Behavioural responses of lynx to declining snowshoe hare abundance

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The behavioural 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 in and near the Kluane Game Sanctuary. Lynx home range size increased from 13.2 to 39.2 km² 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. Lynx concentrated their foraging efforts in areas of relatively high snowshoe hare abundance and abandoned these areas after hares declined. Straight-line daily travel distance remained constant at 2.2–2.7 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 seven radio-tagged lynx dispersed 250 km or more from the study area during the 1982 period of rapid hare decline. No similar long-distance emigrations were recorded after hare densities stabilized at less than 1.0 hares/ha. Trapping mortality was responsible for the loss of seven of nine radio-tagged lynx that travelled outside the game sanctuary. One lynx probably 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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Le comportement du lynx (*Lynx canadensis*) a été étudié à la suite du déclin de la population de lièvres (*Lepus americanus*) dans le sud-ouest du Yukon. D'avril 1982 à juin 1984, 11 lynx ont été munis d'un émetteur-radio et leurs mouvements ont été suivis dans le refuge Kluane Game Sanctuary et aux alentours. L'aire vitale du lynx est passée de 13,2 à 39,2 km² à la suite de la diminution de la densité des lièvres de 14,7 à 0,2/ha. À une densité de moins de 0,5 lièvres/ha, plusieurs lynx ont abandonné leur aire vitale et sont devenus nomades, tout en restant à l'intérieur de la région d'étude. Les lynx concentraient leurs efforts de recherche de nourriture dans les régions où l'abondance des lièvres était relativement élevée et ils abandonnaient ces régions après le déclin de la population de lièvres. La distance parcourue en ligne droite chaque jour est demeurée constante, de 2,2 à 2,7 km/jour lorsque la densité des lièvres était supérieure à 1,0/ha. Sous cette valeur, les distances parcourues en ligne droite chaque jour ont augmenté rapidement, jusqu'à 5,5 km/jour à 0,2 lièvres/ha. Trois des sept lynx marqués se sont éloignés de plus de 250 km de la région d'étude au cours de la période de déclin rapide des lièvres en 1982. De telles émigrations sur une aussi longue distance n'ont plus été observées lorsque la densité des lièvres s'est stabilisée à moins de 1,0 lièvre/ha. Des pièges sont responsables de la perte de sept des neuf lynx porteurs d'émetteurs qui se sont aventurés hors du refuge. Un lynx est probablement mort d'inanition au cours de l'hiver ou du printemps 1984. Le taux élevé de mortalité par piégeage en dehors du refuge souligne l'importance de tels refuges au sein des endroits sauvages pour assurer la survie des populations de lynx au cours des périodes de faible recrutement.

[Traduit par le journal]

Introduction

The close relationship between the 10-year cycle of lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) was noted by Elton and Nicholson (1942). Since then, many aspects of lynx natural history and ecology have been studied (for review, see Parker et al. 1983). Several studies have shown an increase in mortality and a decline in recruitment of lynx with declining snowshoe hare abundance (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). General body condition of lynx has also been shown to be positively correlated with hare abundance.

Except for Nellis et al. (1972), these studies and others have been unanimous in finding that snowshoe hares are the single most important food in the lynx diet during all phases of the 10-year cycle. The fact that lynx recruitment declines and mortality rates increase with declining hare abundance indicates that lynx are energy stressed during the decline and low phases of the hare cycle. One would therefore expect that lynx would exhibit behavioural changes in an effort to continue to fulfill their energetic requirements as hare abundance declines. The mechanisms lynx might use are (*i*) increase their home range size, (*ii*) increase their foraging effort, (*iii*) seek out and con-

centrate their foraging effort in patches of relatively high prey abundance, and (*iv*) switch to other prey.

In this study, we investigated the degree to which lynx utilize each of these possible mechanisms to maximize their energy intake. We present data on lynx dispersal and mortality during a snowshoe hare decline.

This study was centered in the southwestern Yukon, Canada, north of Kluane National Park within and adjacent to Yukon game management zone 6-10 (Fig. 1), a game sanctuary. The area is part of the northern boreal forest zone (Douglas 1974). White spruce (*Picea glauca*) is the dominant tree species and the most abundant shrubs are *Salix glauca*, *Betula glandulosa*, and *Shepherdia canadensis*.

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

Methods

We conducted the study between February 1982 and June 1984. Snowshoe hare abundance was monitored on four live-trapping grids in the study area as part of a concurrent study of their 10-year cycle. Each hare grid was 9 ha and we used 50–80 double-door live traps
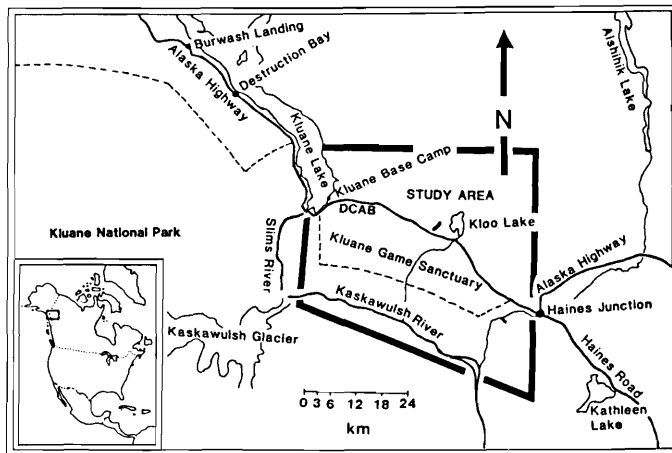
FIG. 1. Map of study area in southwestern Yukon. A, B, C, and D indicate locations of snowshoe hare live-trapping grids.

to catch hares. Grid A (microwave) was a food-addition grid to determine the effect of supplemental rabbit chow on hare abundance. Grids B (beaver pond), C (grizzly), and D (1050) were controls for grid A (Fig. 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 boundary strip (MNA/area of grid).

Trapping to capture and radio tag lynx continued from February through December 1982 and from April to September 1983. Steel leg-hold traps, ranging in size from No. 2 to No. 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 h. A variety of baits ranging from commercial lures to perfume and silver ribbons were used.

Trapped lynx were immobilized with ketaset (concentration, 100 mg/mL; Rogar/STB, division of BTI Products Inc., London, Ont.) at a dosage of approximately 0.2 mL/kg of body weight. The lynx was then weighed, sexed, ear-tagged, and fitted with a radio transmitter prior to release.

Radiotelemetry equipment was produced by Wildlife Materials Inc., Carbondale, IL. Lynx were located using standard radiotelemetry techniques (Cochran 1980) with a combination of hand-held and fixed tower antennas. Accuracy checks on transmitters in known locations indicated that compass bearings using this system were accurate to $\pm 5°$ 95% of the time. Compass bearings were less accurate if the radio-tagged animal was active when the bearing was being taken. If a lynx disappeared from the study area, an effort was made to locate it using radiotelemetry from an aircraft. Radio-collared lynx were located at various times throughout the day and night from April to December 1982, May to 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.

We defined home range as the consistent use of an area over a 3-month period. We therefore subdivided the study into the following 3-month periods for subsequent analysis: April–June 1982, July–September 1982, October–December 1982, April–June 1983, July–September 1983, and April–June 1984.

We 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). We 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.

To determine the effects of relative snowshoe hare abundance on patterns of habitat use by lynx, winter snow track transects were run
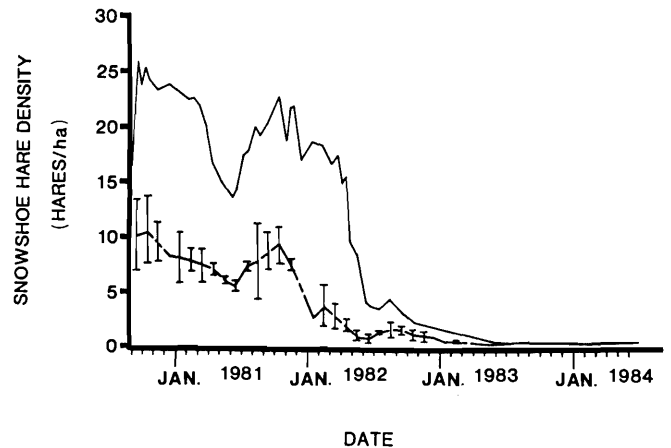

FIG. 2. Snowshoe hare density on supplemental food grid A (—) and control grids B, C, and D (---). Densities are based on total enumeration techniques (Krebs 1966). Vertical bars on dashed line indicate ± 1 SD.

through areas known to have different hare densities. The number of sets of fresh lynx tracks crossing every 600 m of transect was recorded. Counts were conducted each morning when weather and snow conditions permitted throughout April and from late October to early December 1982.

Results

Snowshoe hare abundance

Snowshoe hare abundance on all grids peaked in 1980 and 1981. Maximum fall hare densities in 1981 on grid A were 22.6 hares/ha, while on grids B, C, and D they were 10.3, 8.0, and 10.7 (mean, 9.7) hares/ha, respectively (Fig. 2). Densities began to decline rapidly on grids B, C, and D during the winter of 1981–1982 while remaining relatively high on grid A throughout the winter and into the spring of 1982. In April 1982, when we began monitoring lynx activities, hare abundance on grids B, C, and D was 2.6, 2.4, and 1.4 (mean, 2.1) hares/ha, respectively, while on grid A the hare density was 14.7 hares/ha. By July, hare density had dropped to approximately 1.0 hares/ha on the control grids and to 3.3 on the supplemental food grid. Population densities stabilized or increased slightly on all grids during sunmmer as young were born. During October 1982, however, hare densities began to decline again on all grids. Spring densities in 1983 were equal on all grids at 0.2 hares/ha. By July 1983, densities on all grids had more than doubled, averaging 0.5 hares/ha. Hare densities remained relatively constant at between 0.2 and 0.5 hares/ha on all grids through June 1984.

Lynx trapping success

Eleven lynx (five female and six male) were trapped and radio tagged in approximately 4700 trap nights between April 1982 and September 1983 (Table 1). In addition, one female (No. 307) was recaptured and released approximately 9 months after her initial capture.

Approximate ages of lynx were determined by body size and by the condition of the nipples and genitalia. These age estimates are given in Table 1.

Although it is difficult to assess what proportion of the population we had radio tagged, an estimate can be obtained, for the winters at least, from repeated track transects through the area. We believe that we had radio tagged four of five lynx using grid A in April and May 1982. We expanded the study area

TABLE 1. Summary of lynx trapping success, minimum residency time on study area, and fate of radio-tagged lynx

Lynx No.	Capture date[a]	Age	Sex	Minimum residency on study area	Fate[a]
301	4/4/1982	Adult, ≥2 years	♀	35 days	Dispersed 8/5/1982; killed 700 km north of tagging site, December 1982
302	17/4/1982	Adult, ≥1 year	♂	9 months	Killed within 10 km of tagging site, January 1983
303	21/4/1982	Adult, ≥1 year	♀	7 months	Dispersed 16/10/1982; killed 250 km north of tagging site, December 1982
304	25/5/1982	Adult, ≥1 year	♂	40 days	Dispersed 5/7/1982; killed 250 km north of tagging site, December 1982
305	1/8/1982	Adult, ≥1 year	♂	13 months	Residing in study area, September 1983
306	20/10/1982	Kitten, >1 year	♂	2 months	Killed within 10 km of tagging site, December 1982
307	25/10/1982	Adult, ≥1 year	♀	10 months	Killed within 10 km of tagging site, winter 1983–1984
308	15/7/1983	Adult, ≥1 year	♀	6 months	Found dead 35 km east of tagging site, June 1984
309	19/7/1983	Adult, ≥2 years	♀	11 months	Residing in study area, June 1984
310	29/7/1983	Adult, ≥1 year	♂	11 months	Residing in study area, June 1984
311	1/8/1983	Adult, ≥1 year	♂	4 months	Killed within 10 km of tagging site, January 1984

[a] Dates: day/month/year.

during the summer of 1982 (Fig. 1). By November, we were monitoring five lynx and we suspect that five more 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 sightings were made on the 11 lynx. Minimum residency times for these lynx ranged from 35 days to 13 months.

Snowshoe hare density and lynx home range size

We 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% (Table 2). For comparison with other studies, we present our results as both 100 and 90% home ranges and we use 90% range in our 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, the trend was not consistent or statistically significant (t-test, $P > 0.05$). Therefore, the data were combined for the analysis of the effect of snowshoe hare abundance on lynx home range size.

Hare densities declined rapidly early in the study and more slowly later (Fig. 2). Throughout this decline, lynx home range size increased steadily. Both mean home range size for all individuals at different hare abundances (Fig. 3) and home ranges of individuals monitored through time showed this trend.

Between April and June 1982, the four radio-tagged lynx utilizing grid A (which had a high April hare density of 14.7 hares/ha) had a mean home range size of 13.2 km² (95% confidence interval (CI), 8.8–17.6). These individuals either dispersed or expanded their home ranges as hare density on the grid declined. Lynx residing in areas with hare densities between 1.0 and 4.9 hares/ha had a mean home range size of 25.1 km² (95% CI, 14.5–35.7). When hare densities were less than 1.0 hares/ha, mean lynx home range size was still higher at 39.2 km² (95% CI, 23.7–54.7). This is significantly larger than the mean home range size of lynx residing in areas with hare densities greater than 4.9 hares/ha (t-test, $P < 0.05$).

At densities below about 0.5 hares/ha, there appeared to be a tendency for some lynx to abandon their home ranges and become nomadic. A female (No. 308) that we radio tagged and monitored during summer 1983 travelled extensively in the study area but used no area consistently enough to be identified as her home range. Based on the innermost 90% of our locations for her between July and October 1983, she covered an area of 255 km². In mid-December 1983, she was located alive approximately 35 km east of the initial radio-tagging site. She was found dead in this area in June 1984 and we believe she starved to death during the last half of the winter of 1983–1984.

In addition, two females (Nos. 309 and 310) who had maintained distinct home ranges during the summer 1983, were travelling so widely during May and June 1984 that it was impossible to locate them regularly. Based on seven locations, lynx No. 309 covered a total area of at least 200 km² during this period. Based on 12 locations, lynx No. 310 wandered over a minimum area of 60 km² during the same period.

Ninety percent home ranges of lynx overlapped considerably

TABLE 2. Comparison of 100 and 90% home range areas of lynx

Lynx	Hare density (hares/ha)	100% home range size (km²)	90% home range size (km²)	% difference
301	14.7	12.0 (30)	7.3 (27)	39
302	14.7	33.4 (95)	13.3 (85)	60
	3.3	104.3 (78)	31.0 (70)	70
303	14.7	46.4 (61)	17.7 (54)	62
	1.3	44.9 (63)	43.4 (56)	3
304	14.7	29.7 (54)	14.6 (48)	51
305	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
307	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
306	1.0	55.4 (34)	27.6 (31)	50
309	0.5	61.8 (50)	33.5 (45)	46
	0.2	200.6* (7)		
308	0.5	524.8 (31)	254.7*(28)	51
310	0.5	49.2 (55)	17.8 (49)	64
	0.2	69.6* (12)		
311	0.5	86.7 (61)	53.9 (54)	38

NOTE: Snowshoe hare densities are initial densities at the start of each 3-month period for which individual lynx home ranges were calculated. *, area not defined as a home range because lynx became nomadic. The number of locations used to determine each home range is in parentheses.

within and between sexes throughout the study. Home range overlap averaged 10.5 (95% CI, 0.6−20.5), 24.5 (95% CI, 21.7−27.3), and 22.0 (95% CI, 15.7−28.3) percent for male−male, female−female, and male−female interactions for the whole study, respectively. Male−male overlap was significantly less than male−female overlap (t-test on arc-sine transformed data; P = 0.04), but no significant differences were found between male−male and female−female home range overlaps. Lynx home range overlap remained high throughout the study and was not affected significantly by absolute hare density.

Hare densities and lynx foraging effort

We 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). We 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 (Fig. 4). At 14.7 hares/ha, lynx mean DTD was 2.7 km (95% CI, 1.8−3.7 km). At 1.0 hares/ha, lynx had a mean DTD of 2.4 km (95% CI, 2.0−2.9 km).

Below about 1.0 hares/ha, however, lynx increased their mean DTD rapidly with declining hare density. At hare densities of 0.5 hares/ha, mean DTD was 3.3 km (95% CI, 2.8−3.7 km). As hare density declined to 0.2 hares/ha, mean lynx DTD increased sharply to 5.4 km (95% CI, 3.9−7.0 km).

Hare distribution and lynx foraging patterns

While capturing lynx for radio tagging, we obtained data to show if 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 (Fig. 2). During this period, three lynx (Nos. 301, 302, and 303) were captured in 234 trap nights within a 1 km radius of grid A (Fig. 1). From tracks
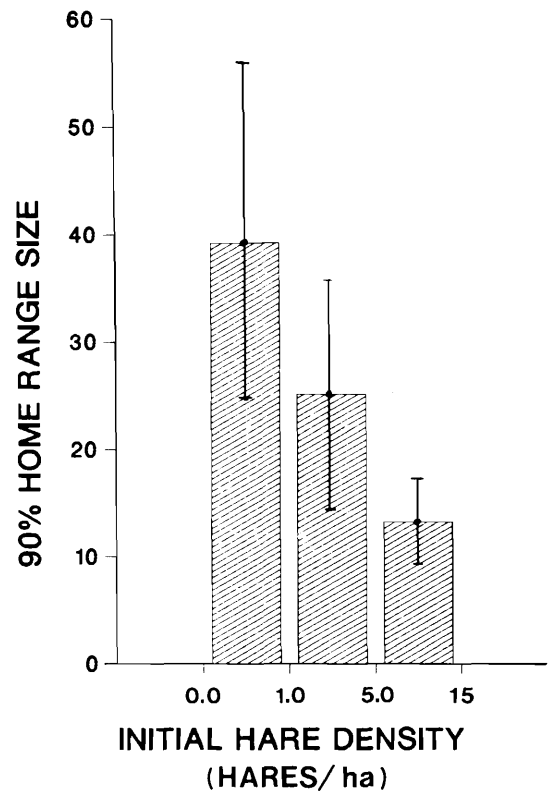

FIG. 3. Mean home range size for lynx residing in areas of varying snowshoe hare densities. Hare density is the initial density at the start of each 3-month period of which home ranges of individual lynx were calculated. Vertical bars indicate 95% confidence limits.

and the capture of another lynx (No. 304) in the same area on May 25, we believe that two other lynx were also using the area at the same time. Subsequent radio tracking of these four lynx indicated a minimum density of one lynx per 7.3 km² around 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 around grid A in October and November resulted in no lynx captures after hares there had declined to approximately 1.8 hares/ha.

Track transects through grids A and B in spring and through grid A during early winter 1982, after hares had declined, also indicated that lynx sought out and concentrated their foraging efforts in areas of relatively high hare abundance (Table 3). In April 1982, lynx used the area of higher hare abundance significantly more (G-test adjusted, P = 0.005).

Lynx abandoned the high-hare areas when they were depleted. As hare density on grid A declined from 14.7 to 2.2 hares/ha, three of the four radio-tagged lynx in the area emigrated. Hare density in the surrounding areas declined 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 lynx trails per 600-m transect declined to 1.2 (95% CI, 0.0−2.3). This is a significant reduction in utlization of the area following the decline in hares (G-test adjusted, P = 0.005).

Lynx emigration and mortality during a decline in snowshoe hares

During this study, only 3 of 11 radio-tagged lynx survived for 1 year or more and remained within the study area. Emigration or human-related mortality were responsible for the loss
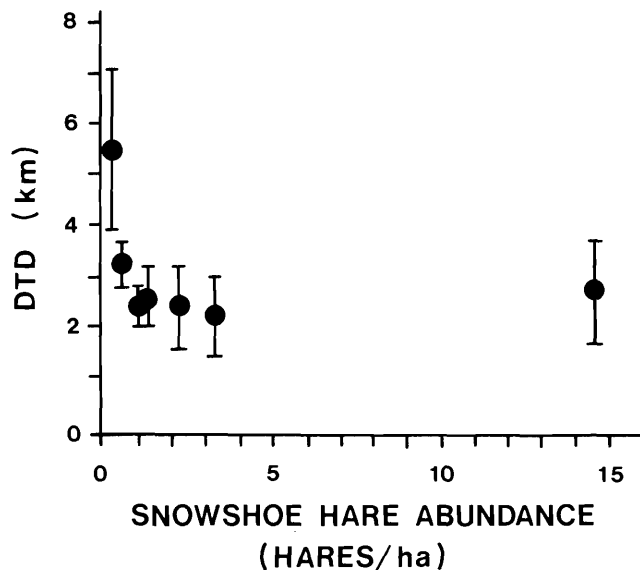
FIG. 4. Mean straight-line daily travel distance (DTD) of lynx versus snowshoe hare abundance. Travel distances are the mean for all individuals at the indicated hare density. Vertical bars indicate 95% confidence limits.

TABLE 3. Effect of relative snowshoe hare density on lynx foraging patterns

Grid, date	Hare density (hares/ha)	No. of lynx caught per 100 trap nights[a]	Sets of lynx tracks per 600-m transect[b]
A, April 1982	14.7	1.3 (234)	5.0c (0.7−9.3)
B, April 1982	2.6	0.0 (234)	0.8d (0.0−1.6)
A, November 1982	1.8	0.0 (246)	1.2d (0.0−2.3)

[a] The total number of trap nights of effort is shown in parentheses.
[b] Mean values followed by a different letter are significantly different (G-test adjusted, $P = 0.005$). The 95% CI is shown in parentheses.

of seven lynx. One lynx died of natural causes in the spring of 1984 (Table 1).

Between April and November 1982, we radio tagged seven lynx. By April 1983, only two lynx were still alive and residing within the study area. Three of the seven lynx (Nos. 301, 303, and 304) dispersed 240−700 km before being killed by trappers. All three 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 (No. 301) was at least 2 years old and the other two individuals were at least 1 year old. When Nos. 301 and 304 emigrated, grid A had significantly higher densities than surrounding areas, but hare density on this grid was declining rapidly (Fig. 2). Lynx No. 301 travelled at least 700 km in the next 8 months before being captured and killed in mid-December in northeastern Alaska. Lynx No. 304 was trapped and killed approximately 250 km north of the study area (at Pelly Crossing) in mid-December 1982.

Lynx 303 moved to approximately 5 km southeast of grid A in July 1982 and emigrated from the study area in October. She was trapped and killed in mid-November within 50 km of the area where No. 304 was killed, near Pelly Crossing, Yukon. These three lynx had minimum dispersal rates of 3.8, 1.7, and 8.3 km/day, respectively, if we assume straight-line travel. All emigration from the study area occurred during the snow-free period from May to October.

Two additional lynx (Nos. 302 and 306) were also trapped and killed within 10 km of their original radio-tagging site during the winter of 1982−1983. All five lynx were trapped within 2.5 months of the start of trapping season. This represents 71% of our radio-tagged population and 100% of the animals that left the game sanctuary. The two lynx (Nos. 307 and 305) that remained in the Kluane Game Sanctuary in late fall 1982 were still present the following spring.

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

During the winter of 1983−1984, two of our six radio-tagged lynx were trapped and killed within 10 km of their initial capture site. This represents 33% of our radio-tagged population and 50% of the lynx known to have travelled outside the game sanctuary.

Trapping was responsible for seven of eight deaths of lynx observed in this study. Furthermore, only two of the nine individuals known to travel outside the game sanctuary during the trapping season were not trapped.

Discussion

Lynx respond behaviourally to declining snowshoe hare abundance. Mean home range size for lynx in this study increased threefold concurrent with a decline in hares from 14.7 to about 0.2 hares/ha. This increase completely overshadowed 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. Although technical differences may explain some of the variation in home range sizes reported for lynx, we feel that the overriding factor is food abundance. Home range sizes reported for lynx in previous studies span 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 hares. Mech (1980) reported lynx home ranges of 51−243 km^2 and suggested that low prey abundance may have caused the large home ranges. Our 90% lynx home ranges span the range from the smallest to the largest previously reported.

The concept of increasing feeding territory or home range size with declining food availability has been discussed in theoretical terms by several authors (e.g., Dill 1978; Harestad and Bunnell 1979; Hixon 1980; McNab 1963). Although increasing home range size would not necessarily 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 our data. 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.

If prey density is not uniform, 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 Keith and Windberg (1978) and Wolff (1980).

Three lynx abandoned their home ranges and became no-

madic 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 settled down when prey abundance increased. Bailey (1981) reported that bobcats that defended territories during periods of prey abundance also became nomadic after prey declined. He suggested that if prey density is unpredictable, or very low, it would be adaptive for bobcats to become transient and search out widely separated 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 abundant prey. If the refugia for hares are widely spaced, it may be necessary for lynx to wander great distances to find them.

Schoener (1968) suggested that territoriality is inversely proportional to the degree of home range overlap between individuals. The high degree of home range overlap within and between both sexes in this study is strong evidence that lynx are not territorial at least during the period of decline of snowshoe hare density.

Previous studies show no consistent trend in the relative exclusiveness of lynx home ranges within and between sexes (Nellis et al. 1972; Brand et al. 1976; Berrie 1974; Mech 1980; Parker et al. 1983; Carbyn and Patriquin 1983). The variability of lynx home range overlap reported by these authors is puzzling. One possible explanation is that the total lynx population within the 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. 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 environmental factors might be or how they might act is evident from a review of past studies. If any behavioural spacing mechanism exists in lynx populations, it is easily overridden by proximate environmental factors such as snowshoe hare density.

Lynx in this study increased their mean straight-line daily travel distance (DTD) 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. How can we reconcile these results?

We found that at hare densities above 1.0 hares/ha, lynx in summer did not increase their DTD significantly with declining hare abundance. Further, if (i) DTD is an inverse function of hunting success in terms of kills per day (Brand et al. 1976; Parker 1981), and (ii) there is no relationship between kills per attempt and hare density (Brand et al. 1976), and (iii) attempted kills per kilometre travelled decline with declining hare density (Brand et al. 1976), then lynx should travel further as hares decline in an effort to fulfill their energetic requirements.

Below hare densities of 1.0 hares/ha, lynx showed a dramatic increase 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 re-

ported only instances where lynx "beds used on consecutive nights could be established with certainty." The most dramatic increase in lynx foraging effort occurs at very low hare densities. Our results above 0.5 hares/ha therefore are in general agreement with those of Brand et al. (1976) and Parker et al. (1983).

If prey are not uniformly distributed, it will always be to the advantage of a predator to concentrate its foraging efforts in the patches of 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.

We do not have data on the patchiness of snowshoe hare distribution, but if the system is similar to that described by Keith and Windberg (1978) and Wolff (1980), snowshoe hare distribution should be very clumped. Wolff (1980) suggested that during the decline and low period of their 10-year cycle, snowshoe hare populations retreat into patches of optimal habitat. It would be adaptive for lynx to seek out and utilize these good patches.

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

Others have also found that lynx tend to concentrate in patches of prey abundance (Brand et al. 1976; Saunders 1963a; Berrie 1974; Bergerud 1971).

Berrie (1974) 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.

Long-distance movements by lynx of from 103 to approximately 800 km (Saunders 1963b; Nellis and Wetmore 1969; Mech 1977; D. Brittel, personal communication) are normally associated with the decline phase of the snowshoe hare cycle. Lynx have invaded 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 emigrants in our 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 elsewhere.

All long movements in this study occurred during the rapid decline in hare numbers. After hare densities had stabilized (below about 1.0 hares/ha), lynx expanded their home ranges 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 because of small sample size is not clear. Once prey density stabilized at a lower level and the lynx acclimated to this new level, they may have been less inclined

towards such dramatic movements.

Human harvesting constituted the single most important mortality factor for lynx in this study. Fur trapping was responsible for seven of eight observed deaths. Only two of nine 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 two animals that were not trapped died of natural causes and presumably starved.

Other studies have also reported high human-related mortality rates in lynx populations (Parker et al. 1983; Mech 1980; Carbyn and Patriquin 1983; Nellis et al. 1972). 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. Combining results of this study with those previous studies (excluding 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 behavioural responses of lynx to declining snowshoe hare abundance should increase lynx vulnerability to trapping. A combination of increased home range size and DTDs 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 capture a relatively large proportion of the lynx population in an area by concentrating in areas of 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 overharvesting during the decline and low in snowshoe hare density.

Acknowledgments

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