BEHAVIORAL RESPONSES OF LYNX
TO
DECLINING SNOWSHOE HARE ABUNDANCE

by

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ABSTRACT

The behavioral responses of lynx (Lynx canadensis) to declines in snowshoe hare (Lepus americanus) abundance were examined in the southwestern Yukon. Between April 1982 and June 1984 11 lynx were radio-tagged and monitored within and near the Kluane Game Sanctuary. Lynx mean home range size increased from 13.2 to 39.2 km^2 concurrent with a decline in snowshoe hare abundance from 14.7 to 0.2 hares/ha. Below about 0.5 hares/ha several lynx abandoned their home ranges and became nomadic, although they remained within the general study area. Track transects through areas known to have different snowshoe hare densities indicated that lynx concentrated their foraging efforts in areas of relatively high snowshoe hare abundance. Lynx abandoned these areas after hare abundance declined. Lynx foraging effort in terms of distance travelled per day showed a curvilinear relationship to snowhoe hare abundance. Straight-line daily travel distance remained constant at 2.2 to 2.7 km/day above 1.0 hare/ha. Below 1.0 hares/ha, straight-line daily travel distances increased rapidly, reaching 5.5 km/day at 0.2 hares/ha. Three of 7 radio-tagged lynx dispersed 250 km or more from the study area during the period of rapid decline in hare abundance in 1982. No similar long distance dispersal was recorded after hare densities stablized at less than 1.0 hares/ha. Trapping mortality was responsible for the loss of 7 of 9 radio-tagged lynx that travelled outside the game sanctuary. One lynx died, and is believed to have starved, during the winter or spring of 1984. The high rate of trapping mortality outside the game sanctuary suggests that refugia in wilderness areas are important in maintaining lynx populations during periods of low recruitment.

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Dr. A.R.E. Sinclair also acted as academic supervisor during a portion of this study. He also provided office supplies during the write-up phase of the study. Thanks Tony.

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INTRODUCTION

The close relationship between the ten year cycles of lynx (Lynx canadensis) and the snowshoe hare (Lepus americanus) was first noted in the ecological literature by Elton and Nicholson (1942). Since then many aspects of lynx natural history and ecology have been studied (see Parker et al. 1983 for a review). In view of the close relationship between lynx and snowshoe hare numbers, surprisingly little of the previous work has related lynx ecology to snowshoe hare abundance.

Several studies, however, have related hare abundance to lynx reproduction and mortality (van Zyll de Jong 1963, Stewart 1973, Nava 1970, Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979, Parker et al. 1983). These studies have shown an increase in mortality and a decline in recruitment of lynx with declining snowshoe hare abundance. General body condition of lynx has also been shown to be positively correlated with hare abundance.

Studies of the effects of hare abundance on other aspects of lynx ecology have been reported by Nellis and Keith 1968, Nellis et al. 1972, Nellis 1975, and Brand et al. 1976. These studies were part of a long term study of snowshoe hare population dynamics in Alberta (Keith and Windberg 1978). Parker et al. (1983) also report on a study of prey abundance and lynx ecology in Nova Scotia.

These studies and others have been unanimous in finding that snowshoe hares are the single most important food item in the diet of the lynx during all phases of the 10 year cycle

(Table 1). The fact that lynx recruitment declines and mortality rates increase with declining hare abundance clearly indicates that lynx are severely energy stressed during the decline and low phases of the hare cycle. One would therefore expect that lynx would exhibit major behavioral changes in an effort to continue to fulfill their energetic requirements as hare abundance declines. The most obvious mechanisms lynx might use are: 1) increase their home range size; 2) increase their foraging effort and 3) seek out and concentrate their foraging effort in patches of relatively high prey abundance.

In this study I investigated the degree to which lynx utilize each of these possible mechanisms to maximize their energy intake. I present data on lynx dispersal and mortality during a snowshoe hare decline. Finally, the factors structuring the lynx social system and the management implications of my findings are discussed.

Table 1. A summary from past studies of the importance of snowshoe hares in the diet of lynx.

Study	Hare cycle phase	Season	Most important item in lynx diet	Next most important item in lynx diet
Nellis et al. 1972 Alberta	decline	winters 1964-67	hares 76% of biomass	9.8% carrion
	low	winter	carrion 52% of biomass	hares 43% of biomass
Brand et al. 1976 Alberta	high	winter	hares 100% of biomass	-------
	high	summer	hares 91% of biomass	2% mice and voles
More 1976 south-western N.W.T.	low	winter	hares 79-100% freq. of occurance in scats	25-64% red squirrel
van Zyll De Jong 1963 Alberta	start of decline	winter	hares 79% freq. of occur. in gut contents	10% microtine
		summer	hares 52% freq. of occur. in gut contents	31% microtine
Saunders 1963 Nfld.	?	winter	hares 85% of biomass	13% moose
		summer	hares 60% of biomass	30% microtine

METHODS AND STUDY AREA

Study Area

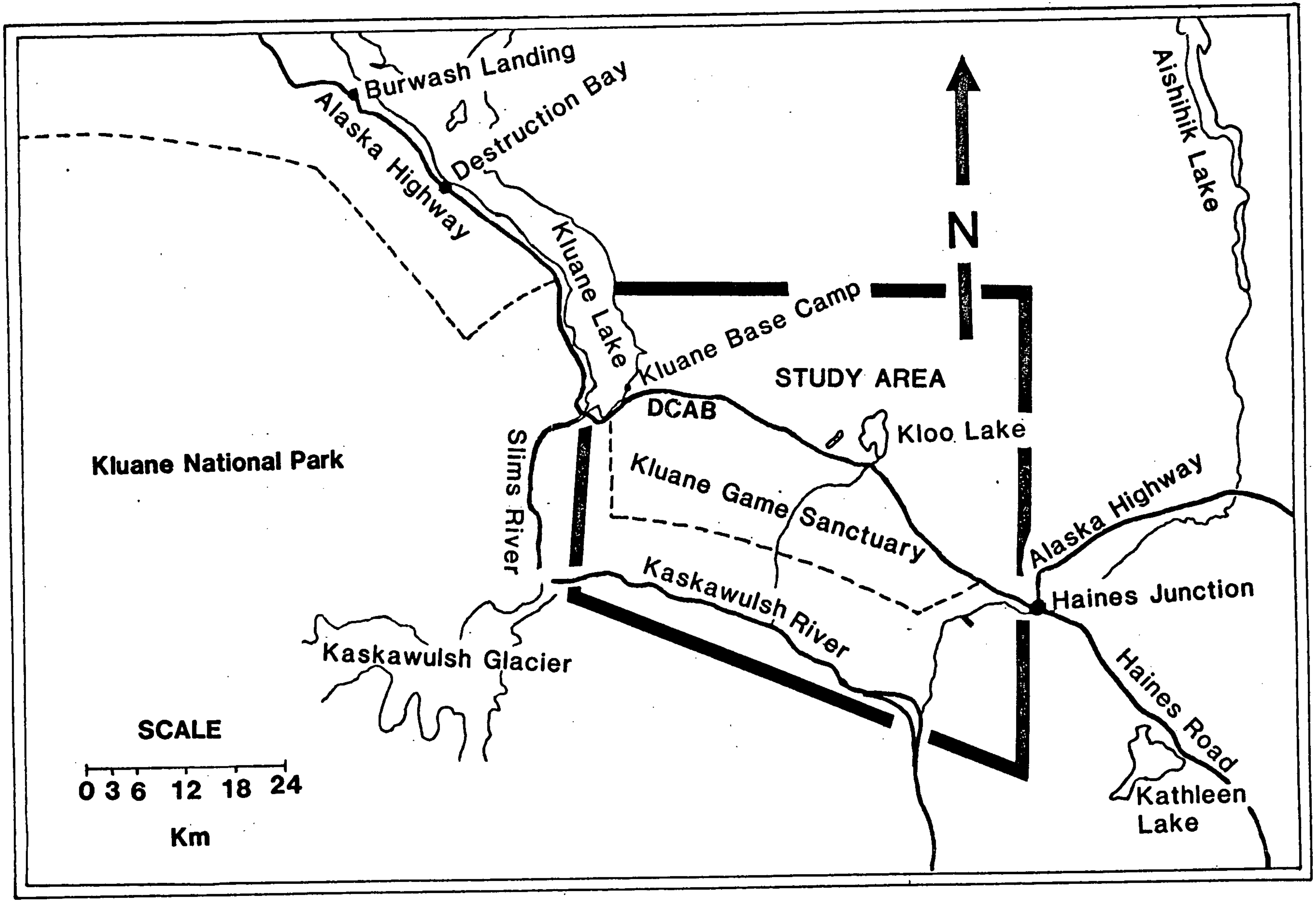
The study was centered in the southwestern Yukon, north of Kluane National Park within and adjacent to Yukon Game Management Zone 6-10 (Figure 1). This is classified as a game sanctuary with no hunting or trapping permitted. The area is part of the northern boreal forest zone as described by Douglas (1974). White spruce (*Picea glauca*) is the dominant tree species, with a variety of willows (*Salix spp.*) and other less abundant shrubs species making up the understory.

The study area is dissected by a number of old mining and exploration roads which facilitated travel. Winter travel was accomplished by snowmobile, snowshoeing and skiing. Summer travel was by four wheel drive truck, trail bike and walking.

Timing and Emphasis of Study

I conducted the study between February 1982 and June 1984. Between February and May 1982 I focused my efforts around grids A (Microwave) and B (Beaver Pond) (Figure 1). I expended equal trapping effort for both lynx and snowshoe hares on each grid during this period. Winter snow-tracking effort was also equal on each grid. After May 1982, grid B was abandoned for lynx trapping and snow-tracking due to its relative inaccessibility

Figure 1. Map of study area in southwestern Yukon. A, B, C and D indicate locations of snowshoe hare live-trapping grids. See text for a description of the grids.


Burwash Landing
Destruction Bay
Alaska Highway
Kluane Lake
N
Aishihik Lake
Kluane Base Camp
STUDY AREA
DCAB
Kloo Lake
Kluane National Park
Slims River
Kluane Game Sanctuary
Alaska Highway
Haines Junction
Kaskawulsh River
Kaskawulsh Glacier
Haines Road
Kathleen Lake
SCALE
0 3 6 12 18 24
Km

although I continued to monitor hare abundance on the grid. Lynx and snowshoe hare monitoring continued to be most intensive within the Kluane Game Sanctuary to take advantage of the road system in this area. Careful records of the number and distribution of lynx tracks in the sanctuary were kept so that an estimate could be made of the proportion of lynx in the area that were radio-tagged. The total study area was expanded as necessary to maintain contact with the radio-tagged lynx (Figure 1).

Estimation of Snowshoe Hare Abundance

Snowshoe hare abundance was monitored on four live-trapping grids in the study area as part of a concurrent study of their ten year cycle. Grid A (Microwave) was a food addition grid to determine the effect of supplemental food on hare abundance. Grids B (Beaver Pond), C (Grizzly) and D (1050) were controls for A (Figure 1). Live-trapping techniques on these grids are described by Boutin (1980). Hare abundance was determined using the minimum number alive (MNA) method (Krebs 1966). Hare densities on the grids were calculated without the addition of a boundry strip (MNA/area of grid). Bondrup-Nielsen (1983) discussed the bias introduced into density estimates resulting from the use of relatively small grid size in live-trapping programs. His model suggests that my density estimates may be 2 to 3 times too high.

Lynx Trapping and Radio Tagging

Trapping efforts to capture and radio-tag lynx continued from February through December 1982 and from April to September 1983. Initially , an attempt was made to capture lynx using box traps but this proved ineffective. Later trapping efforts were similar to those employed by professional trappers. Steel leghold traps, ranging in size from #2 to #4, with the jaws padded with either cloth tape or rubber were used in "cubby" type sets (see Anonymous,1982). Sets were placed along trails and roads within the study area and checked at least once every 24 hours. A variety of baits ranging from commercial lures to perfume and silver ribbons were used.

Once a lynx was trapped, it was immoblized with ketaset (concentration 100mg/ml: rogar/STB, division of BTI Products Inc., London, Ontario) at a dosage of approximately 0.2 ml per kg of body weight. The lynx was then weighed, sexed, ear-tagged and fitted with a radio transmitter prior to release.

Radio Telemetry and Home Range Determination

Radio telemetry equipment was produced by Wildlife Materials Inc., Carbondale, Illinois. Lynx were located using standard radio-telemetry techniques (Cochran 1980) with a combination of handheld and fixed tower antennas. Accuracy checks on transmitters in known locations indicated that compass bearings using this system were accurate to ± 5 degrees 95% of the time. Compass bearings were less accurate if the radio-tagged animal was active when the bearing was being taken. If it was felt that the error introduced by activity was excessive, no compass bearings was recorded. A minimum of 2 compass bearings were required to produce each location. If a lynx disappeared from the study area, an effort was made to locate it using radio-telemetry from an aircraft. The lynx were located at various times throughout the day and night from April and December, 1982 and between May and October, 1983 and during May and June 1984. Once fitted with a radio transmitter, each lynx was followed until it dispersed from the area, it was trapped by professional trappers, or the transmitter stopped working.

I defined home range as the consistent use of an area over a 3 month period. I therefore subdivided the study into the following 3 month periods for subsequent analysis:

PERIOD	MONTHS
1	April-June 1982
2	July-September 1982
3	October-December 1982
4	April-June 1983
5	July-September 1983
6	April-June 1984

I used a minimum of 30 point locations within each period to determine home range. Home range size was estimated by the convex polygon method (Mohr 1947) with the following modification. I eliminated the outermost 10% of locations in calculating home range size after the method of Boutin (1980). This reduced the inclusion of occasional wanderings by lynx in the assessment of its home range.

Track Transects

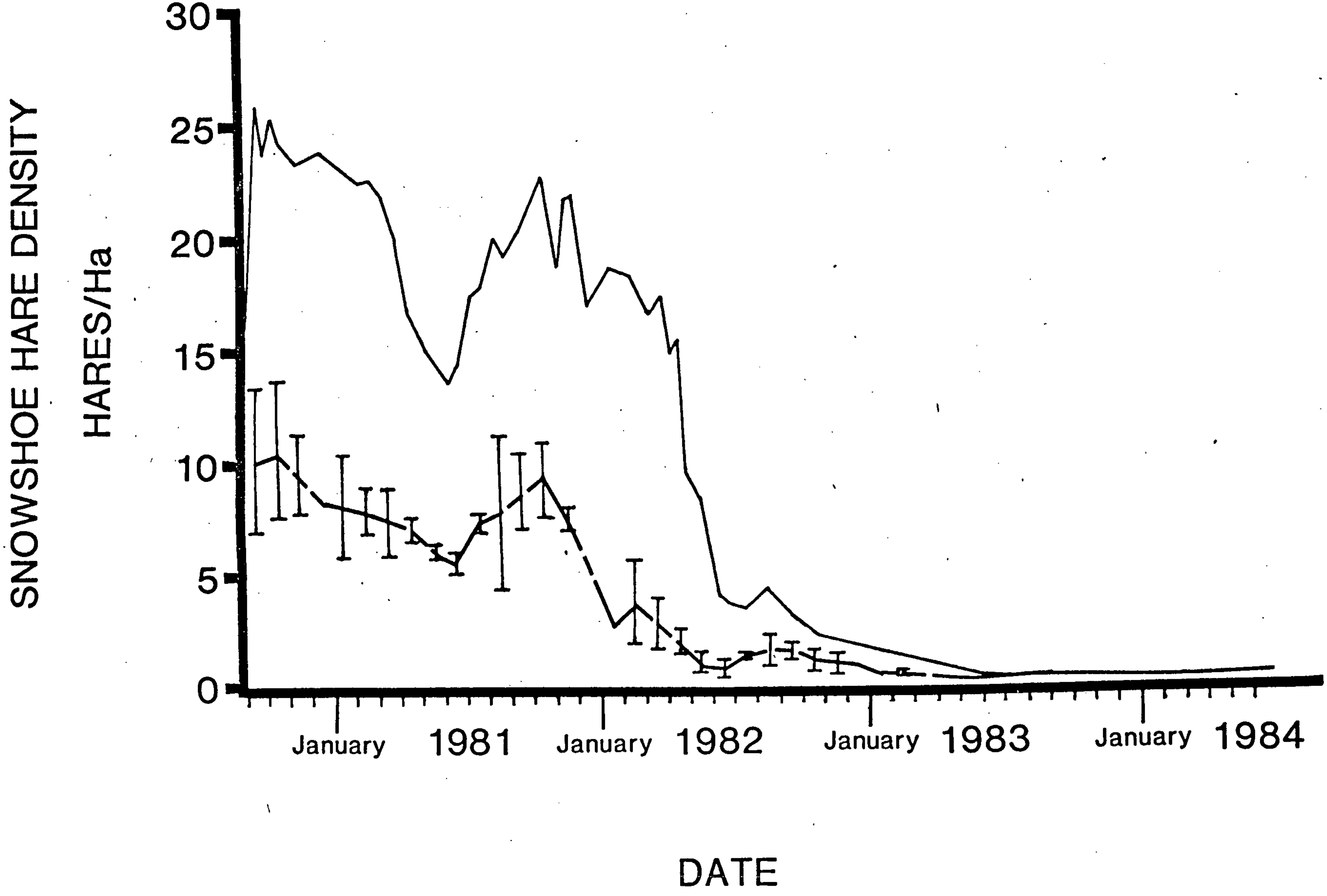
To determine the effects of relative snowshoe hare abundance on patterns of habitat use by lynx, winter snow track transects were run through areas known to have different hare abundances. The number of sets of fresh lynx tracks crossing every 600 meters of transect was recorded. Transects were conducted each morning when weather and snow conditions permitted throughout April and from late October to early December 1982.

RESULTS

Snowshoe Hare Abundance

Hare abundance on grids A (supplemental food grid), C and D peaked in the fall of 1980. Grid B reached its maximum density in the fall of 1981. Maximum fall snowshoe hare densities in 1981 on grid A were 22.6 hares/ha, while on grids B, C and D they were respectively 10.3, 8.0 and 10.7 (mean 9.7 ±1.2) hares/ha (Figure 2). Densities began to decline rapidly on grids B, C and D in January 1982 while remaining relatively high on grid A throughout the spring of 1982. In April 1982 when I began monitoring lynx activities, hare abundance on grids B, C, and D respectively was 2.6, 2.4 and 1.4 (mean 2.1 ±0.5) hares/ha while on grid A hare density was 14.7 hares/ha. By July hare density had dropped to approximately 1.0 ±0.4 hares/ha on the control grids and to 3.3 on the supplemental food grid. Population densites levelled off or increased slightly on all grids during the summer months as young of the year were born. During October, however, densities began to decline again on all grids. Spring densities in 1983 were equivalent on all grids at 0.2 ±0.1 hares/ha. By July densities on all grids had increased slightly, averaging 0.5 ±0.2 hares/ha. Snowshoe hare densities remained relatively constant at between 0.2 and 0.5 hares/ha on all grids through June 1984.

Figure 2. Snowshoe hare density on supplemental food grid A (solid line) and control grids B, C and D (dashed line). Densities are based on total enumeration techniques (Krebs 1966). Vertical bars on dashed line indicate ±1 standard deviation.


SNOWSHOE HARE DENSITY
HARES/Ha
30
25
20
15
10
5
0
January
1981
January
1982
January
1983
January
1984
DATE

Lynx Trapping Success

Eleven lynx (5 females and 6 males) were trapped and radio-tagged in approximately 4700 trap-nights between April 1982 and September 1983 (Table 2). In addition, one female (Jean) was recaptured and released approximately 9 months after her initial capture.

It was not possible to determine the precise age of the individuals but from the condition of the nipples and genitalia it was evident that two of the females (Joy and Jennifer) had bred previously and were therefore at least 2 years old. Jean, showed no signs of previous breeding but her weight (10.7 kg) and the fact that she was travelling alone, suggests that she was also at least one and a half years old at the time of her initial capture. Scruff and Rene showed no signs of previous breeding and may have been yearlings when I radio-tagged them. With the exception of Scottie, all males had adult body weights, fully developed penises, scrotal testes and were travelling alone, indicating that they were at least 1 year old. Scottie had adult body weight, but an incompletely developed penis, non-scrotal testes and was travelling with another lynx, presumably his mother, suggesting that he was a young of the year 1982.

From the limited data obtained, females would seem to lose body conditon more rapidly than males as hare abundance declines (Table 3). All males captured and radio-tagged in this study appeared to be excellent body condition. In fact body weights of 2 males captured late in the study were equivalent to or higher than those captured early in the study. Females captured

Table 2. Summary of lynx trapping success, minimum residency time on study area and fate of radio-tagged lynx.

Lynx	Capture date (D/M/YR)	Age	Sex	Minimum residency on study area	Fate
Joy	4/4/82	adult =>2 yrs.	F	35 Days	dispersed 8/5/82. killed 700 km N of tagging site, December 1982.
Sid	17/4/82	adult =>1 yr.	M	9 Months	killed within 10 km of tagging site, January 1983.
Scruff	21/4/82	adult =>1 yr.	F	7 Months	dispersed 16/10/82. killed 250 km N of tagging site, Nov. 1982.
Charlie	25/5/82	adult =>1 yr.	M	40 Days	dispersed 5/7/82. killed 250 km N of tagging site, Dec. 1982.
Carlos	1/8/82	adult =>1 yr.	M	13 Months	residing in study area September 1983.
Scottie	20/10/82	kitten < 1 yr.	M	2 Months	killed within 10 km of tagging site, December 1982.
Jean	25/10/82	adult =>1 yr.	F	10 Months	killed within 10 km of tagging site, winter 1983-84.
Rene	15/7/83	adult =>1 yr.	F	6 Months	found dead 35 km east of tagging site, June 1984.
Jennifer	19/7/83	adult =>2 yrs.	F	11 Months	residing in study area, June 1984.
Enrique	29/7/83	adult =>1 yr.	M	11 Months	residing in study area, June 1984.
Paul	1/8/83	adult =>1 yr.	M	4 Months	killed within 10 km of tagging site, January 1984.

Table 3. Body weights for individual lynx at time of capture. Means are not significantly different (T-test P> 0.05). * indicates recapture.

Date	Male capture weights (Kg)	Female capture weights (Kg)
April to December 1982	Sid 8.8 Charlie 8.6 Carlos 8.3 Scottie 9.7 mean = 8.9 95% c.i. = 8.0-9.7	Joy 9.5 Scruff 8.3 Jean 10.6 mean = 9.5 95% c.i. = 7.3-11.6
April to September 1983	Enrique 10.4 Paul 9.5 mean = 10.0 95% c.i. = 8.0-11.9	Jean * 9.9 Rene 7.7 Jennifer 7.5 mean = 8.4 95% c.i. = 5.9-10.8

early in the study had body weights similar to those of males and appeared to be in good condition. Those captured later in the study (Rene and Jennifer) however, were emaciated and had lower body weights. Jean also lost 0.8 kg (7.5% of her initial body weight) between her initial capture in October 1982 and her recapture in July 1983.

Although it is difficult to assess accurately what proportion of the population I had radio-tagged, an estimate can be obtained, for the winters at least, from repeated track transects through the area. I believe that I had radio-tagged 4 of 5 lynx using grid A in April and May 1982. As previously mentioned, I expanded to study area during the summer of 1982 (Figure 1). By November I was monitoring 5 lynx and I suspect that 5 more lynx were residing in the area. Further evidence that a large proportion of the lynx population was radio-tagged is that only 1 of 10 lynx sighted during the study was untagged.

During the 26 months of the study, over 1300 telemetry locations and visual sightings were made on the 11 lynx. Minimum residency times for these lynx ranged from 35 days to 13 months.

Effect of Snowshoe Hare Abundance on Lynx Home Range Size

As described in the methods, I eliminated the outermost 10% of locations when calculating lynx home range size. The loss of these outermost points results in a reduction of home range size of from 3 to 70 percent (Figure 3a, b, c and d). For comparison with other studies I present my results as both 100% and 90% home ranges (Table 4) and I use 90% range in my analysis and discussion.

Although there was a slight trend for females to have smaller home ranges than males within a given range of snowshoe hare densities, it was not consistent or statistically significant (t-test, $P>0.05$). The data are therefore combined for the analysis of the effect of snowshoe hare abundance on lynx home range size.

During the summer of 1983 Rene did not use any area consistently. Jennifer and Enrique also did not use areas consistently during the spring of 1984. These movements do not fit my definition of home range and are therefore omitted from the following analysis of the effect of hare abundance on lynx home range size. Including these movements in the following analysis would strengthen the observed trend.

As previously discussed (Figure 2), hare densities declined rapidly through the early phases of the study and at a lesser rate later in the study. Throughout this decline, lynx showed a steady increase in the size of their home ranges. Both mean home range size for all individuals at different hare abundances (Figure 4) and home ranges of individuals monitored through time

Figure 3. Examples of 100% (solid line) and 90% (dashed line) home range estimates. Figure 3a,b and c represent the home range of Sid at hare densities of 14.7, 3.3 and 2.2 hares/ha respectively. Figure 3d represents the home range of Carlos at 0.5 hares/ha.

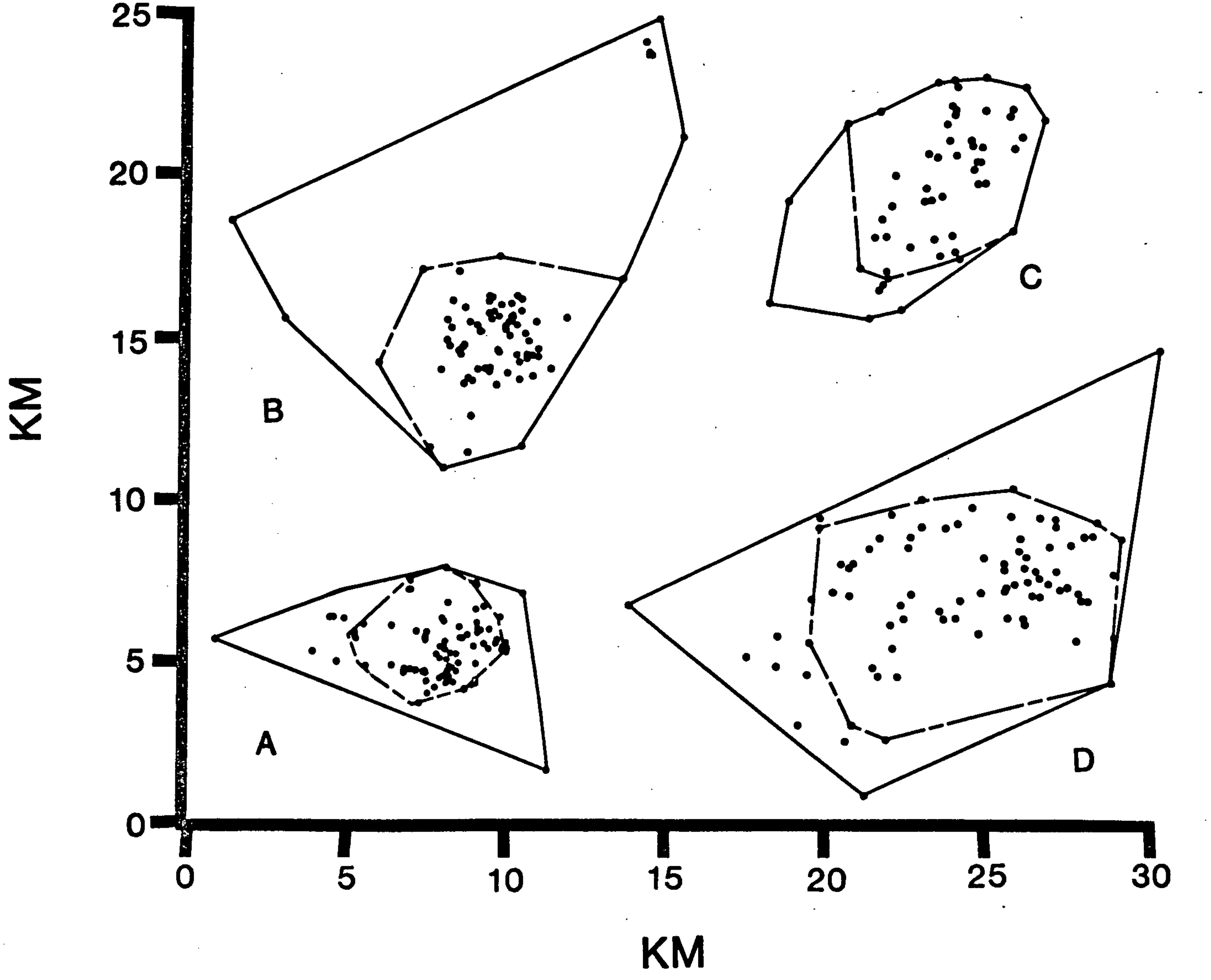
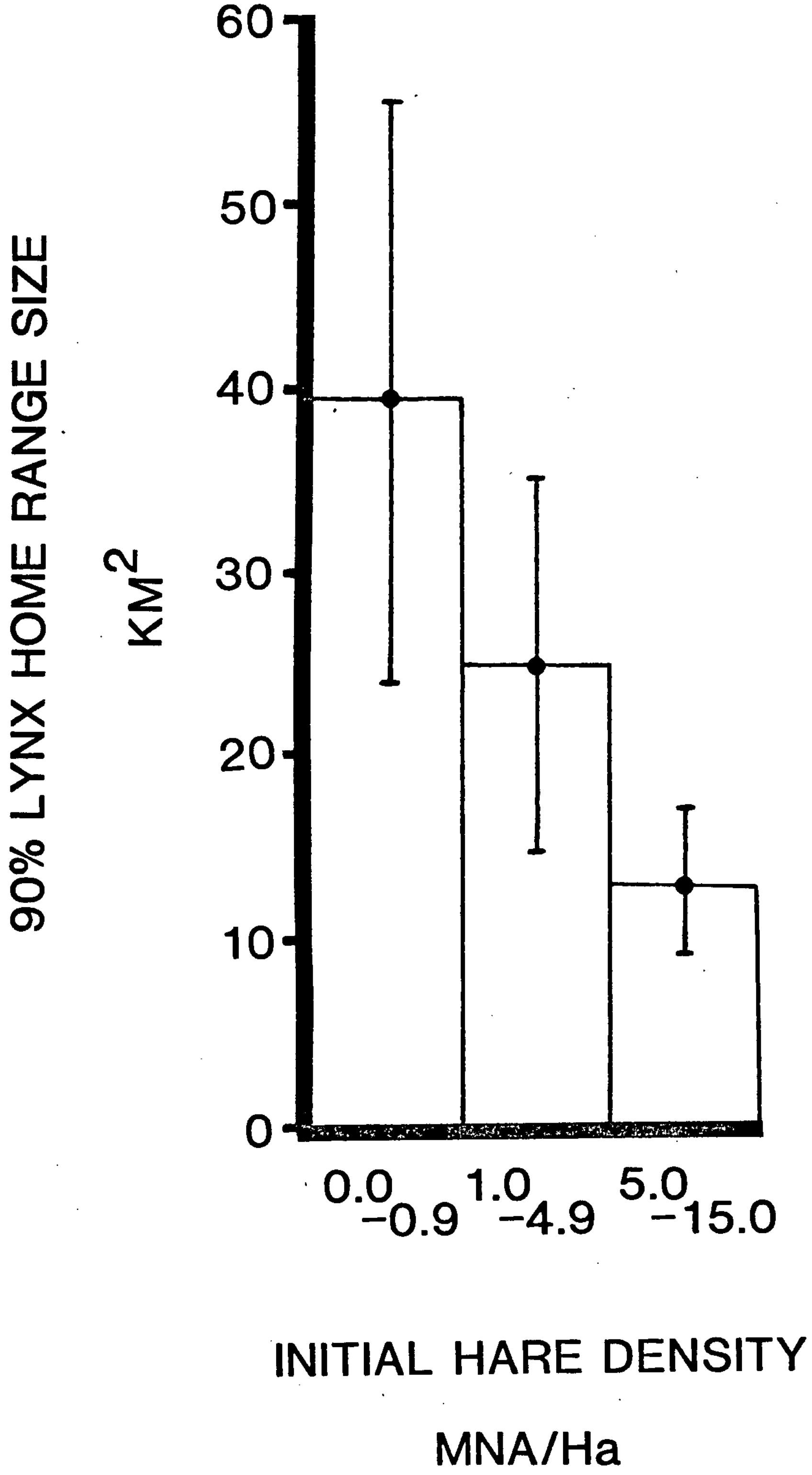

25
20
15
10
5
0
KM
0
5
10
15
20
25
30
KM
A
B
C
D

Table 4. Comparison of 100% and 90% home range areas of lynx. Snowshoe hare densities are initial densities at the start of each 3 month period for which individual lynx home ranges were calculated. Lynx home ranges are in square kilometers. * indicates that area not defined as a home range. See text for explanation. Number of locations used to determine each home range is in parentheses.

Lynx	Hare density (hares/Ha)	100% home range size (km²)	90% home range size (km²)	Percent difference
Joy	14.7	12.0 (30)	7.3 (27)	39
Sid	14.7	33.4 (95)	13.3 (85)	60
	3.3	104.3 (78)	31.0 (70)	70
	2.2	41.7 (53)	27.9 (47)	33
Scruff	14.7	46.4 (61)	17.7 (54)	62
	1.3	44.9 (63)	43.4 (56)	3
Charlie	14.7	29.7 (54)	14.6 (48)	51
Carlos	1.3	28.8 (45)	15.8 (40)	45
	1.0	22.4 (46)	16.1 (41)	28
	0.5	113.9 (69)	58.1 (62)	49
	0.2	76.8 (85)	52.4 (76)	32
Jean	1.0	17.1 (31)	13.7 (28)	20
	0.5	68.5 (65)	30.3 (58)	56
	0.2	34.0 (97)	28.1 (87)	17
Scottie	1.0	55.4 (34)	27.6 (31)	50
Jennifer	0.5	61.8 (50)	33.5 (45)	46
	0.2	200.6* (7)		
Rene	0.5	524.8 (31)	254.7* (28)	51
Enrique	0.5	49.2 (55)	17.8 (49)	64
	0.2	69.6* (12)		
Paul	0.5	86.7 (61)	53.9 (54)	38

Figure 4. Mean home range size for lynx residing in areas with indicated snowshoe hare densities. Hare density is the initial density at the start of each 3 month period for which home ranges of individual lynx were calculated. Vertical bars indicate 95% confidence limits of mean.

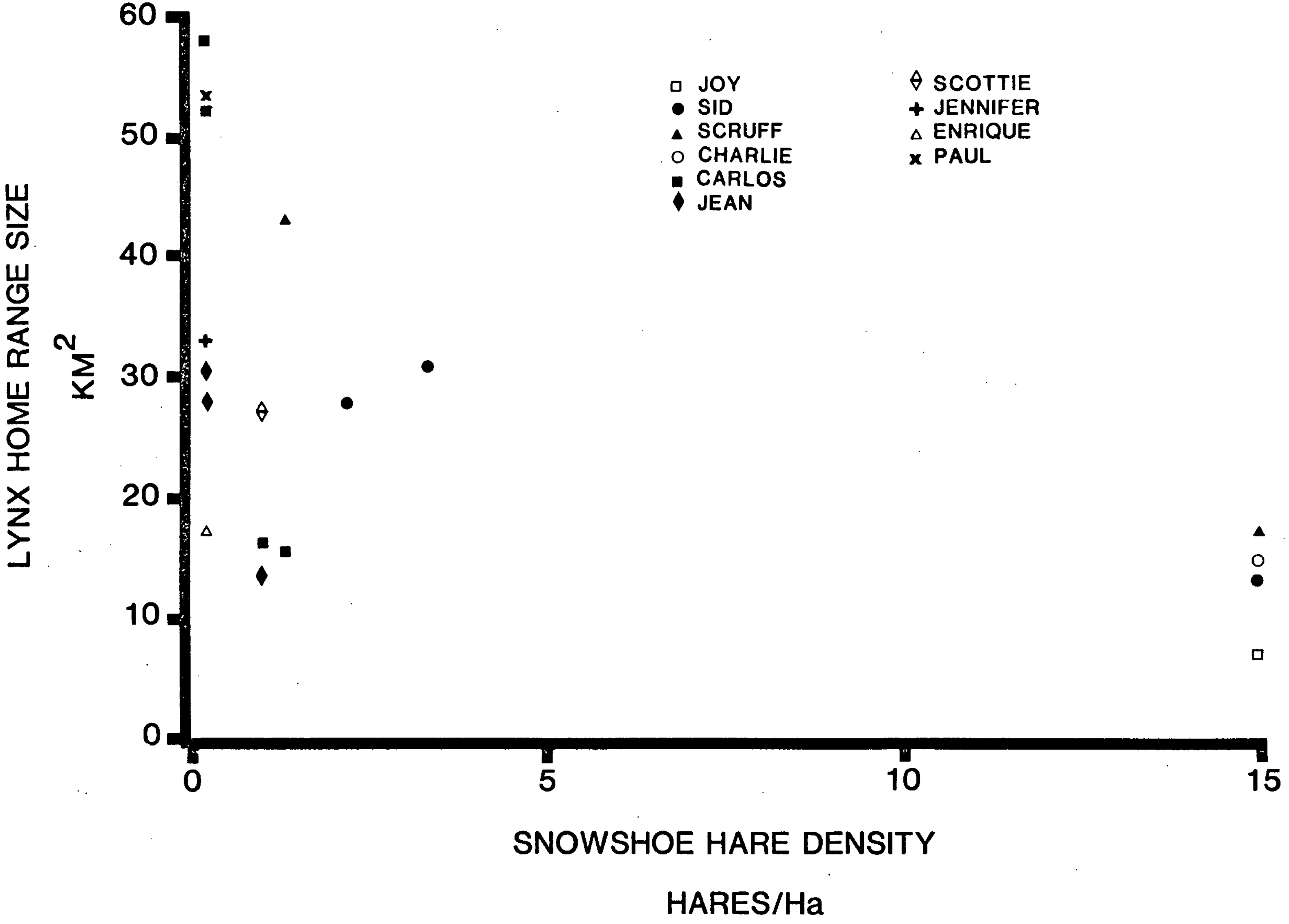

60
50
40
30
20
10
0
90% LYNX HOME RANGE SIZE
KM^2
0.0 -0.9
1.0 -4.9
5.0 -15.0
INITIAL HARE DENSITY
MNA/Ha

(Figure 5) showed this trend. This trend was similar when plotted against either initial hare densities or mean densities for each three month period. Using initial densities reduced the variance and gave clearer trends. These results are therefore presented as a function of initial hare densities in each 3 month period.

Between April and June 1982, the 4 radio-tagged lynx utilizing grid A (early April hare density 14.7 hares/ha) had a mean home range size of 13.2 (95% c.i. 8.8 to 17.6) km^2. These individuals either dispersed or expanded their home ranges as hare density on the grid declined. Because hare densities on grid A declined at a different rate than surrounding areas, home range data for individuals residing in the 2 areas in different time periods are lumped based on hare density. Lynx residing in areas with hare densities between 1.0 and 4.9 hares/ha had a mean home range size of 25.1 (95% c.i. 14.5 to 35.7) km^2. This is not a significant increase in home range size over lynx residing in the area with an initial hare density of 14.7 hares/ha. During the low part of the hare cycle when densities were less than 1.0 hares/ha mean lynx home range size was still higher at 39.2 (95% c.i. 23.7 to 54.7) km^2. Although this is not a significant increase over lynx residing in areas with hare densities between 1.0 and 4.9 hares/ha, it is significantly larger than the mean home range size of lynx residing in areas with hare densites greater than 4.9 hares/ha (t-test, $P<0.05$)

In addition to the overall trend towards larger home ranges as hare abundance declined, individual lynx monitored through

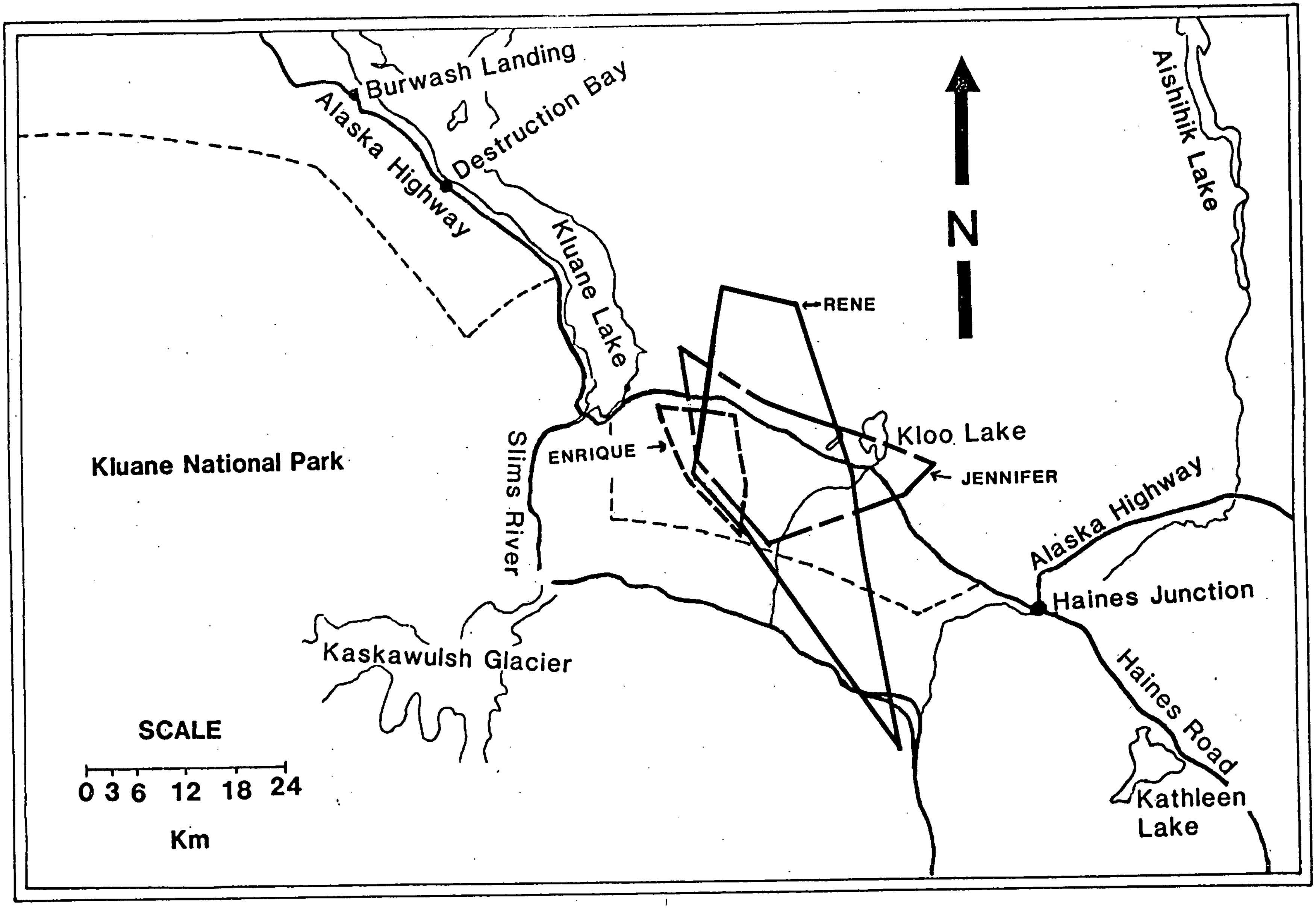
Figure 5. 90% home range sizes of individual lynx at indicated snowshoe hare density. Hare density is the initial density at the start of each 3 month period for which home range were calculated.


LYNX HOME RANGE SIZE
KM^2
60
50
40
30
20
10
0
0
5
10
15
SNOWSHOE HARE DENSITY
HARES/Ha
□ JOY
● SID
▲ SCRUFF
○ CHARLIE
■ CARLOS
♦ JEAN
◊ SCOTTIE
✚ JENNIFER
△ ENRIQUE
x PAUL

more than one 3 month time period increased their home range size as hare abundance declined (Figure 5). The only exception to this trend was a slight decrease in the home range size of Sid, concurrent with a decline in hare abundance from 3.3 to 2.2 hares/ha in the fall of 1982. With the exception of the slight decline in the home range size of Sid after a previous increase, no trend towards changes in home range size with season was observed either for individuals or in general.

At densities below about 0.5 hares/ha there appears to be a tendency for some individuals to abandon their home ranges and become nomadic. A female (Rene), that I radio-tagged and monitored during the summer of 1983, travelled extensively in the general study area but used no area consistently enough to be identified as her home range (Figure 6). After being radio-tagged in late July 1983, she remained in the area for several days before travelling approximately 35 km S during the next week. She crossed several large streams and a fast flowing river on this trek. Within a month she had returned to the initial tagging area. She remained in the area for a week before disappearing for 4 days. On her return, she travelled widely within the general study area until late September. During this period she travelled as much as 25 km to the SE on several occasions. Although she did not use any area consistently enough to be identified as her home range, a summation of the innermost 90% of my locations for her between July and October, amounts to an area of 255 km^2. In mid December 1983, she was located approximately 35 km E of the

Figure 6. Map of areas delineated by joining outermost observed locations of "nomadic" individuals.


Burwash Landing
Destruction Bay
Alaska Highway
Kluane Lake
N
RENE
Aishihik Lake
Kluane National Park
ENRIQUE
Kloo Lake
JENNIFER
Slims River
Alaska Highway
Haines Junction
Kaskawulsh Glacier
Haines Road
Kathleen Lake
SCALE
0 3 6 12 18 24
Km

initial radio-tagging site and I believe she starved during the previous winter. She was found dead in this area in June 1984.

In addition, Jennifer and Enrique who, during the summer of 1983, had maintained distinct home ranges, were travelling so widely during May and June 1984 that it was impossible to maintain continuous contact with them. Based on 7 locations, Jennifer covered a total area of at least 200 km^2 during this period (Figure 6). Based on 12 locations, Enrique wandered over a minimum area of 60 km^2 during the same period. These areas would undoubtedly have been larger if it had been possible to monitor their movements more fully.

Ninety percent home ranges of lynx overlapped considerably within and between sexes throughout the study. Over the course of the study, home range overlap averaged 10.5 (95% c.i. 0.6 to 20.5), 24.5 (95% c.i. -21.7 to 74.6), and 22.0 (95% c.i. 15.7 to 28.3) percent for male-male, female-female and male-female interactions respectively. Male-male overlap was significantly less than male-female overlap (t-test on arcsin transformed data, P=0.04). No significant difference was found between male-male and female-female home range overlap (t-test P=0.18). There was also no significant difference between female-female and female-male home range overlap (t-test P=0.70).

Lynx home range overlap remained high throughout the study and was not affected significantly by absolute hare density in an area. Overlap for the 4 individuals occupying the area of relatively high hare abundance (14.7 hares/ha) averaged 24.8 (95% c.i. 16.0 to 33.5) percent. Between July and September

1983 hare density on my four grids was about 0.5 hares/ha. Home range overlap for 5 lynx residing in an adjacent area during this period was 20.5 (95% c.i. 13.9 to 27.1) percent. This is not a significant difference (t-test on arcsin transformed data, P=0.67). Based on snow tracking I am confident that I had the majority of lynx in these two areas radio-tagged in these two time periods. Home range overlap for radio-tagged individuals monitored at hare densities between these extreme high and low densities ranged from 0.0 to 36.9 percent (mean 15.3, 95% c.i. -1.0 to 26.4). This indicates a high degree of home range sharing at all hare densities, although variation in degree of overlap between individuals was high.

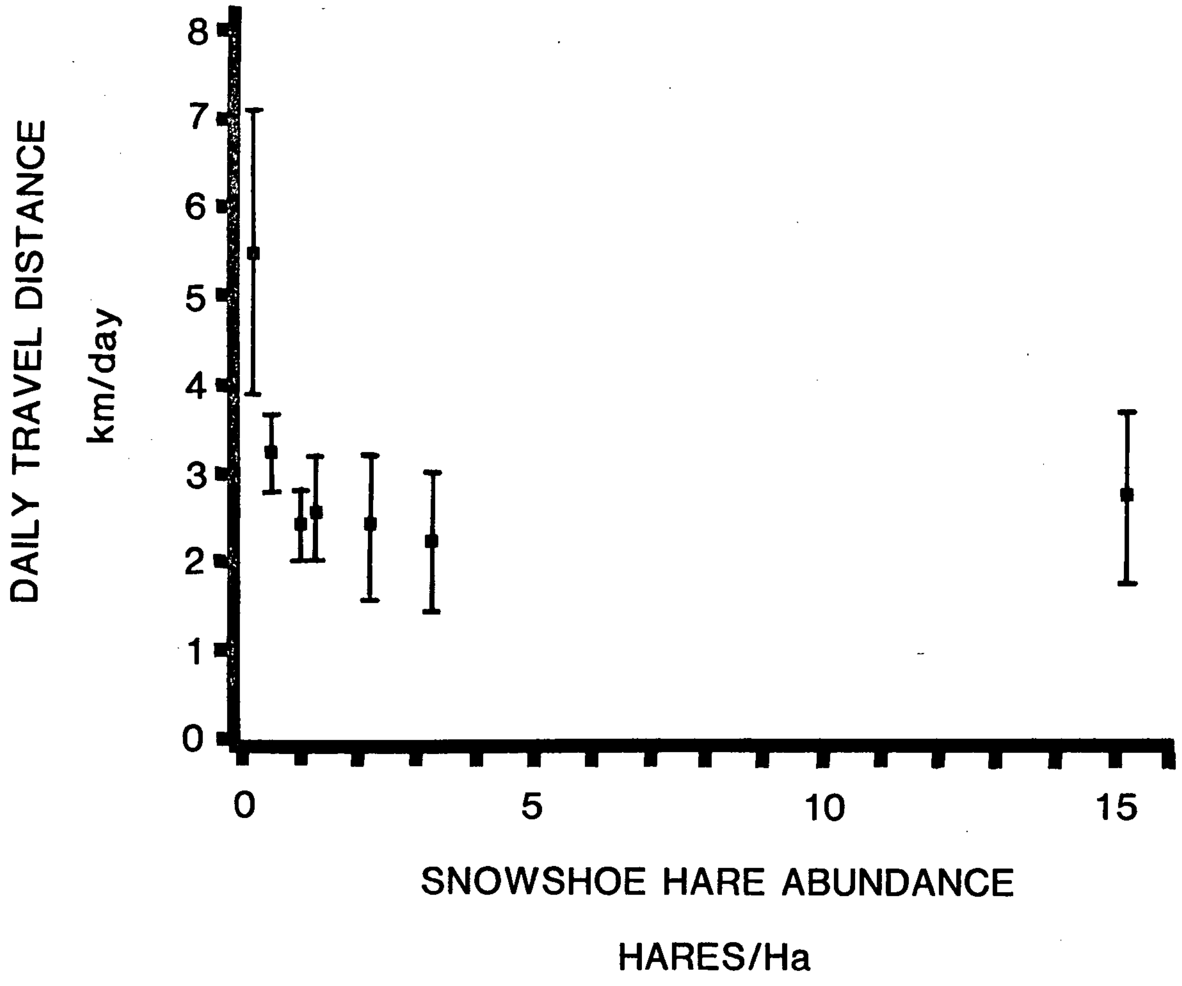
Effect of Snowshoe Hare Abundance on Lynx Foraging Effort

I assumed that lynx are foraging whenever they are travelling as did Brand et al. (1976). Lynx foraging effort was estimated by the straight-line distance travelled per day (DTD). I calculated this by measuring the distance between the points where an individual was located on consecutive days.

Lynx showed no significant change in their foraging effort at snowshoe hare densities above about 1.0 hares/ha (Figure 7). At 14.7 hares/ha lynx mean DTD was 2.7 km (95% c.i. 1.8 to 3.7 km). At 1.0 hares/ha lynx had a mean DTD of 2.4 km (95% c.i. 2.0 to 2.9 km).

Below about 1.0 hares/ha, however, lynx increase their mean DTD rapidly with declining hare density. At hare densities of

Figure 7. Mean straight-line daily travel distance of lynx versus snowshoe hare abundance. Travel distances are the mean for all individuals at the indicated hare density. Vertical bars indicate 95% confidence limits of mean.


DAILY TRAVEL DISTANCE
km/day
8
7
6
5
4
3
2
1
0
0
5
10
15
SNOWSHOE HARE ABUNDANCE
HARES/Ha

0.5 hares/ha, mean DTD was 3.3 km (95% c.i. 2.8 to 3.7 km). As hare density declined still further to 0.2 hares/ha mean lynx DTD increased sharply to 5.3 km (95% c.i. 3.9 to 7.2 km). This is a significantly larger distance than that travlled at 1.0 hares/ha (t-test $P < 0.05$).

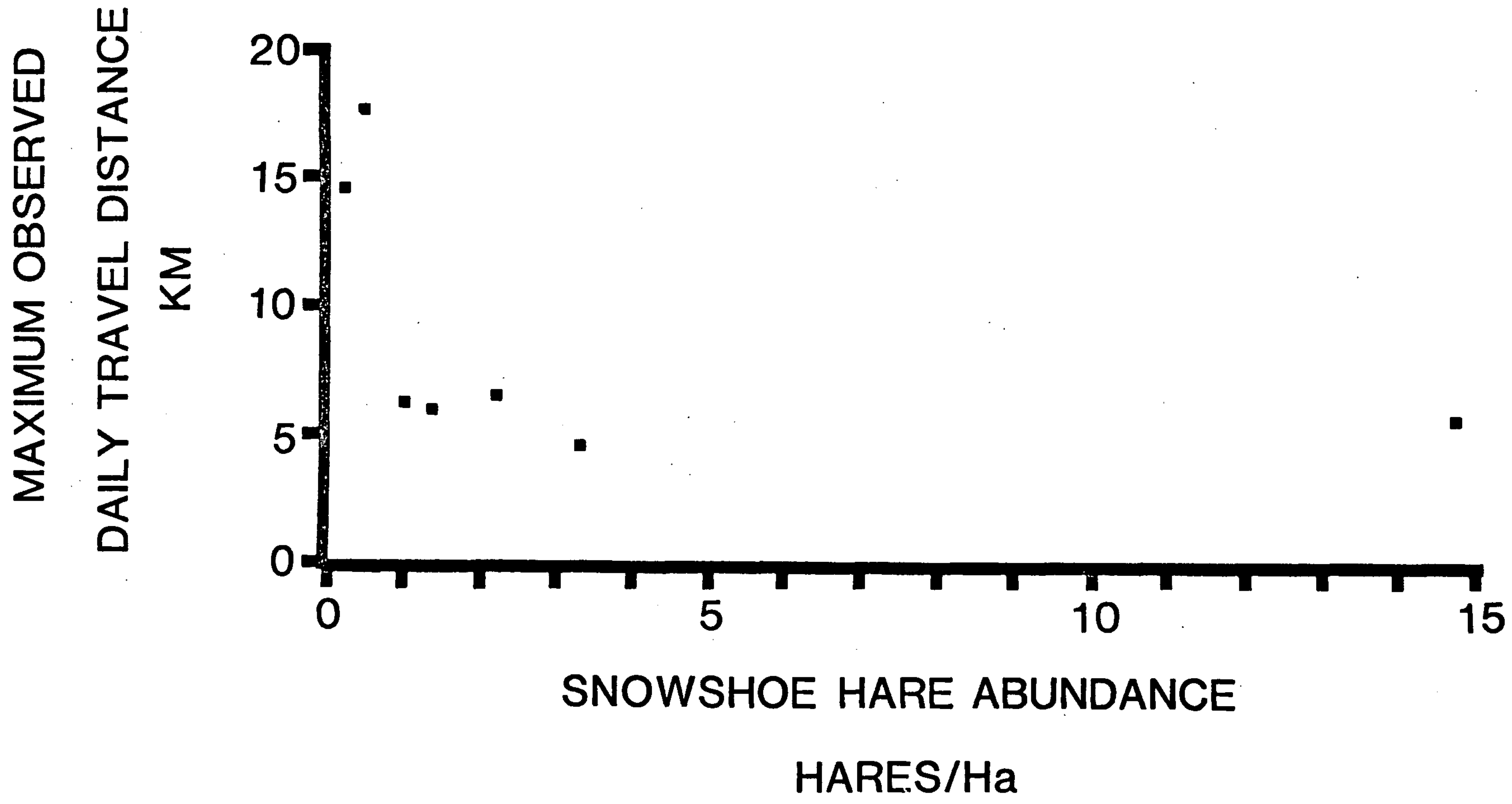
Additional evidence supporting the idea that lynx increase foraging effort with declining hare abundance is the maximum daily travel distance recorded at high and low hare density (Figure 8). These data show the same general trend as do mean DTD. At 14.7 hares/ha, the maximum DTD I recorded was 5.8 km. This stayed relatively constant to 1.0 hares/ha when maximum recorded DTD was still 6.3 km. As hare densities declined to 0.5 and then to 0.2 hares/ha maximum DTD increased to 17.5 and 14.6 km respectively, showing a decrease at extremely low hare density.

<u>Effect of Snowshoe Hare Distribution on Lynx Foraging Patterns</u>

While trying to capture lynx for radio-tagging, I obtained data to show how they were concentrating in areas of high prey density.

Between April 1 and May 10 1982, hare density on grid A declined from 14.7 to 8.4 hares/ha while hare density on grid B declined from 2.6 to 0.4 hares/ha (Figure 2). During this period, 3 lynx (Joy, Scruff and Sid) were captured in 234 trap-nights within a 1 km radius of grid A (Table 1). From tracks and the capture of another lynx (Charley) in the same area on

Figure 8. Maximum observed straight-line travel distance for all lynx in each 3 month period for which home ranges were calculated.


MAXIMUM OBSERVED
DAILY TRAVEL DISTANCE
KM
0
5
10
15
20
0
5
10
15
SNOWSHOE HARE ABUNDANCE
HARES/Ha

May 25, it is believed that two other lynx were also utilizing the area at the same time. Subsequent radio-tracking of these four lynx indicated a minimum density of 1 lynx per 7.3 km^2 in the area of grid A. An equal number of trap-nights on grid B during the same period resulted in no captures.

Two hundred and forty six trap-nights in the area of grid A in October and November 1982, after hare density on the grid had declined to approximately 1.8 hares/ha, resulted in no captures.

Track transects through both grids A and B in the spring and through grid A during the early winter of 1982, after hare densites had declined, also indicated that lynx sought out and concentrated their foraging efforts in areas of relatively high hare abundance (Table 5). In April 1982 when hare density dropped from 14.7 to 9.5 hares/ha on grid A, the mean number of sets of lynx tracks crossing a 600 m transect was 5.0 (95% c.i. 0.7 to 9.3). At the same time, when hare density on grid B was declining from 2.7 to 1.2 hares/ha, the mean number of sets of lynx tracks crossing each 600 m transect was 0.8 (95% c.i. -0.1 to 1.6). Thus, lynx used the area of higher hare abundance significantly more (Gadj. test P= 0.005).

Lynx abandoned the areas of relatively high hare abundance when they were depleted. As hare density on grid A declined from 14.7 to 2.2 hares/ha, 3 of the 4 lynx I had radio-tagged in the area dispersed. Hare density in the surrounding areas was declining from 1.9 to 1.4 hares/ha during this period.

In November 1982 when hare density on grid A had declined to 1.8 hares/ha, the mean number of sets of lynx tracks per 600

Table 5. Effect of relative snowshoe hare abundance on lynx foraging patterns. $*^1$ and $*^2$ indicate a significant difference (Gadj. Test P= 0.005). TN indicates the total number of trap-nights of effort.

Grid	Hare density (hares/Ha)	Number of lynx caught/100 trap-nights	Sets of lynx tracks/600 meter transect (mean & 95% c.i.)
A April/82	14.7	1.3 (234 TN)	5.0 (0.7 to 9.3) *1 *2
B April/82	2.6	0.0 (234 TN)	0.8 (-0.1 to 1.6 *1
A Nov./82	1.8	0.0 (246 TN)	1.2 (0.0 to 2.3) *2

m transect declined to 1.1 (95% c.i. 0.0 to 2.3). This is a significant reduction in utilization of the area following the decline in hare abundance (Gadj. test,P= 0.005). There was no significant difference in the intensity of lynx use of grid B in April and grid A in November when hare densities were similar (Gadj. test P>0.05).

A second area of lynx concentration was noted between July and September 1983 approximately 15 km SE of grid A along the old Alaska Highway. Five lynx resided within a total area of 99 km^2 for a density of 1 lynx per 19.8 km^2. This density is lower than that noted on grid A. As previously mentioned, the degree of home range overlap for individuals residing on grid A and this second area of concentration was not significantly different. The degree of home range overlap in these 2 areas was generally higher than noted elsewhere in the study. Unfortunately, I do not have data on hare distribution in this second area.

Lynx Dispersal and Mortality during a Decline in Snowshoe Hare Abundance

During the study only 3 of the 11 radio-tagged lynx survived for 1 year or more and remained within the study area. Dispersal or human related mortality were responsible for the loss of 7 lynx. One lynx died of natural causes in the spring of 1984 (Table 2).

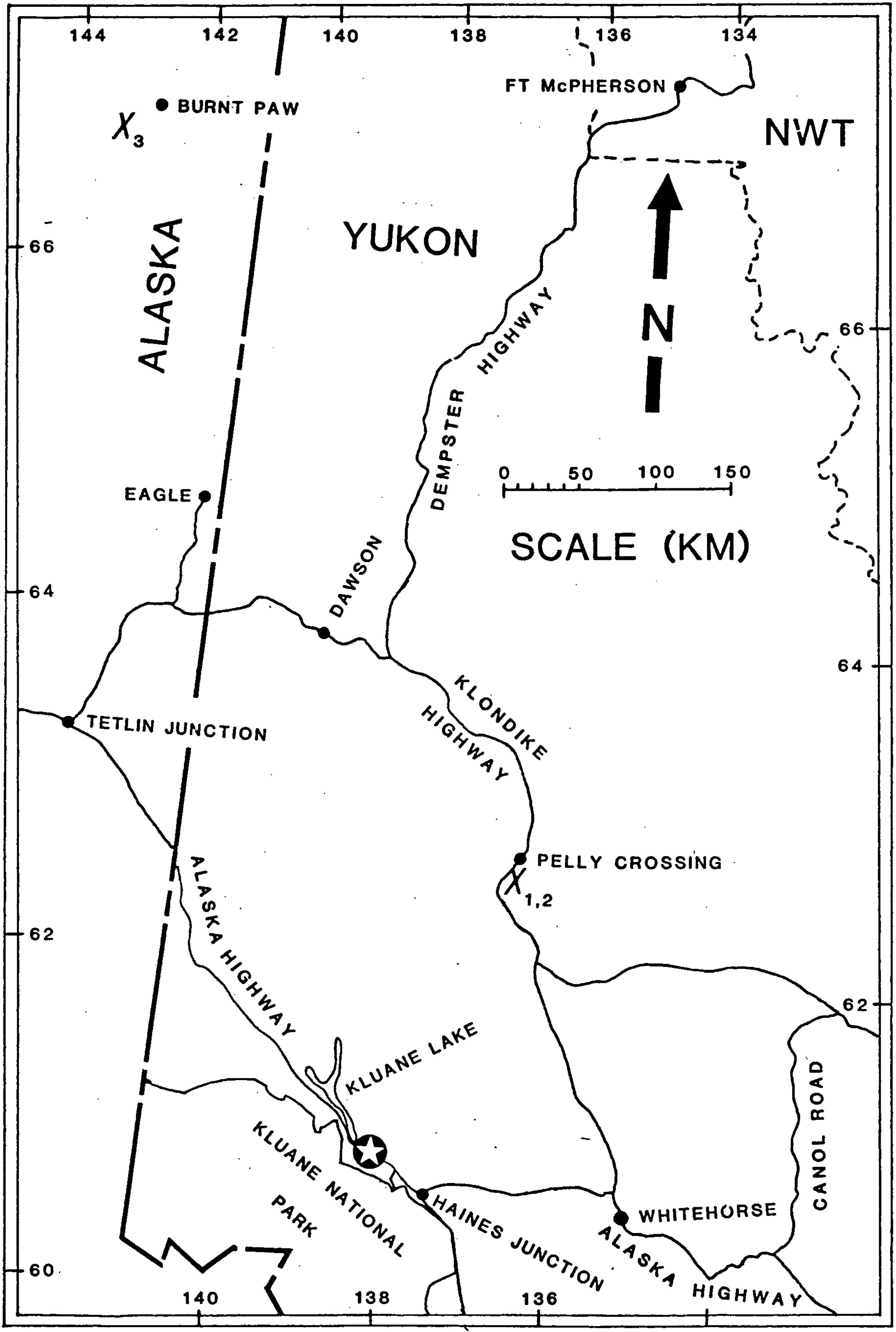
Between April and November 1982, I radio-tagged 7 lynx. By

April, 1983, only 2 were still alive and residing within the study area. Three of the 7 (Joy, Charley and Scruff) dispersed 250-700 km before being trapped and killed by professional trappers (Figure 9). All 3 of these lynx were radio-tagged on grid A between April 4 and May 25 1982. These individuals had minimum residency times in the area of 35 days, 40 days and 7 months respectively. One of the females (Joy) was at least 2 years old and the other 2 individuals were at least 1 year old. During the period when Joy and Charley dispersed, grid A had significantly higher densities than surrounding areas but hare density on the grid was declining rapidly (Figure 2). Joy travelled at least 700 km in the next 8 months before being captured and killed in mid-December in NE Alaska. Charley was trapped and killed approximately 250 km N of the study area in mid-December 1982.

Scruff moved her home range to approximately 5 km SE of grid A in July 1982 and dispersed from the study area in October. She was trapped and killed in mid-November within 50 km of the area where Charley was killed near Pelly Crossing, Yukon. Joy, Charley and Scruff had minimum dispersal rates of 3.8, 1.7 and 8.3 km/day respectively to travel the distances covered by these lynx in the time taken, if I assume straight-line travel. All dispersals from the study area occurred during the snow-free period from May to October.

Two additional lynx (Sid and Scottie) were also trapped and killed within 10 km of their original radio-tagging site during the winter of 1982-83. All 5 lynx were trapped within 2.5

Figure 9. Map of long distance dispersals undertaken by lynx. Star indicates initial radio-tagging site for all individuals. $X_{1,2}$ and X_3 indicate sites where Charlie and Scruff and Joy respectively were trapped and killed. See Table 2 and text for date of initial radio-tagging, date killed and dispersal rates.


144
142
140
138
136
134
FT McPHERSON
BURNT PAW
X_3
NWT
YUKON
ALASKA
66
64
62
60
DEMPSTER HIGHWAY
N
0 50 100 150
SCALE (KM)
EAGLE
DAWSON
TETLIN JUNCTION
KLONDIKE HIGHWAY
PELLY CROSSING
$X_{1,2}$
ALASKA HIGHWAY
KLUANE LAKE
KLUANE NATIONAL PARK
HAINES JUNCTION
WHITEHORSE
CANOL ROAD
140
138
136

months of the start of trapping season. This represents 71% of my radio- tagged population and 100% of the animals that left the game sanctuary. The 2 lynx (Jean and Carlos) that remained in the Kluane Game Sanctuary in late fall 1982 were still present the following spring.

Between July and September 1983, 4 additional lynx were radio-tagged within the game sanctuary. I observed no long distance dispersal, of the type observed the preceding year during rapid decline in snowshoe hare abundance.

During the winter of 1983-84, 2 of my 6 radio-tagged lynx were trapped and killed within 10 km of their initial capture site. This represents 33% of my radio-tagged population and 50% of the lynx known to have travelled outside the game sanctuary. One lynx (Rene) starved and was found dead in June 1984 north of Haines Junction, 35 km east of her initial capture site. The carcass was extremely emaciated, and I believe she starved during the winter.

Trapping was responsible for 7 of 8 deaths of lynx observed in this study. Furthermore, only 2 of the 9 individuals known to travel outside the game sanctuary during the trapping season were not trapped.

DISCUSSION

The results of this study indicate that lynx respond behaviorally to declining snowshoe hare abundance. In the following sections I will discuss the effectiveness of these responses in the lynx's efforts to continue to fulfill its energetic needs as hare abundance declines.

Lynx Home Range Size

Mean home range size for lynx in this study increased 3 fold concurrent with a decline in snowshoe hare abundance from 14.7 to about 0.2 hares/ha. This increase was sufficient to completely overshadow any effect of sex, age, or season on home range size.

In contrast to this study, Brand et al. (1976) found no relationship between lynx home range size and either lynx or snowshoe hare density. The reason for this difference is unclear but may be at least partially a function of differences in the technique used to assess home range size. The work of Brand et al. (1976) was conducted using winter snow tracking. The limitations of this technique have been pointed out by Mech (1980): "(1) errors are possible in identifying individual lynxes by tracks from day to day, (2) observations are restricted to winter, (3) the area of search is limited, and (4) the sexes of the study animals often cannot be determined".

Points 1 and 3 may be responsible for the lack of an increase in home range size found by Brand et al. (1976). It is possible that the expansion of individual lynx home ranges into unmonitored areas went undetected. If an individual expanded its home range into the range of another, this expansion may have gone undetected because of misidentification of the tracks. Brand et al. also stated that home range size was a function of sampling intensity, and home ranges in their study would probably have continued to increase with additional kilometers of snow-tracking.

Although technical differences may explain some of the variation in home range sizes reported for lynx, I feel that the over-riding factor is food abundance. Home range sizes reported for lynx in previous studies span over an order of magnitude. Brand et al. (1976) and Parker et al. (1983), working in areas of relatively high snowshoe hare abundance, reported lynx home ranges between 7.9 and 49.5 km^2. Carbyn and Patriquin (1983) found lynx home ranges of between 138 and 221 km^2 during a period of rapid increase in hare abundance. Mech (1980), reported lynx home ranges of 51 to 243 km^2 and suggested that low prey abundance may have been responsible for the large home ranges. Saunders (1963b) found lynx home ranges between 15.5 and 20.7 km^2 at low hare densities. His estimates are based on limited winter snow tracking which may not have been sufficient to delineate the entire home ranges. If I include the area covered by Rene during the summer of 1983, my 90% home ranges span from the smallest to the largest previously reported.

The concept of increasing feeding territory or home range size with declining food abundance is intuitively reasonable and has been discussed in theoretical terms by several authors (Dill 1978, Harestad and Bunnell 1979, Hixon 1980, and McNab 1963 among others). Field evidence for increasing home range size has come from such wide ranging systems as reptlies (Krekorian 1976, Simon 1975), birds (see Dill, 1978 and Schoener, 1968 for reviews), mammals (Haber et al. 1976) and fish (Slaney and Northcote 1974). Although increasing home range size would obviously not increase foraging success in terms of catch per unit effort, it would mean that the food resources within the individuals home range would not be depleted as rapidly. This is evident from my data. The 4 lynx using the area around grid A in May 1982 had a mean home range size of 13.2 km^2. Assuming uniform hare density throughout the area each lynx home range would contain about 19,400 hares. If a lynx had exclusive use of this home range and required 0.5 hares/day for maintenance, this hare population would last the lynx over 106 years. Even with the 4 lynx sharing a total area of 29.2 km^2 this hare density would last them 58.8 years. It therefore seems that lynx home ranges at this time were well in excess of their immediate needs. Furthermore, it seems unlikely that the decline in the hare population in this area can be attributed to lynx predation alone. At 2 hares/ha when lynx home ranges averaged 25.1 km^2 the standing crop of hares within its home range, again assuming exclusive use, would last an individual lynx 27 years. At 0.5 hares/ha the existing hare population within the average lynx home range of 39.2 km^2 would last about 10.7 years. Overlapping home ranges would decrease this time still further and the hare population (without recruitment) within the 99.0 km^2 shared by 5 residents in the summer of 1983 would last them only about 5.4 years. These calculations show that the increase in lynx home range size in response to declining hare abundance was not sufficient to maintain a constant size hare population within their home range. These estimates obviously over-estimate the amount of time that lynx could survive on the hares existing within its home range. It assumes that lynx are sufficiently efficient predators to totally deplete their home range. Prey abundance within a predators home range cannot be extrapolated directly to prey availability for the predator. As prey abundance declines the predator will have to expend more effort to find and capture each prey item. A doubling of a lynx's home range size in response to a halving of snowshoe hare abundance would therefore not result in equivalent prey availability for the lynx. It also assumes that no other predators are harvesting snowshoe hares within the lynx's home range. I noted in this study that raptors and other mammals were also important predators on snowshoe hares, and also seemed to concentrate in areas of relatively high prey abundance.

If prey distribution is not uniform within the environment, by expanding its home range, the individual would also increase the chance of having relatively good patches of prey within its home range. This would be especially important to a lynx during a snowshoe hare decline if the few remaining hares are concentrated within refugia as suggested by Wolff (1980). This will be discussed in more detail in the later section on patch utilization by lynx.

Three lynx abandoned their home ranges and became nomadic at hare densities below about 0.5 hares/ha. Similar patterns have been reported for other felids. Hanby and Bygott (1979) found that the number of nomadic female lions wandering through the suboptimal habitat of the Serengeti Plains declined and some of these previously nomadic females became resident when prey abundance increased. Bailey (1981) reported that bobcats that defended territories during periods of prey abundance also became nomadic after prey abundance declined. He suggested that if prey abundance is unpredictable, or very low, it would be adaptive for bobcats to become transient and search out widely seperated concentrations of prey. These arguments hold equally well for lynx. At densities below about 0.5 hares/ha, lynx may not be able to fulfill their energetic requirements and must seek out patches of relatively high prey abundance. I do not have good information on the spatial and temporal distribution snowshoe hares in my area but if the refugia are widely spaced it may be necessary for lynx to wander great distances in search of them.

Mean home range overlap for lynx exceeded 10.5% both within and between sexes throughout this study. Further, absolute snowshoe hare density had no effect on the degree of home range overlap between lynx. The degree of home range overlap at extreme high and low hare densities in this study were not significantly different.

Schoener (1968) suggested that territoriality is inversely proportional to the degree of home range overlap between individuals. Bailey (1974) found home ranges of territorial bobcats overlapped 0.1 and 2.0 percent for male with males, females with females respectively. The high degree of home range overlap within and between all sexes in this study is strong evidence that lynx are not territorial at least during the period of decline and low snowshoe hare abundance.

Previous studies show no consistent trend in the relative exclusiveness of lynx home ranges within and between sexes. Nellis et al. (1972) reported that lynx tend to be separated in time and space. Brand et al. (1976) reiterated this stating that " avoidance behavior appears to separate lynx in both time and space, but probably does not act locally as a density-limiting mechanism". Berrie (1974) found that female lynx were "less tolerant of each other than were males". In his study the home ranges of males overlapped with each other and with neighbouring females while female home ranges did not overlap. Mech (1980) reported that female home ranges overlapped while those of males did not. In his study, home ranges of male lynx also overlapped little with those of females. Parker et al. (1983) reported extensive overlap in the home ranges of the adult male and female in his study. The home ranges of these two adults did not overlap with that of a juvenile female which he presumed to to be the offspring of his adult female. Carbyn and Patriquin (1983) found the home ranges of two females with kittens overlapped but it was uncertain whether the home range of the male in their study overlapped with that of the females.

The lack of a consistent pattern in the degree of lynx home range overlap is puzzling. One possible explanation is that the total lynx population within the study areas of these studies was not monitored. The home ranges of unmonitored lynx may have overlapped extensively with those of monitored lynx in some cases. The patterns of overlap reported in the literature would therefore be a function of which animals in the population happened to be monitored. A second possibility is that the spatial distribution of lynx is a function of subtle environmental variables. Under various conditions different degrees of home range overlap within and between sexes is tolerated. No indication of what these enironmental factors might be or how they might act is evident from a review of past studies. If any behavioral spacing mechanism exists in lynx populations, it is easily over-ridden by proximate environmental factors such as snowshoe hare distribution (see discussion of patch utilization by lynx).

Effect of Snowshoe Hare Abundance on Lynx Foraging Effort

Lynx in this study increased their mean straight-line daily travel distance from 2.7 km/day at high hare density to 5.3 km/day at low hare density. In contrast, Nellis and Keith (1968), Brand et al. (1976), Parker (1981) and Parker et al. (1983) all found no correlation between snowshoe hare abundance and the distance that lynx travelled per day.

Nellis and Keith (1968) and Brand et al. (1976) found that winter daily travel distances (DTD) of lynx fluctuated markedly from year to year, independent of hare abundance. Brand et al. (1976) found a significant negative correlation between lynx daily travel distance and hunting success. Parker (1981) found that lynx daily travel distance remained constant at about 8 km/day as hare abundance declined through one winter. He found, however, that hunting success, in terms of kills per attempt, increased through the winter. He concurred with Nellis and Keith (1968), and Brand et al. (1976) that daily travel distance was primarily a function of hunting success in terms of kills/km. Brand et al. (1976) and Parker (1981) suggest that hunting success, and therefore daily travel distance, is a function of snow conditions and individual hunting skills.

I found, however, that at hare densities above 1.0 hares/ha lynx did not increase their DTD significantly with declining hare abundance in summer, when snow conditions could not be affecting hunting success. Further, if (1) daily travel distance is an inverse function of hunting success in terms of kills per day and (Brand et al. 1976, Parker 1981), (2) there is no relationship between kills per attempt and hare density (Brand et al. 1976), and (3) attempted kills per km travelled decline with declining hare density (Brand et al. 1976), lynx should travel further as hare abundance declines in an effort to fulfill their energetic requirements.

Below hare densities of 1.0 hares/ha, however, lynx showed a dramatic increased in foraging effort in all seasons. The studies of both Brand et al. (1976) and Parker et al. (1983), were conducted at hare densities of 0.7 hares/ha or higher. Nellis and Keith (1968) worked at hare densities below 0.7 hares/ha. They used winter snow-tracking to collect their data and reported only instances where lynx "beds used on consecutive nights could be established with certainty". It may be that on days when lynx travelled unusally long distances, it was not possible for them to establish the total distance travelled and these data were therefore omitted. In any event, the most dramatic increase in lynx foraging effort occurs at very low hare densities. My results above 0.5 hares/ha therefore are in general agreement with those of Brand et al. (1976) and Parker et al. (1983).

I calculated expected total daily travel distances for lynx at different hare densities using the equation:

$$\begin{bmatrix}\text{expected}\\ \text{daily}\\ \text{travel}\\ \text{distance}\end{bmatrix} == \frac{\begin{bmatrix}\text{maintenance level}\\ \text{energy requirement}\end{bmatrix}}{\begin{bmatrix}\text{Y intercept of}\\ \text{regression line}\\ \text{for attempted}\\ \text{kills per km}\end{bmatrix} + \begin{bmatrix}\text{slope of}\\ \text{regression}\\ \text{line}\end{bmatrix} \text{x} \begin{bmatrix}\text{hare}\\ \text{density}\\ \end{bmatrix} \text{x} \begin{bmatrix}\text{attack}\\ \text{success}\\ \text{rate}\end{bmatrix}}$$

Using data from Brand et al. (1976) I set at following parameter values;

maintenance level energy requirement = 0.5 hares/day

Y intercept of regression line = 17.5

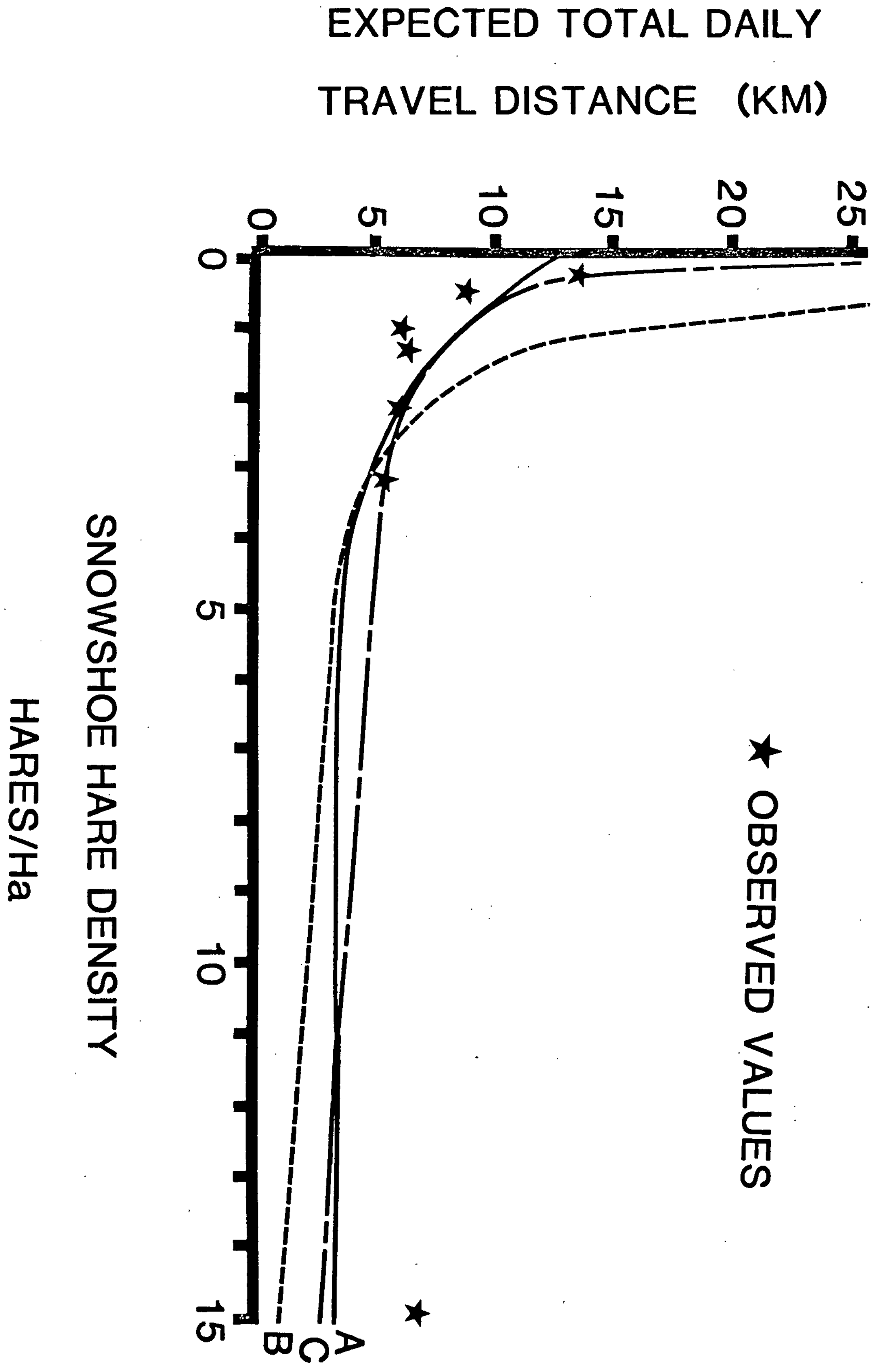
slope of regression line = 0.075

attack success rate (proportion of successful attacks) = .23

In contrast to Brand et al.(1976), Parker et al. (1983) found that lynx kill an average of 1 hare per day. Substituting this higher kill rate in the above equation would result in a doubling of the expected daily travel distances. Parker (1981) also reported an average individual hunting success rate of 17%. This lower value would again tend to increase the expected daily travel distances.

Using a range of hare abundances I derived the expected daily travel distance curve shown as line A in Figure 10. From

Figure 10. Observed and expected total daily travel distances for lynx versus snowshoe hare abundance. For derivation of lines A, B and C see text.


EXPECTED TOTAL DAILY TRAVEL DISTANCE (KM)
0
5
10
15
20
25
SNOWSHOE HARE DENSITY HARES/Ha
0
5
10
15
A
C
B
★ OBSERVED VALUES

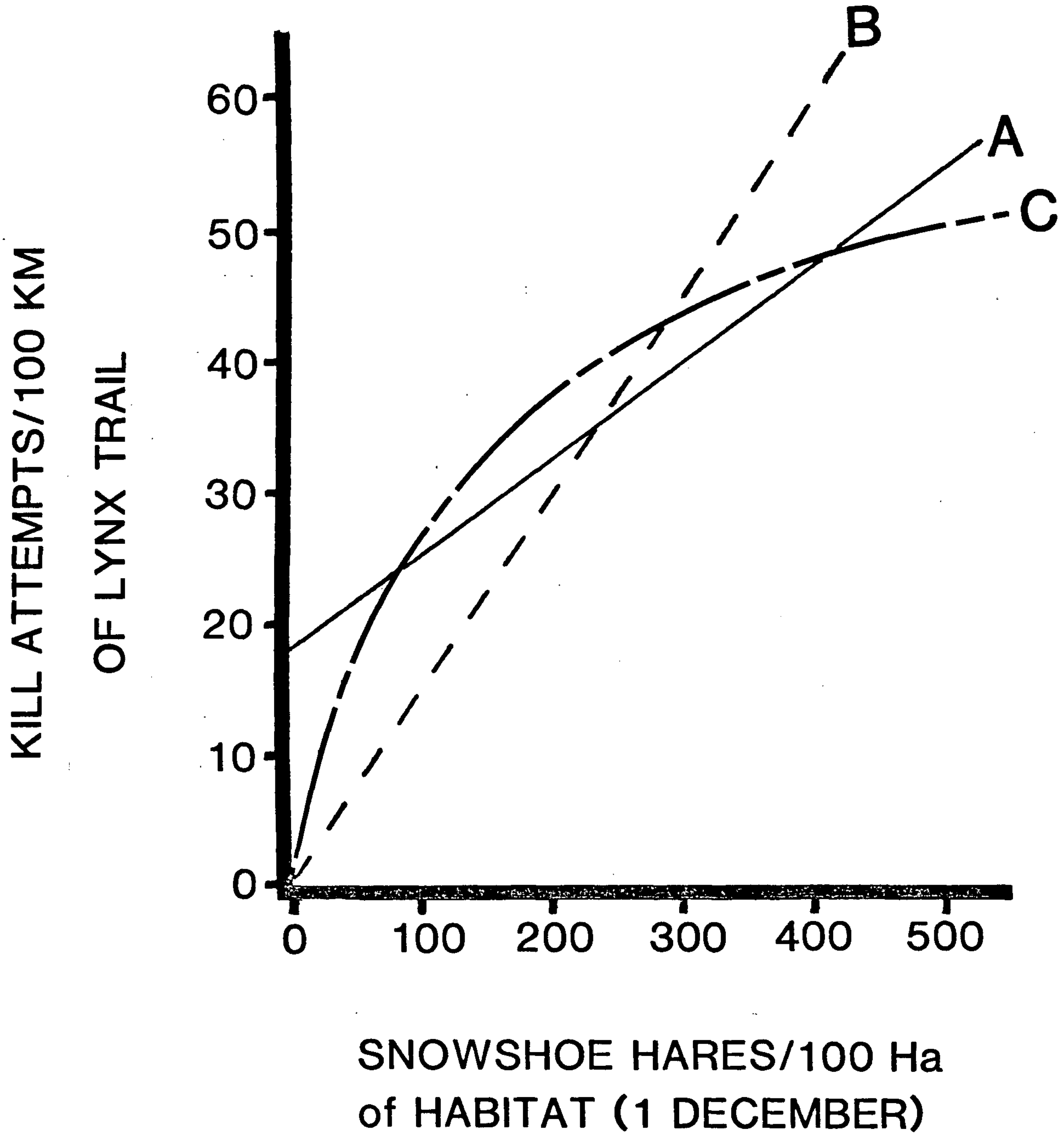
Nellis and Keith (1968) and Saunders (1963b) I calculated total daily travel distance to straight-line daily travel distance ratios of 3.0 and 1.9 respectively. I therefore multiplied my straight-line daily travel distances by 2.5, the mean of these values, to estimate total daily travel distance. These are also plotted in Figure 10.

Although the curve through the expected values is similar to my observed values, the inflection point is not sharp enough to mimic my data accurately. Daily travel distances are therefore under-estimated at very high and very low hare abundances and over-estimated at intermediate densities.

Estimates for the Y intercept and slope parameters used in the above equation are derived from Figure 2 of Brand et al. (1976). Although the correlation coefficient for their regression line is good,($r^2=0.91$) these values are biologically unreasonable. A Y intercept considerably higher than zero suggests that lynx are continuing to attempt to kill hares long after there are no hares left to attempt to kill. Clearly to be biologically reasonable the regression line must run through the origin or intersect the x-axis near the origin. Two possible lines can be drawn through the origin to intersect their data (Fig. 11); a straight line regression or a curve similar to a type II functional response (Holling 1959). Both result in a larger slope for the regression line at low hare densities. The type II functional response curve also results in a smaller slope at high hare densities.

Line B of Figure 10 shows predicted values for the straight

Figure 11. Reproduction of Figure 2, Brand and Keith (1979), with 2 additional regression lines added. Line A is the original regression line presented by Brand and Keith (1979). Lines B and C are alternative, more biologically reasonable regressions passing through the origin. See text for explanation and justification of line B and C.


B
A
C
60
50
40
30
20
10
0
0
100
200
300
400
500
KILL ATTEMPTS/100 KM OF LYNX TRAIL
SNOWSHOE HARES/100 Ha of HABITAT (1 DECEMBER)

line regression through the origin (line B Fig. 11) using the above equation with a Y intercept of zero and a slope of 0.13. The resulting r^2 value of 0.11 for this line is far less than that of 0.91 reported by Brand et al. (1976) It is however, more biologically reasonable.

The inflection point of the resulting line (line B, Fig. 10), although more closely resembling the observed data, occurs at too high a hare density. This line also grossly over-estimates travel distance at low hare densities and under-estimates it at high hare densities.

I therefore plotted the data from Figure 2 of Brand et al. (1976) on log-log scale, the equivalent of calculating a best fit hyperbolic curve through their data to the origin (line C, Fig.11). The r^2 value for this line is 0.87, only slightly lower than 0.91 reported by Brand et al. (1976). Furthermore, this line is again biologically reasonable because it goes through the origin. This is also the general form of the type II functional response (Holling, 1959) that is common for many vertebrate predators (Krebs 1978). Using the slope and Y intercept from this transformation we again calculated expected travel distances with the above equation. These are plotted as line C on figure 10.

Although this line slightly over-estimates daily travel distance at low densities and under-estimates travel distances at extremely high hare densites, the inflection point is the correct form and occurs at the right point to mimic my observed data so that the fit of this line is surprisingly good. The slight over-estimation of travel distance at low hare densities may be due to physiological constraints on the lynx. Lynx may not be able to travel far enough per day at low hare densities to meet their energetic requirements. This, in turn, would result in the decline in general body condition of lynx at low hare densities. The under-estimation of travel distance at extremely high hare densities may be due to lynx continuing to travel and sample the environment after their energetic requirements have been met. Parker et al. (1983) found evidence that lynx often continue to travel after consuming the first kill of the day. This model also demonstrates that my data and those of Brand et al. (1976) are in strong accord.

Although the explanations of Brand et al. (1976) and Parker et al. (1983) may be sufficient to explain why there is no apparent increase in lynx foraging effort at hare densities above 1.0 hares/ha, they cannot be extrapolated to lower densities. Lynx foraging effort increases dramatically at hare densities below 1.0 hare/ha but the increase is not sufficient for lynx to continue to fulfill their energetic requirements.

Effect of Snowshoe Hare Distribution on Lynx Foraging Patterns

If prey are not uniformly distributed throughout the environment it will always be to the advantage of a predator to concentrate its foraging efforts in the patches of relatively high prey abundance (Krebs 1978). This will become increasingly important as the relative difference between the good patches and the surrounding areas increases and it becomes difficult for the predator to fulfill its energetic requirements outside the good patches.

I do not have good data on the patchiness of snowshoe hare distribution but if the system is similiar to that described by Wolff (1980) snowshoe hare distribution should have been very clumped. Wolff (1980) suggested that during the decline and low period of their ten year cycle, snowshoe hare populations retreat into patches of optimal habitat. It would seem reasonable then that it would be adaptive for lynx to seek out and utilize these good patches.

In this study I found three independent lines of evidence indicating that lynx do seek out and concentrate their foraging efforts in patches of high snowshoe hare abundance. First, my lynx trapping success was higher in an area of relatively high hare abundance. Second, track transects through areas of different hare abundance also indicated that lynx used areas of high hare abundance more intensively than surrounding areas. Third, lynx density was higher within the patch of relatively high prey abundance than elsewhere in the study. Further, I found that lynx abandoned these good patches when they became depleted.

Others have also found that lynx tend to concentrate in patches of relatively high prey abundance. Brand et al. (1976) state that one of the three hunting methods used by lynx was to concentrate their efforts in areas of hare activity, especially during cyclic lows in hare abundance. He did not quantify this. Saunders (1963a) reported that lynx concentrated in an area of abundant carrion during a period of low hare numbers and then dispersed after the carrion became unavailable. Berrie (1974), Koehler et al. (1979) and Bergerud (1971) also note that lynx tend to concentrate in areas of relatively high food abundance.

Berrie (1974) further suggested that refugia for snowshoe hare were important for the survival of lynx through the low of the cycle and that the expansion of the lynx population out of these refugia followed that of the snowshoe hare population during the increase phase. That lynx cannot meet their energetic needs at hare densities below 0.5 hares/ha, as previously suggested, supports this idea.

As discussed above, absolute hare density has little effect on the degree of aggregation of lynx, but relative prey abundance (patchiness of distribution) may play a large role in determining the spatial distribution of lynx. The high degree of home range overlap found between the 4 lynx during April-June 1982 was a function of their sharing a patch of relatively high prey abundance. Although I do not have data on prey distribution in the area of lynx home range overlap at low hare density, it is possible that this area also had relatively high prey abundance. Lynx home range overlap may then be a function of relative prey abundance. Lynx home ranges may overlap extensively in areas of relatively high prey density and not overlap in areas of relatively low prey density. This might also explain the large variation in degree of home range overlap between lynx at intermediate hare densities in this study. Lynx density was also higher in the two areas of high home range overlap than elsewhere in the study.

Lynx Dispersal and Mortality

During the period of rapid decline in snowshoe hare numbers (January through December 1982) 3 of the 7 lynx that I had radio-tagged dispersed between 250 and 700 km before being trapped by professional trappers. Other long distance dispersals by lynx of from 103 to approximately 800 km have been reported elsewhwhere by other researchers (Saunders 1963b, Nellis and Wetmore 1969, Mech 1977, D. Brittel pers. comm.). These dispersals are normally associated with the decline phase of the snowshoe hare cycle and lynx have been reported to invade areas well south of their normal range (Adams 1963, Mech 1973, Gunderson 1978). This and other studies have shown that adults as well as juveniles undertake such long movements.

The three dispersers in my study had minimum daily straight line travel distances similar to or larger than those recorded for resident lynx during the same period. This suggests that once these animals abandoned their home ranges they did not resettle in other areas.

It is interesting to note that all the long distance movements recorded in this study occurred during the rapid decline in snowshoe hare numbers. After hare densities had stablized at a low level, (below about 1.0 hares/ha.) lynx expanded their home range dramatically, or became nomadic but remained within the general study area. Whether this represents a change in the response of lynx to different environmental conditions, or is merely a chance occurrence due to small sample size is not clear. It might be that the long distance movements exhibited by these lynx were a response to rapidly changing and unfamilar conditions. These lynx may have been seeking conditions similar to those they had experienced in the past. Once prey abundance became stable again at a lower level and the lynx acclimated to this new level of resource abundance they may have been less inclined towards such dramatic movements.

Man was the single most important mortality factor for lynx in this study. Professional trapping was responsible for 7 of 8 of observed deaths. Only 2 of 9 radio-tagged individuals that were known to travel outside Kluane Game Sanctuary were not trapped; most were trapped within 2.5 months of the beginning of trapping season. One of the 2 animals that were not trapped (Rene) died of natural causes and presumably starved.

Other studies have also reported high human-related mortality rates in lynx populations. Parker et al. (1983) found 65% of a local lynx population was trapped in the first open season after a one year closure. Mech (1980) reported that 3 of 5 lynx radio-tagged in 1972 were killed by humans within five months and a fourth was killed within a year. In total, 7 of his 14 lynx were killed by humans. Carbyn and Patriquin (1983) report that all three lynx they radio-tagged in Riding Mountain National Park were trapped and killed outside the park. Two were trapped within 4 months of radio-tagging and one was trapped two years and three months later. Nellis et al. (1972) reported 3 of 9 adult lynx tagged between August 1964 and February 1965 were trapped within one year of tagging. The fate of the remaining 6 is unknown. Of eight lynx tagged between August 1965 and February 1968, 1 was dead within 1 year and 3 were recaptured after at least 1 year. Koehler et al. (1979) believed that one of two lynx he had radio-tagged was predated by a mountain lion. The fate of his second animal is apparently unknown. Brand and Keith (1979) estimated annual trapping mortality rates of 10% during the early increase phase of the hare cycle and 17-29% during the early decline phase. Non-trapping mortality rates for adults were estimated at 7 to 38% during early decline phase. Their estimates contain several assumptions that makes them suspect, including an assumption that all non-trapping mortality occurs before the start of trapping season (i.e. from May to November). It would be surprising if natural mortality were highest during the most benign time of year. Further, his estimates of trapping mortality are low and his non-trapping mortality rates are high compared to data from the above tagging studies. Combining the results of this study with those previous studies (excluding the estimates of Brand and Keith 1979), man is the single most important mortality factor in lynx populations. The deaths of 55% of all lynx tagged in these studies were human-related. Of those animals for which the cause of death is known, man is responsible for 95% of the mortality. In contrast, natural mortality in this and the above studies was responsible for an annual loss of only 5.6% of tagged lynx.

The behavioral responses of lynx to declining snowshoe hare abundance should increase lynx vulnerability to trapping. A combination of increased home range size and daily travel distances with declining prey abundance should bring the lynx into contact with more traps. When prey are scarce, lynx might be more easily attracted to trap baits, thus increasing trapping success. Finally, because lynx aggregate in areas of relatively high snowshoe hare abundance, it would be possible for a trapper to trap a relatively large proportion of the lynx population in an area by concentrating his efforts in areas of relatively high hare abundance. If these factors are important, they should have most effect when recruitment into the lynx population is lowest. This may result in lynx populations being especially sensitive to over- harvesting during the decline and low in snowshoe hare abundance.

Lynx Social Structure

The social structure of any mammalian species is a function of the environment in which it lives (Fisler 1969). In this section, I will discuss the social organization observed in lynx populations and the environmental factors that have selected for it.

Lynx, like most felids are solitary animals. Although lynx were occasionally near each other in this study, the only signs of extended sociality involved females and their young of the year.

The degree of sociality observed in populations of carnivores is generally considered to be a function of preferred prey size and hunting strategy. Bouliere (1963) noted that solitary carnivores typically prey on animals smaller than themselves while social carnivores often select larger prey. Kruuk (1972, 1975) developed this observation to suggest that sociality in carnivores is an adaptation for capturing relatively large prey, and this has been used to explain sociality in lions (Schaller 1972, Kruuk 1972, Bertram 1978,1979, Gittleman 1983, Macdonald 1983). Kruuk's test of this hypothesis for felids, however, was inconclusive. Packer (in press) suggests instead that sociality in lions results from a combination of three factors: 1) preference for large prey, 2) the openess of the habitat in which they live and 3) the high population densities which they attain.

Lynx inhabit dense boreal forests and consume primarily snowshoe hares which weigh only 10-15% of the adult body weight of a lynx. The relatively small size of lynx prey and life in dense boreal forest would therefore not favor sociality in lynx. Further, Kleiman and Eisenberg (1973) suggest that hunting by stealth, the primary hunting strategy of lynx, demands a solitary life style. In areas of high prey abundance, however, lynx can reach population densities equal to those of lions.

It is interesting to note, however, that hunting success for lynx increases with group size. Parker et al. (1983) found that hunting success rates (percent of chases that are successful) for family units of one, two, three and four were 14, 17, 38 and 58 percent respectively. There may therefore be little disadvantage to group living in lynx during periods of high snowshoe hare abundance. Further, group living might benefit lynx when snowshoe abundance is low by enabling them to capture larger prey items, such as caribou, Dall sheep and perhaps moose calves. Why lynx are not social may be related to Packer's second point. Lynx live in dense cover while lions are typically open country animals and it may not be possible to coordinate group hunts for large prey in dense cover where visibility is low. Wolves hunt cooperatively in closed forest habitat but use vocalizations to coordinate their efforts (Peterson 1977). Lynx do not vocalize.

Based on the high degree of home range overlap, lynx in this study were not territorial. As discussed by Davies (1978), if a limiting resource is stable and predictable in time and space then it is to the advantage of the predator to to defend exclusive use areas (territories). If the resource is not stable and predictable in time and space, however, there is no benefit to defending a territory in which the resource is likely to disappear.

Territoriality within sexes, have been described for several felid species. Female tigers (Sunquist 1981), bobcats (Bailey 1974), leopards (Bertrum 1982), and European wildcats (Corbett 1979: cited in Packer in press) have been reported to have exclusive home ranges. Food is generally considered to be the defended resource in these systems. Coalitions of male cheetahs (Frame 1980) and lions (Schaller 1972) are also been reported to defend territories against other coalitions of males. Females are generally considered to be the resource being defended by these male coalitions. Home range overlap between sexes is common in felids. Male-female home range overlap has been reported for tigers (Sunquist 1981), jaguars (Schaller and Crawshaw 1980), cougars (Seidensticker et al. 1973), European wildcats (Corbett 1979), and bobcats (Bailey 1974).

Snowshoe hare numbers, the limiting resource for lynx populations, are unstable in both time and space and are likely unpredictable to the lynx. Areas which may have high hare densities at the cyclic peak may be virtually empty within months of the start of the decline. Under these conditions it would be maladaptive for a lynx to expend energy maintaining a territory.

In summary, snowshoe hare abundance and distribution seem to be the proximate structuring forces controlling lynx abundance and distribution. Absolute abundance of lynx is a function of snowshoe hare abundance. Cycles in lynx abundance lag behind those of hares by one to two years (Elton and Nicholson 1942, Brand et al. 1976, Parker et al. 1983). Lynx distribution in space is dependent on snowshoe hare distribution. Lynx concentrate in areas of relatively high hare abundance (Saunders 1963a, Bergerud 1971, Berrie 1974, Koehler et al. 1979 and this study) and disperse after these areas of relative abundance have been depleted (this study).

MANAGEMENT IMPLICATIONS

Introduction

Effective management of wildlife populations exhibiting marked fluctuations in recruitment rates require management plans that vary harvest rate directly with changes in recruitment rate. Failure to reduce the harvest rate during periods of low recruitment can inhibit the populations ability to increase when conditions again become favourable (Caughley 1977).

Recruitment of lynx into the population fluctuates from near zero during periods of low snowshoe hare abundance to 3 to 4 young per female per year during periods of high hare abundance. Management strategies currently being used for lynx, however, do not take into account fluctuations in recruitment rate. Lynx populations are therefore especially susceptible to over-harvesting. In addition, evidence from this and past tagging studies, suggests that man is responsible for an annual loss of over 55% of lynx populations. Other factors cause the loss of 5.6% of lynx populations each year. During periods of decline and scarcity in snowshoe hare abundance both trapping and natural mortality rates can be expected to be higher than these figures. During 2 years of declining hare abundance, I found annual mortality rates of 100 and 75 percent of my tagged lynx which were known to leave Kluane Game Sanctuary.

I therefore produced 2 simulation models to assess the effect of the observed harvest rates on lynx population dynamics through their ten year cycle.

The Models

I developed the models using population parameters (Table 6) from my work and that of Brand and Keith (1979). In both models I subdivided the snowshoe hare cycle into 3 years of high hare abundance, 2 years of intermediate hare abundance during increase and decline phases and 3 years of low hare abundance at the bottom of the cycle. I assumed a 1:1 sex ratio in the lynx population. I set the initial spring lynx age distribution at 7% yearlings and 93% adults, similar to the age distribution found by Brand and Keith (1979) after 3 years of low hare abundance and just prior to the start of the increse phase of the hare cycle. Estimates of <u>in utero</u> litter size and pregnancy rates for yearling and adult females at low, intermediate and high hare abundance were taken from Table 5 of Brand and Keith (1979). I allowed kittens 100% survival from birth to the start of the trapping season (May to November) during periods of high hare abundance. Estimates of kitten survival during periods of intermediate and low hare abundance were taken from Brand and Keith (1979) and set at 35 and 8 % respectively.

In model A (see appendix 1a for details of the model), annual kitten production by yearling and adult females was calculated by the equation:

$$NK = (NY * .5 * RY) + (NA * .5 * RA)$$

Table 6. Parameter estimates used in lynx population simulation models. Adult and yearling mortality rates are per year. Kitten summer mortality rates are birth to November. Post November kitten mortality rates were assumed equal to adult mortality rates. Lynx pregnancy rates, litter sizes, kitten mortality rates and adult mortality rates for model B are from Brand and Keith (1979). I assume lynx have a maximum of 1 litter per year. See text for derivation of adult mortalty rates for model A.

PARAMETER	SNOWSHOE HARE ABUNDANCE		
	LOW	INTERMEDIATE	HIGH
Adult lynx pregnancy rate	0.33	0.46	0.73
Yearling lynx pregnancy rate	0.0	0.0	0.4
Adult lynx in utero litter size	3.4	3.9	4.6
Yearling lynx in utero litter size	---	---	3.9
Lynx kitten summer mortality rate	0.92	0.65	0.0
Trapping mortality rate (model A)	0.55	0.55	0.55
Natural mortality rate (model A)	0.06	0.06	0.06
Trapping mortality rate (model B)	0.14	0.14	0.14
Natural mortality rate (model B)	0.35	0.35	0.35

where

* = multiplied by

NK = number of kittens in the fall;

NY = number of yearlings in the spring population;

RY = pregnancy rate * *in utero* litter size for yearling females * summer survival rate for kittens;

NA = number of adults in the spring population;

RA = pregnancy rate * *in utero* litter size for adult females * summer survival rate for kittens

I assumed that November to May mortality rates were equal for all age classes and that all yearling and adult mortality occurred in this period. I assumed no density dependence in mortality rates. I set annual trapping and non-trapping mortality rates at 55% and 6% respectively (see previous section on lynx mortality for derivation of these values). Post trapping season (May) adult lynx population numbers were calculated by the equation:

$$NAS = (NAF + NYF) * S$$

where

* = multiplied by

NAS = number of adults in May

NAF = number of adults in November

NYF = number of yearlings in November

S = survival rate November to May

May yearling population numbers was calculated by the equation:

NYS = NKF * S

where

NYS = number of yearlings in spring;
NKF = number of kittens in fall;

Brand and Keith (1979) also modelled the dynamics of a lynx population through a decline to the following peak. Model A contained several qualitative and quantitative differences from their model. To determine if these differences would have an effect on the dynamics of the modelled population, I modified model A to reflect the assumptions and parameter estimates of Brand and Keith (1979)(Table 6)(see appendix 1b for details of model B).

Calculation of kitten recruitment into the lynx population was the same in models A and B. As in model A, Brand and Keith (1979) assumed that trapping and non-trapping mortality were additive and that trapping mortality was similar in all age classes. Brand and Keith (1979), however, assumed that all non-trapping mortality occurred from May to November. Brand and Keith (1979) estimated total annual mortality at 44%, similar to the value used in my first model. They estimated annual natural mortality losses at 35% of the spring lynx population and trapping mortality at 14% of the fall population. Model B therefore calculates independent estimates for spring and fall yearling and adult numbers using their estimates of trapping and non-trapping mortality rates.

Results and Discussion

I ran both models through 5 complete cycles (50 years) starting with 2 years of increase phase hare abundance. The lynx population in model A was virtually extinct at the end of one full cycle of 10 years (Fig. 12). Even during periods of high hare abundance mortality exceeded recruitment into the lynx population. In fact the lynx population declined to virtual extinction when total annual mortality rates (trapping + natural) were 0.30 or larger (Fig. 13). All past tagging studies for which I could determine annual mortality rates (this study, Parker et al. 1983, Mech 1980, Carbyn and Patriquin 1983, Nellis et al. 1972, Koehler et al. 1979) have reported rates in excess of 0.30.

The lynx population in model B also declined to virtual extinction, although at a slower rate than in model A (Fig 14). It is interesting to note that in Brand and Keith (1979)'s simulation from the start of the cyclic decline in lynx abundance to the following peak in abundance, 8 years later, the modelled lynx population showed a decline in numbers of approximately 0.4%. This suggests that, allowed to run through a number of cycles their population may also have continued to decline.

Figure 12. Dynamics of simulated lynx population using model A and observed mortality rates. See Table 6 and Appendix 1a for parameter estimates and simulation model program.

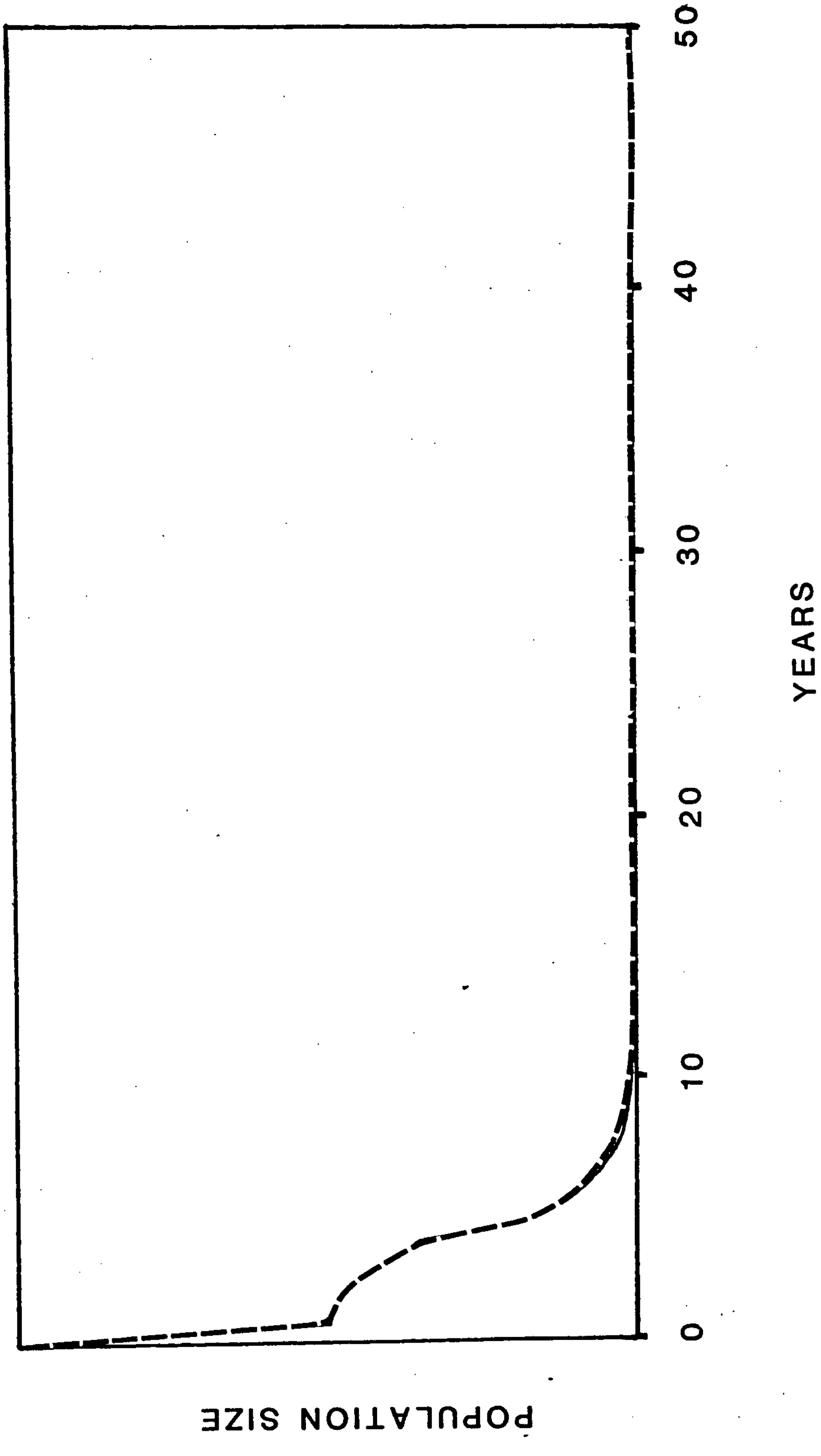

0
10
20
30
40
50
YEARS
POPULATION SIZE

Figure 13. Dynamics of simulated lynx population using model A with total annual mortality rate set at 0.30. See Table 6 and Appendix 1a for parameter estimates and simulation model program.

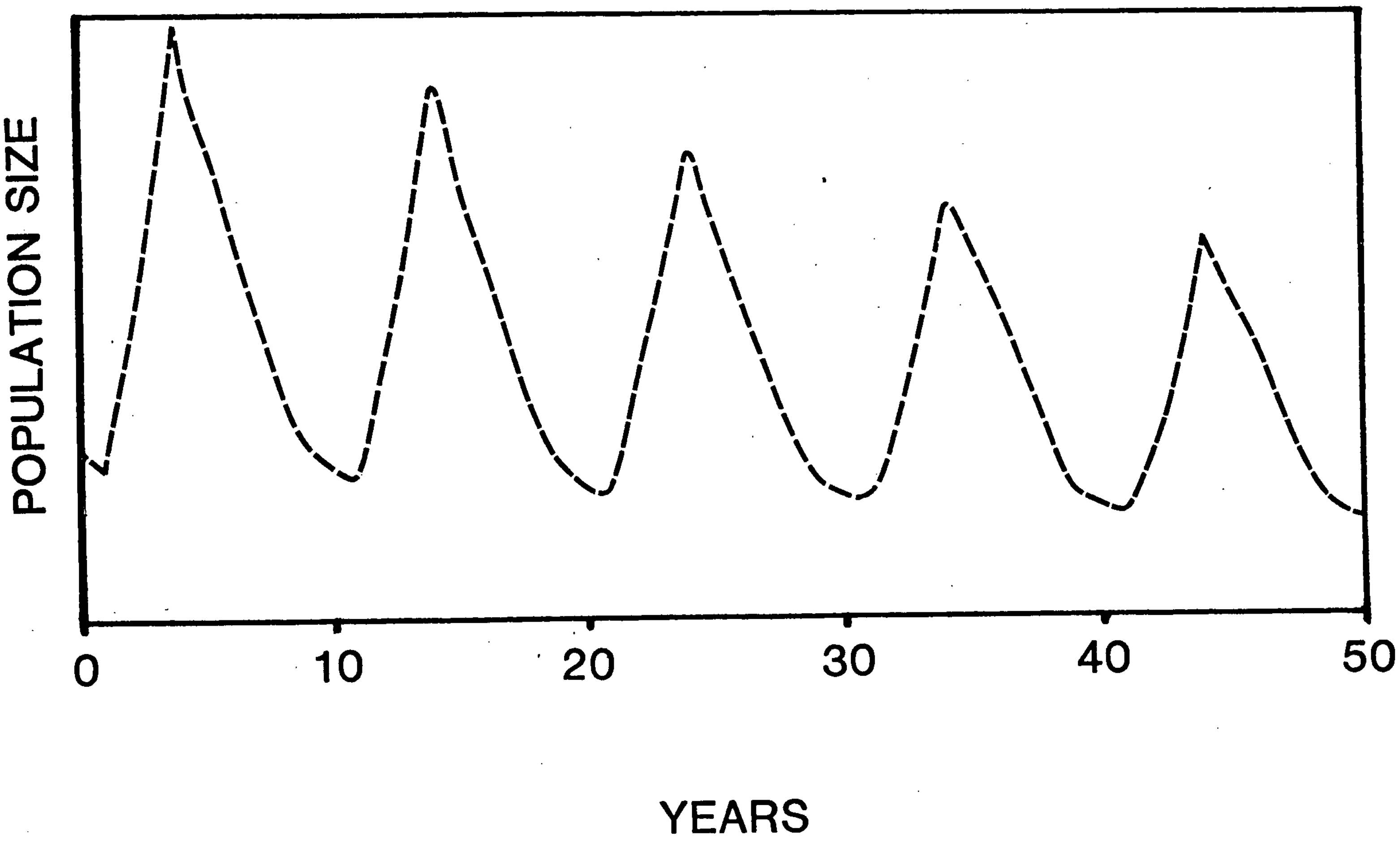
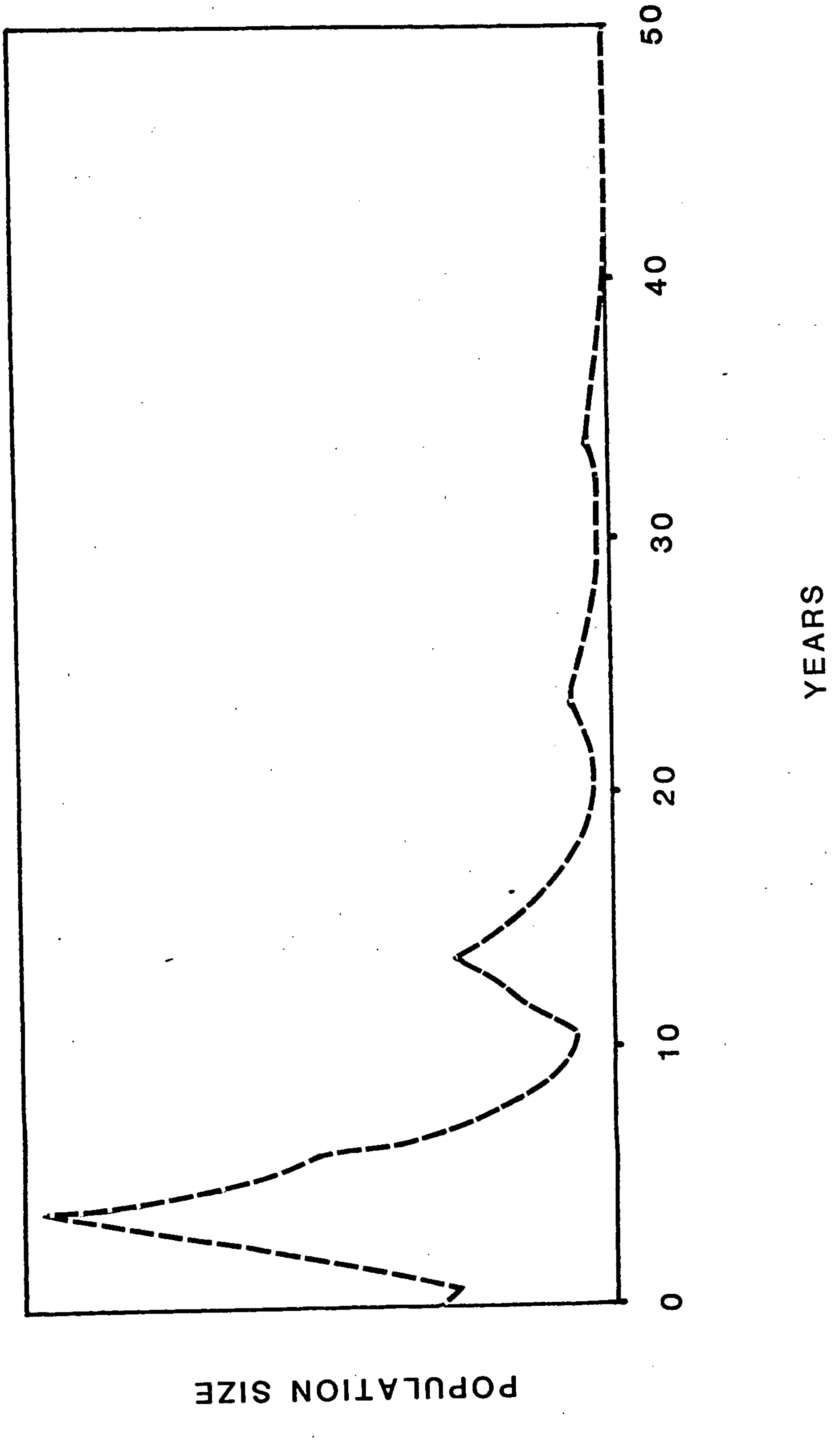

POPULATION SIZE
0
10
20
30
40
50
YEARS

Figure 14. Dynamics of simulated lynx population using model B and mortality rate estimates from Brand and Keith (1979). See Table 6 and Appendix 1b for parameter estimates and simulation model program.


POPULATION SIZE
YEARS
0
10
20
30
40
50

Lynx populations in nature certainly do not decline at the rate indicated by these simulations. The surprisingly rapid decline in simulated populations must result from estimates of lynx recruitment that are too low, or estimates of mortality rates that are too high. My estimates of recruitment into the lynx population are based on pregnancy rates, and on in utero litter sizes found by Brand and Keith (1979) in carcasses collected from trappers. They therefore seem to be well founded. It is therefore likely that both my and Brand and Keith (1979)'s estimates of mortality rates are too high. Two components of mortality are included in my models: 1) kitten mortality from birth to the start of their first trapping season (May to November) and 2) trapping and non-trapping mortality following initial kitten mortality.

I assumed no kitten mortality at high hare abundance, clearly erring in favor of higher recruitment than could actually be occurring in nature. Estimates of kitten mortality rates at intermediate and low hare abundances were derived from Brand and Keith (1979) and set at 65 and 92% respectively. Kitten mortality rates may be lower at intermediate and low hare abundance than those estimated. Evidence from this and other studies do, however, suggest extremely low kitten survival during periods of low hare abundance. Both Brand and Keith (1979) and I, saw no evidence of kittens on our study areas during periods of low hare abundance. Brand and Keith (1979) also found less than 3 percent kittens in carcass collections during periods of low hare abundance. During periods of high hare abundance, kittens comprised 18 to 30 percent of trapped samples. In any event, even with 100% kitten survival at intermediate and low hare abundance, lynx populations should continue to decline under the observed mortality rates.

Adult mortality rates in model A were derived from this and past lynx tagging studies. These estimates may be too high for two reasons. First, these estimates are based on a total of 36 tagged lynx. The high mortaliy rates observed might therefore be due to random chance within the small sample. The fact that the 6 studies from which these 36 animals were drawn all had mortality rates in excess of 0.30, the maximum annual mortality rate that recruitment into the population could sustain, suggests that low sample size is not the complete answer.

Alternatively, the mortality rates observed in these studies may be representative of mortality rates in areas similar to those in which the studies took place. For reasons of logistic ease, field studies on lynx, as with other mammals, are most often undertaken in areas of relatively high accessibility. These are also the areas where trapping pressure is likely to be most intense. Trapping mortality rates in remote areas where access is limited may be far lower. Average trapping mortality rates over large areas would therefore be considerably less than those noted in areas of high accessiblity. If this is the case, remote areas may be extremely important in maintaining lynx populations during the declines and lows in hare abundance. The importance of remote areas in maintaining lynx populations through periods of low recruitment was first suggested by Berrie (1974). With continually increasing access into these remote areas, lynx populations may be subjected to uniformly high human mortality rates throughout large parts of their range resulting in unsustainable harvest rates. The importance of remote areas in maintaining lynx populations clearly needs more research.

Concern for the continued existance of lynx populations under intensive trapping pressure has been expressed by several researchers (Parker et al. 1983, Todd 1983, Carbyn and Patriquin 1983, Brand and Keith 1979 and Berrie 1974). Caughley (1977) suggested that a "tracking strategy", where harvest rates vary directly with recruitment into the harvestable population, was the only workable strategy for populations with dynamics similar to those of lynx. Researchers were in fact recommending a tracking strategy for the harvesting of lynx populations years prior to the publication of Caughley's (1977) book. Berrie (1974), in an insightful discussion of the future of lynx populations in Alaska, recommended that no lynx trapping be allowed for as much as 3 years during the cyclic low in hare abundance. He suggested that with improved access to wilderness areas and continued trapping throughout the cyclic low would result in a decreased cyclic amplitude by reducing the number of individuals available to breed when conditions improved. Brand and Keith (1979) reiterated this recommendation with the help of 2 simulation models of trapped and untrapped lynx populations. Their models indicated a 28% increase in the total harvestable lynx population through one complete cycle if trapping were curtailed during the three years of lynx population decline and low. Parker et al. (1983) noted that the lynx harvest in Nova Scotia was curtailed during a period of snowshoe hare scarcity and low recruitment into the lynx population. He recommended that a system of harvest curtailment be continued during future periods of snowshoe hare scarcity and low recruitment into lynx populations. Todd (1983) also presented a case for curtailment of lynx trapping in Alberta for 3 to 4 years during the cyclic decline and low in lynx population numbers.

The underlying assumption in Caughley's tracking strategy, and the harvest plans recommended for lynx by previous researchers, is that trapping mortality is largely additive to non-trapping mortality. That is, lynx that are trapped would otherwise survive through the the low in hare abundance to reproduce when conditions improved. Alternatively, trapping mortality may be compensatory for non-trapping mortality during periods of low prey abundance. Individuals which are trapped during periods of low prey availability would die of natural causes anyway before conditions improved. Trapping mortality, or some proportion of it, would therefore have no effect on the number of individuals surviving to breed when conditions improved.

In our simulations of the dynamics of lynx populations, both Brand and Keith (1979) and I assumed trapping and non-trapping mortality were additive . Brand and Keith (1979) supported this assumption with the observation that lynx resident on their study area at the end of one trapping season but were not present the following winter. They concluded that the lynx must have died during the summer and their mortality was therefore additive to trapping mortality. They extrapolate to assume that all non-trapping mortality occurs outside the trapping season.

It would be surprising if all non-trapping mortality occurred during the most benign time of year from May to November. In my study, 42% of radio-tagged lynx dispersed during the period of rapid decline in hare abundance and all dispersal occurred during the snow-free period. It is possible then, that the lynx in Brand and Keith's (1979) study dispersed from the area rather than died. Also, the death of one of my lynx, presumably to starvation, during the low in hare abundance suggests that not all lynx would survive the cyclic low in hare abundance even without trapping.

Brand and Keith (1979)'s model suggested that with natural mortality up to 50% compensatory for trapping mortality, a net gain in harvestable lynx through a complete cycle would be achieved by curtailing trapping during the 3 years of low lynx recruitment. Trapping mortality may be more than 50% compensatory for non-trapping mortality during periods of low hare abundance. If this is the case, continuing to harvest lynx through the low in hare abundance would have little or no affect on the recovery of lynx populations when hare abundance increased.

Therefore, although I applaud the efforts of Brand and Keith (1979) and others who have attempted to develop sound management schemes for lynx, it would be premature to impliment these plans without further testing. The effectiveness of any plan can only be determined if it is conducted within the confines of a sound experimental design. This would entail setting up replicate study areas. One study area would be trapped continuously, as under current management schemes for lynx, and in the second area trapping would be curtailed during the period of low lynx recruitment as suggested in Brand and Keith (1979)'s management plan. By monitoring lynx recruitment rates, trapping and non-trapping mortality rates and total lynx harvest in the 2 areas the effectiveness of "tracking strategy" could be assessed. This type of experiment is essential in assessing the effectiveness of any new management strategy (Romesburg 1981, Walters and Hilborn 1976).

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APPENDIX

Appendix 1a. Program for simulation model A. Program is written in BASIC for APPLE IIc microcomputer and compiled with micro simcon population simulation package (Walters 1982). See Table 6 for parameter estimate and their derivation.

```
100  IF TI > 0 THEN 200
105 T = .55:N = .06: REM  T=TRAPP
     ING MORTALITY RATE AND N= NA
     TURAL MORTALITY RATE
110 NY = 7:NA = 93: REM  NY= NUMB
     ER OF YEARLINGS IN INITIAL P
     OPULATION AND NA = NUMBER OF
      ADULTS IN INITIAL POPULATIO
     N
120 A = 0
200  IF A <  = 1 THEN 207
201  IF A > 1 AND A <  = 4 THEN 2
     06
202  IF A > 4 AND A <  = 6 THEN 2
     07
204  IF A > 6 AND A <  = 9 THEN 2
     08
205 : REM  IN LINES 206 TO 208 RY
     =AVERAGE NUMBER OF KITTENS P
     RODUCED PER YEARLING FEMALE
     PER YEAR; RA = AVERAGE NUMBE
     R OF KITTENS PRODUCED PER AD
     ULT FEMALE PER YEAR
206 RY = 1.6:RA = 3.4: GOTO 210
207 RY = 0:RA = .6: GOTO 210
208 RY = 0:RA = .1
210 NK = NY * .5 * RY + NA * .5 *
     RA: REM  NK=YEARS PRODUCTION
      OF KITTENS
220 NA = NY + NA - (NY + NA) * (T
      + N)
230 NY = NK - NK * (T + N)
240 NT = NY + NA: REM  NT= TOTAL
     PRE-BREEDING SEASON POPULATI
     ON
241  IF A <  = 9 THEN A = A + 1
242  IF A > 9 THEN A = 0
250 Z(1,TI) = NT
251 Z(2,TI) = NA
252 Z(3,TI) = NY
253 Z(4,TI) = NK
```

Appendix 1b. Program for simulation model B. Program is written in BASIC for APPLE IIc microcomputer and compiled with micro simcon population simulation package (Walters 1982). See Table 6 for parameter estimate and their derivation.

```
100  IF TI > 0 THEN 200
105 T = 0.14:N = 0.35: REM  T= TR
     APPING MORTALITY RATE AND N=
     NATURAL MORTALITY RATE
110 NY = 7:NA = 93: REM  NY=NUMBE
     R OF YEARLINGS IN INITIAL PO
     PULATION AND NA=NUMBER OF AD
     ULTS IN INITIAL POPULATION
120 A = 0
200  IF A <  = 1 THEN 207
201  IF A > 1 AND A <  = 4 THEN 2
     06
202  IF A > 4 AND A <  = 6 THEN 2
     07
204  IF A > 6 AND A <  = 9 THEN 2
     08
205 : REM  IN LINES 206 TO 208 RY
     =AVERAGE NUMBER OF KITTENS P
     RODUCED PER YEAR PER YEARLIN
     G FEMALE AND RA= AVERAGE NUM
     BER OF KITTENS PRODUCED PER
     ADULT FEMALE PER YEAR
206 RY = 1.6:RA = 3.4: GOTO 210
207 RY = 0:RA = .6: GOTO 210
208 RY = 0:RA = .1
210 NK = NY * .5 * RY + NA * .5 *
     RA: REM  NK= YEARS PRODUCTIO
     N OF YOUNG
215 NA = NA - (NA * N): REM  CALC
     ULATION OF ADULT POPULATION
     PRIOR TO TRAPPING SEASON
217 NY = NY - (NY * N): REM  CALC
     ULATION OF YEARLING POPULATI
     ON PRIOR TO TRAPPING SEASON
220 NA = NA + NY - (NA + NY) * T:
      REM  CALCULATION OF POST TR
     APPING SEASON ADULT POPLUATI
     ON
230 NY = NK - NK * (T): REM  CALC
     ULATION OF POST TRAPPING SEA
     SON YEARLING POPULATION
240 NT = NY + NA: REM  CALCULATIO
     N OF TOTAL POPULATION SIZE I
     N SPRING
241  IF A <  = 9 THEN A = A + 1
242  IF A > 9 THEN A = 0
250 Z(1,TI) = NT
251 Z(2,TI) = NA
252 Z(3,TI) = NY
253 Z(4,TI) = NK
```