region						Total
		Tanana Basin			Tanana Basin	Yukon Basin	Copper Basin	
		Fairbanks	Delta	Tok				
1961-62	Kit	0	0	3	3	1	0	4
	Yrlg	0	0	0	0	0	0	0
	Adult	0	0	0	0	0	0	0
	Total	0	0	3	3	1	0	4
1962-63	Kit	7	4	3	14	0	2	16
	Yrlg	11	3	6	20	2	14	36
	Adult	8	5	4	17	1	8	26
	Total	26	12	13	51	3	26	78
1963-64	Kit	115	46	67	228	7	63	298
	Yrlg	110	53	70	233	17	48	298
	Adult	33	22	34	89	12	48	149
	Total	258	121	171	550	36	159	745
1964-65	Kit	11	6	8	25	5	76	106
	Yrlg	139	87	51	277	50	99	426
	Adult	40	20	26	86	50	75	211
	Total	190	113	85	388	105	250	743
1965-66	Kit	3	3	2	8	2	71	81
	Yrlg	21	11	22	54	2	215	271
	Adult	91	62	118	271	61	227	559
	Total	115	76	142	333	65	513	911
1966-67	Kit	0	0	0	0	0	3	3
	Yrlg	1	0	0	1	3	22	26
	Adult	24	11	13	48	19	60	127
	Total	25	11	13	49	22	85	156
1967-68	Kit	0	0	1	1	1	0	2
	Yrlg	1	0	0	1	1	3	5
	Adult	8	0	6	14	14	27	55
	Total	9	0	7	16	16	30	62
1968-69	Kit	6	0	2	8	11	2	21
	Yrlg	0	0	0	0	0	0	0
	Adult	8	0	10	18	15	26	59
	Total	14	0	12	26	26	28	80
1969-70	Kit	3	1	3	7	19	15	41
	Yrlg	0	0	0	0	14	3	17
	Adult	8	5	4	17	5	14	36
	Total	11	6	7	24	38	32	94
1970-71	Kit	6	0	1	7	13	16	36
	Yrlg	8	3	7	18	35	10	63
	Adult	3	0	1	4	2	9	15
	Total	17	3	9	29	50	35	114
1972-73	Kit				21	0	3	24
	Yrlg				44	0	11	55
	Adult				54	0	8	62
	Total				119	0	22	141

^a kit = 0-12 months, yrlg = 13-24 months, adult = 25+ months.

Appendix 13. Regions^a of Alaska with winter to winter differences^b in the age structure of female lynx carcasses, 1962-63 through 1972-73.

Winter	Winter								
	1963-64	1964-65	1965-66	1966-67	1967-68	1968-69	1969-70	1970-71	1972-73 ^c
1962-63	T	--	T	TC	TC	TC	T	C	T
1963-64		YT	YTC	YTC	YTC	TC	YT	Y	T
1964-65			YTC	YTC	YTC	TC	YT	YT	T
1965-66				TC	C	YTC	YT	YTC	T
1966-67					--	YT	YTC	YTC	TC
1967-68						YT	YC	YTC	TC
1968-69							YC	YTC	C
1969-70								T	--
1970-71									T

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
'--' denotes $P \geq 0.05$.

^c Data available from Tanana and Copper Basins only.

Appendix 14. Regional^a differences^b in the age distribution of female lynx carcasses in Alaska, 1962-63 through 1972-73.

Winter	Regional Difference
1962-63	--
1963-64	T vs. YC
1964-65	T vs. YC
1965-66	C vs. YT
1966-67	C vs. T
1967-68	--
1968-69	C vs. YT
1969-70	Y vs. T
1970-71	--
1972-73	--

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
'--' denotes $P \geq 0.05$.

Appendix 15. Percentage of female lynx carcasses from the Yukon Basin, Alaska with corpora lutea (CL)^a and recent placental scars (RPS)^b, 1962 through 1972.

Year	Yearlings				Adults			
	% with CL	n	% of ovulators with RPS	n	% with CL	n	% of ovulators with RPS	n
1962	100.0	2	100.0	2	100.0	1	100.0	1
1963	100.0	16	56.2	16	100.0	11	90.0	10
1964	78.7	47	43.2	37	97.7	43	53.6	41
1965	50.0	2	100.0	1	98.4	61	55.2	58
1966	0	2	0	1	94.7	19	33.3	18
1967	100.0	1	100.0	1	100.0	13	50.0	14
1968 ^c		0		0	100.0	12	80.0	15
1969 ^c	92.3	13	53.8	13	100.0	4	100.0	4
1970	96.9	32	70.4	27	100.0	2	50.0	2
TOTAL		<u>115</u>		<u>98</u>		<u>166</u>		<u>163</u>

^a Includes CL from recent and previous ovulations.

^b Calculated from females with CL present.

^c Drawings of uteri were unavailable so the RPS values may include faded placental scars also, thus may be a slight overestimate.

Appendix 16. Percentage of female lynx carcasses from the Tanana Basin, Alaska with corpora lutea (CL)^a and recent placental scars (RPS)^b, 1962 through 1972.

Year	Yearlings				Adults			
	% with CL	n	% of ovulators with RPS	n	% with CL	n	% of ovulators with RPS	n
1962	100.0	20	84.2	19	100.0	15	93.3	15
1963	99.5	218	80.7	218	98.8	85	86.9	84
1964	82.1	262	48.4	213	98.6	71	74.3	70
1965	44.0	50	39.1	23	92.7	262	63.0	243
1966	0	1		0	90.2	41	25.6	39
1967	0	1		0	91.7	12	33.3	12
1968 ^c		0		0	100.0	18	50.0	18
1969 ^c		0		0	93.8	16	67.0	15
1970	87.5	16	66.7	12	100.0	4	67.0	3
1972	100.0	44	58.5	41	100.0	54	57.7	52
TOTAL		<u>612</u>		<u>526</u>		<u>578</u>		<u>551</u>

^a Includes CL from recent and previous ovulations.

^b Calculated from females with CL present.

^c Drawings of uteri were unavailable so the RPS values may include faded placental scars also, thus may be a slight overestimate.

Appendix 17. Percentage of female lynx carcasses from Copper Basin, Alaska with corpora lutea (CL)^a and recent placental scars (RPS)^b, 1962 through 1972.

Year	Yearlings				Adults			
	% with CL	n	% of ovulators with RPS	n	% with CL	n	% of ovulators with RPS	n
1962	100.0	13	69.2	13	100.0	8	87.5	8
1963	97.7	43	82.9	41	100.0	43	92.7	41
1964	89.9	89	68.4	79	96.4	56	81.5	54
1965	82.1	196	57.5	160	94.1	205	56.7	194
1966	11.1	18	33.3	3	90.0	50	54.2	48
1967	33.3	3	100.0	1	100.0	23	7.7	26
1968 ^c		0		0	100.0	25	76.9	26
1969 ^c	100.0	2	0	2	100.0	9	70.0	10
1970	80.0	10	100.0	6	100.0	8	100.0	8
1972	100.0	10	30.0	10	100.0	8	37.5	8
TOTAL		<u>384</u>		<u>315</u>		<u>435</u>		<u>423</u>

^a Includes CL from recent and previous ovulations.

^b Calculated from females with CL present.

^c Drawings of uteri were unavailable so the RPS values may include faded placental scars also, thus may be a slight overestimate.

Appendix 18. Mean number of corpora lutea per ovulating yearling lynx in three regions of Alaska, 1962 through 1972.

Year	Region								
	Yukon Basin			Tanana Basin			Copper Basin		
	Mean	±95% CI	n	Mean	±95% CI	n	Mean	±95% CI	n
1962	5.0	0	2	5.6	0.83	20	5.2	0.63	13
1963	5.6	0.80	16	6.3	0.27	217	6.1	0.64	42
1964	4.8	0.70	37	4.5	0.15	215	5.5	0.47	80
1965	4.0	0	1	4.6	0.60	22	5.1	0.29	161
1966			0			0	5.0	0	2
1967	3.0	0	1			0	4.0	0	1
1969	5.6	1.24	12			0	3.0	0	2
1970	7.5	1.27	31	6.8	2.52	14	5.5	0.98	8
1972			0	5.2	0.41	44	4.8	0.57	10

Appendix 19. Mean number of corpora lutea^a per ovulating adult lynx in three regions of Alaska, 1962 through 1972.

Year	Region								
	Yukon Basin			Tanana Basin			Copper Basin		
	Mean	±95% CI	n	Mean	±95% CI	n	Mean	±95% CI	n
1962	5.0	0	1	12.2	2.54	15	11.6	3.25	8
1963	9.5	2.05	11	16.9	1.49	84	17.9	2.64	43
1964	10.0	1.52	42	12.4	1.29	70	13.6	1.99	54
1965	9.8	1.59	60	9.6	0.77	243	9.0	0.90	193
1966	7.4	1.72	18	10.6	2.29	37	9.4	1.98	45
1967	10.5	2.70	13	7.3	2.20	11	5.8	1.28	23
1968	10.8	1.99	12	8.8	1.86	18	8.2	1.85	25
1969	16.0	6.60	4	13.3	3.27	15	11.6	3.01	9
1970	18.0	9.80	2	15.5	0.57	4	14.8	3.39	8
1972			0	7.5	0.87	54	10.4	2.25	8

^a Includes corpora lutea from recent and previous ovulations (see Methods).

Appendix 20. Regions^a of Alaska with annual differences^b in the mean number of corpora lutea per ovulating yearling lynx, 1962 through 1972.

Year	Year							
	1963	1964	1965	1966 ^c	1967 ^c	1969 ^c	1970	1972 ^d
1962	--	T	T	--	--	C	--	--
1963		T	TC	--	--	C	T	TC
1964			-	--	--	C	Y	T
1965				--	--	C	-	-
1966 ^c					--	--	--	--
1967 ^c						--	Y	--
1969 ^c							C	--
1970								--

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
'--' denotes $P \geq 0.05$.

^c Sample sizes ≤ 2 for two or more regions.

^d Data available from Tanana and Copper Basins only.

Appendix 21. Regions^a of Alaska with annual differences^b in the mean number of corpora lutea per ovulating adult lynx, 1962 through 1972.

Year	Year								
	1963	1964	1965	1966	1967	1968	1969 ^c	1970 ^d	1972 ^e
1962 ^c	T	--	TC	--	TC	C	--	Y	T
1963		TC	TC	TC	TC	TC	--	--	T
1964			TC	YTC	TC	TC	--	--	T
1965				--	C	--	YTC	TC	T
1966					C	Y	YTC	YTC	--
1967						--	TC	TC	C
1968							TC	TC	--
1969 ^c								--	T
1970 ^d									T

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
 '--' denotes $P \geq 0.05$.

^c Sample size from Yukon Basin <5.

^d Sample size from Yukon and Tanana Basins <5

^e Data available from Tanana and Copper Basins only.

Appendix 22. Mean number of recent placental scars (RPS) per adult lynx with RPS, 1962 through 1972. Data from carcasses collected in three regions of Alaska.

Year	Region								
	Yukon Basin			Tanana Basin			Copper Basin		
	Mean	±95% CI	n	Mean	±95% CI	n	Mean	±95% CI	n
1962	5.0	0	1	6.3	1.17	14	5.0	1.66	7
1963	4.1	1.48	9	5.8	0.40	73	5.2	0.72	38
1964	4.2	0.76	22	4.6	0.51	52	4.5	0.60	44
1965	3.9	0.54	32	3.9	0.28	153	3.5	0.28	110
1966	4.2	0.33	6	4.2	1.36	10	3.8	0.61	26
1967	2.0	0.74	7	3.0	1.38	4	2.0	0	2
1968 ^a	3.8	1.13	12	3.2	1.12	9	3.2	0.48	20
1969 ^a	5.8	2.02	4	4.4	1.02	10	4.6	1.27	7
1970	8.0	0	1	3.5	0.98	2	4.6	1.57	8
1972			0	3.7	0.74	30	4.3	2.61	3

^a Drawings of the uteri were unavailable so the RPS values may include faded placental scars also, thus may be a slight overestimate.

Appendix 23. Regions^a of Alaska with annual differences^b in the mean number of recent placental scars (RPS) per adult lynx with RPS, 1962 through 1972.

Year	Year								
	1963 ^c	1964	1965	1966	1967 ^d	1968	1969 ^c	1970 ^e	1972 ^f
1962 ^c	--	T	TC	T	TC	TC	T	--	T
1963 ^c		T	TC	TC	YTC	TC	T	--	T
1964			TC	--	YC	TC	--	--	T
1965				--	Y	--	--	--	--
1966					Y	--	--	--	--
1967 ^d						Y	YC	Y	--
1968							C	--	--
1969 ^c								--	--
1970 ^e									--

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b Kruskal-Wallis Pairwise Comparison ($P < 0.05$);
'--' denotes $P \geq 0.05$.

^c Sample size from Yukon Basin <5.

^d Sample size from Tanana and Copper Basins <5.

^e Sample size from Yukon and Tanana Basins <5.

^f Data available only from Tanan and Copper Basins; the Copper Basin sample was only 3.

Appendix 24. Mean number of recent placental scars (RPS) per yearling lynx with RPS, 1962 through 1972. Data from carcasses collected in three regions of Alaska.

Year	Region								
	Yukon Basin			Tanana Basin			Copper Basin		
	Mean	±95% CI	n	Mean	±95% CI	n	Mean	±95% CI	n
1962	5.0	0	2	4.2	0.88	16	4.0	1.22	9
1963	3.6	1.27	9	4.4	0.23	176	4.2	0.52	34
1964	4.5	0.76	16	4.2	0.25	103	4.2	0.36	54
1965	4.0	0	1	3.8	0.85	9	3.5	0.32	92
1966			0			0	4.0	0	1
1967	2.0	0	1			0	2.0	0	1
1969 ^a	3.3	0.56	7						0
1970	3.9	0.82	19	3.8	1.10	8	2.8	1.47	6
1972			0	3.6	0.71	24	3.7	1.73	3

^a Drawings of uteri were unavailable so the RPS values may include faded placental scars also, thus may be a slight overestimate.

Appendix 25. Regional^a differences in ovulation and implantation in yearling and adult lynx from Alaska, 1962 through 1972. CL = corpora lutea, mCL = mean number of CL, RPS = recent placental scars.

Year	Yearlings			Adults		
	% with CL ^b	mCL for ovulators ^c	% ovulators with RPS ^b	% with CL	mCL for ovulators ^c	% ovulators with RPS ^b
1962	d	-- ^e	f	d	--	f
1963	d	--	TC > Y	d	TC > Y	f
1964	--	C > YT	C > YT	d	TC > Y	TC > Y
1965	C > T ^g	--	C > T ^g	-- ^g	--	--
1966	f		f	-- ^g	--	C > TY
1967	f	--	f	-- ^d	C < Y	C < Y ^g
1968				-- ^d	--	--
1969	f	C < Y ^g	f	-- ^d	--	f
1970	f	--	-- ^g	-- ^d	--	f
1972 ^g	-- ^d	--	--	-- ^d	C > T	f

^a Y = Yukon Basin, T = Tanana Basin, C = Copper Basin.

^b χ^2 Contingency Tables ($P < 0.05$).

^c Kruskal-Wallis Pairwise Comparison or Mann-Whitney ($P < 0.05$).

^d Cell sizes too small for χ^2 analysis but most regions had values close to 100%.

^e '--' denotes $P > 0.05$.

^f Cell sizes too small for χ^2 analysis.

^g Large enough sample size (or cell size) to test for difference between only two regions.

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Personal Communications

John R. Cary, Department of Wildlife Ecology, University of Wisconsin,
226 Russell Lab, Madison, WI 53706.

Craig Gardner, Alaska Department of Fish and Game, P.O. Box 47,
Glennallen, AK 99588.