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RH: Lynx Population Dynamics Slough and Mowat

**LYNX POPULATION DYNAMICS IN AN UNTRAPPED REFUGIUM**

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Abstract: Refugia from trapping are believed to be important to support a long-term sustainable harvest of Canada lynx (Lynx lynx), but long-term studies in unharvested areas are lacking. We studied lynx population characteristics in relation to snowshoe hare (Lepus americanus) densities in a 301 km<sup>2</sup> refugium in the Yukon Territory between 1986 and 1994. Lynx carcasses were collected from adjacent trapping concessions for analysis of attributes of the harvested population. Hare density peaked in summer 1990 and began to decline in the winter of 1990-91. Lynx density in March varied with hare density from 2.7/100 km<sup>2</sup> in 1987 to 44.9/100 km<sup>2</sup> in 1991-92. The lynx population doubled annually for 4 years when reproduction and kit and adult survival were high, and immigration balanced or exceeded emigration. High mortality and emigration characterized the lynx decline. Proportions of breeding adults were 100% most years, including the first year of declining hare densities, but zero in the following 2 years. Yearling females reproduced only in the 2 years of highest hare numbers. Kit survival, which was 0% in 1986-87, peaked at 75% for kits of adult females and 26% for kits of yearlings in 1990-91. Emigration peaked annually from March-June, was lowest Sept.-Oct., and was not sex-biased. At least 16% ( $n=22$ ) of

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emigrants were trapped or shot. Seventeen lynx (14M, 3F) emigrated 100-1100 km. Annual natural mortality rates were under 11% for the first 6 years of study, including 2 years of hare decline, 60% in 1992-93 and 25% in 1993-94. The carcass sample contained 36% fewer kits, 40% more yearlings, and 4% fewer adults than were present on the study area, reflecting the lower birth and survival rates of kits of yearling females and trapping bias. Mean annual lynx home range size did not vary with hare density, until 1992-93 when male ranges increased markedly, and 1993-94 when female ranges increased. We recommend a network of permanently assigned untrapped areas to facilitate normal lynx population responses to changing snowshoe hare densities, to prevent local extinctions, and to maximize lynx harvests over a complete population cycle.

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Lynx abundance throughout most of its range in the boreal forests of North America follows a high amplitude cycle in response to population numbers of its main prey, the snowshoe hare (Elton and Nicholson 1942, Brand et al. 1976, Brand and Keith 1979). Historically, the lynx has been in high demand by the fur industry, with average pelt prices paid to Yukon trappers reaching a high of C\$720 in 1984-85 (an increase of C\$510 in 5 yr) during a cyclic population low. Lynx are susceptible to trappers using traditional foothold traps and accessing lynx habitat with improved transportation methods and

infrastructure. Previous lynx population studies documented annual rates of trapping mortality in excess of recruitment rates throughout the population cycle (Bailey et al. 1986, Quinn and Thompson 1987, Ward and Krebs 1985). State and provincial furbearer managers, trappers, and animal welfare groups presumed that lynx were being overexploited, reducing the amplitude of their response to the snowshoe hare cycle, and threatening local populations (Todd 1985), as suggested by De Vos and Matel (1952). A tracking strategy (Caughley 1977) was suggested for lynx management, whereby trapping is curtailed during the 3-4 years of low lynx recruitment (Brand and Keith 1979, Parker et al. 1983, Bailey et al. 1986). Another strategy, employing untrapped refugia, had been proposed to maintain normal lynx population dynamics while providing a sustainable harvest (Butler 1942, Ward and Krebs 1985, Bailey et al. 1986, Slough 1995). The objective of the study was to determine the significance of an untrapped refugium in maintaining lynx populations subjected to trapping.

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#### **STUDY AREA**

Field studies were conducted between December 1986 and June 1994 on a 301 km<sup>2</sup> study area, located 100 km southeast of Whitehorse, Yukon Territory (60°15'N, 135°20'W; [Fig. 1]). The area was closed to trapping during the study and had been trapped in only 1 season since the mid-1940s (9 lynx harvested in 1976). The study area was surrounded by registered trapping concessions (RTCs) averaging 350 km<sup>2</sup>. RTCs are tenured trapping rights granted to individuals or groups of trappers for specific land areas for renewable 5-year terms (Slough et al. 1987). They reduce competition for the furbearer resource and foster a sense of stewardship among trappers. The lynx harvest from 60 RTCs in a 100 km radius of the study area varied between 30 and 350 annually, taken between 1 November and 10 March.

The study area was on the Teslin plateau (Bostock 1965), characterized by weathered mountains dissected by creek valleys. Elevations ranged from 800 to 1,950 m above sea level (asl). The area, in the Lake Laberge Ecoregion (Oswald and Brown 1986), was burned in 1958, and was 73% regenerating lodgepole pine (Pinus contorta), white spruce (Picea glauca), trembling aspen (Populus tremuloides), subalpine fir (Abies lasiocarpa), and willows (Salix spp.). Residual patches of mature timber covered 9% of the area, riparian willows 4%, alpine tundra, which occurred above 1220 m asl, 11%, and lakes 3%. Eleven of the adjacent RTCs were burned in 1958, and the remainder were mature boreal forest.

Mean annual temperature was -1.1C with extremes of -55C (Dec 1992) and 31C (Aug 1990). The average mean temperature of the warmest month, July, was 13.7C, and the coldest, January, was -19.5C. Mean annual precipitation was 40.7 cm, 60% of which fell as rain. The mean annual maximum snow depth of 65.8 cm (range 53-74 cm) occurred between January and March.

We accessed the area by aircraft or snowmachine. We cut over 75 km of snowmachine trails, to reach most of the major drainages. The study area was used by hunters for moose (Alces alces) in August to October and fishers for lake trout (Salvelinus namaycush), but otherwise received little human use. Other predators and possible competitors of lynx included wolverine (Gulo gulo), red fox (Vulpes vulpes), coyote (Canis latrans), wolf (C. lupus), black bear (Ursus americanus), brown bear (U. arctos), and raptors such as the great horned owl (Bubo virginianus), northern goshawk (Accipiter gentilis), and golden eagle (Aquila chrysaetos). Alternative prey included gallinaceous birds and red squirrels (Tamiasciurus hudsonicus).

## **METHODS**

### **Snowshoe Hare Abundance**

We counted snowshoe hare fecal pellets in 360 (1987-89) or 480 (1990-94) permanent 0.155 m<sup>2</sup> quadrats placed along 11 transects each June. An attempt was made to sample pellets in major vegetation types throughout the study area. We calculated average hare densities for the preceding 12 months with a modified version of the equation found in Krebs et al. (1987) ( $\log_{10}$  hares/ha =  $\{[(0.812727 \times \log_{10} \text{ pellets}) - 0.235869] \times 2.302585093\} + 0.2773423$ ; C.J. Krebs, pers. commun.). We assessed differences among years with a 1-way analysis of variance (ANOVA) and Tukey's Studentized Range Test (HSD).

### **Lynx Live-capture**

Lynx were live-trapped annually December-April, 1986 through 1994, with techniques described by Mowat et al. (1994). Annual trapping effort averaged 5100 trap nights, employing 14 box traps and 80 foot snare traps. We distributed trapping effort across the study area, systematically traversing all potential lynx home ranges. Immobilization and handling of lynx were described by Poole et al. (1993).

Lynx were sexed, weighed, and eartagged in both ears with serially numbered tags (size 3, style 1005 monel tags, Natl. Band and Tag Co., Newport, Ky.). Age was estimated as kitten or yearling/adult from body weight and other physical characteristics (Poole 1994). Among males, kits weighed an average of 6.9 kg December-April, whereas yearlings and adults averaged 11.2 and 11.7 kg, respectively. For females, kits averaged 6.5 kg, yearlings were 8.8 kg, and adults were 10.3 kg. An incisor (usually  $I_3$ ) was extracted from adults and females weighing 7-8 kg for age determination and separation of yearling and adult classes by the acellular cementum annuli technique (Crowe 1972, Kvam 1984, Lieberman and Meadow 1992). Teeth were prepared with standard methods (Fancy 1980). The technique is based on the belief that the first cementum annulus is deposited late in the second winter of life (Nava 1970, Crowe 1972) and subsequent bands are deposited annually (Lieberman and Meadow 1992).

Fifty-eight male lynx and 45 females we trapped were fitted with collar-mounted radiotransmitters weighing 240 g (Model 400, Telonics Inc., Mesa, Az. or Model LMRT-3; Lotek Eng. Inc., Aurora, Ont.). Collars placed on kittens were padded with open-cell foam.

#### **Lynx Population Parameters**

##### Movements.--

Radiocollared lynx were located weekly from a Maule M-7 or similar Cessna (e.g. 185) aircraft. Signals were isolated within 360° aircraft turns with 100-m radii, 100-150 m aboveground. Ground locations of lynx capture or natural mortality, both on and off the study area, and close range snowtracking of radiocollared lynx were also used to detect movements.

Locations were recorded on 1:50,000 scale National Topographic System maps (Can. Dep. Energy, Mines and Resour., Ottawa, Ont.). Universal Transverse Mercator coordinates from the mapped locations were recorded to the nearest 100

m. Accuracy of telemetry was examined with test transmitters, dead radiocollared lynx, and dropped radiocollars, situations unknown to the observer at the time. The mean distance between 80 estimated and actual locations was 282 m, with a tracking precision (SD) of 208 m, incorporating errors of both telemetry and plotting. The 95% confidence ellipse (Marzluff et al. 1994) around each point was 52 ha.

Home ranges were calculated as 95% minimum convex polygons with RANGES IV software (Kenward 1990). Plots of incremental areas indicated that ranges of individuals with <20 locations were not asymptotic so these were excluded from the analyses. Obvious outliers, <1% of locations, were also removed (White and Garrott 1990). Data were grouped in annual periods from 16 May 16-15 May, corresponding to the onset of the birth-pulse in late May. Differences in home range areas of sex and age classes among years were determined with ANOVA and HSD. Unpaired Students *t*-tests were used for comparison of intersexual differences within years.

#### Density.--

Three methods were used to estimate lynx density at March 1 annually: (1) the minimum number alive (MNA), based on live-captures, (2) the MNA plus the number of untagged lynx estimated from track sightings in relation to home ranges of radiocollared animals, and (3) at higher densities in 1990-91 and 1991-92 the number of kits was estimated by applying survival rates determined through snowtracking (Mowat et al. 1996b) to the estimated number of kits born the previous year (no. resident females  $\times$  birth rate  $\times$  mean litter size for yr1 and ad). We included the estimated number of untagged females in these calculations.

Lynx population changes were calculated as  $\lambda$ , the finite rate of increase (Caughley 1977). Sex ratios were compared with unity, and age structure was compared between years with likelihood-ratio Chi-square statistics. We assessed differences in the mean age of adults among years with ANOVA and HSD tests.

#### Emigration and Mortality.--

Lynx were classed as emigrants if they were radiocollared or eartagged in the study area and later located  $\geq 10$  km from the study area and did not return, or if they were not located on the study area and radio failure was not suspected. Only 1 transmitter was known to have failed suddenly. Telemetry coverage was frequently extended 25 km beyond the study area to locate emigrants. Emigration was also ascertained from reports of trapped or killed lynx that had been radiocollared or eartagged in the study area. Sex ratios and age structure of emigrants were tested against parity with likelihood-ratio Chi-square statistics.

Mortalities  $\leq 25$  km from the study area were confirmed with ground-based radiotelemetry to locate lynx stationary for  $\geq 2$  consecutive aerial locations. Trapping (including shooting) mortalities were reported by trappers and a lynx killed by a vehicle was reported by the motorist. Annual natural and trapping mortality rates and emigration rates were calculated after Pollock et al. (1989) with STAGENTD software. Mortality and emigration rates were compared between years with log-rank tests to obtain approximate Chi-square statistics (Pollock et al. 1989).

#### Immigration and Recruitment.--

Lynx were classed as immigrants if they were  $\geq 1$  year old and not present the previous winter, including those detected by fresh track sightings relative

to known locations of radiocollared lynx. Annual immigration rates were estimated as the proportion of immigrants in the March 1 population. Sex ratios of age classes and age structure of immigrants were compared with parity with likelihood ratio Chi-square statistics.

Recruitment was assessed at 2 periods annually; the number of kits at natal dens between late-May and July and the number of kits surviving until 30 March, when family breakup and dispersal typically began.

Natal dens were located by monitoring activities of radiocollared females on 4-10 consecutive days between late-May and late-June. Parturition was inferred if females were stationary and proven by ground-based radio-telemetry.

Birthdates were estimated from a linear regression of weight on date for a captive lynx kit 21-42 days of age (J. Weaver, pers. commun.), including a data point from a stillborn kit (175 g)  $\{\text{Age [days]} = (\text{wt}-190.1 \text{ g.})/19.8\}$ ,  $r = 0.997$ ,  $n = 6$ ,  $P < 0.001$ . Found litters were estimated to be an average of 19 days of age (range 1 to 33 days). Litter sizes were compared among years with ANOVA and between age classes within years with Student's  $t$ -tests.

Kits were sexed (1 litter in 1989 and all litters subsequently), weighed (except in 1989), and eartagged (size 2, style 1005 monel tags, Ntl. Band and Tag Co., Newport, Ky.). Lynx kits were sexed by assessing the relative distance between the urogenital opening and the anus, which was greater in males (Mowat et al. 1996b). The survival of tagged kits to the following winter suggested that handling did not increase the likelihood of litter failure (Mowat et al. 1996b). Sex ratios of litters were compared to unity with likelihood-ratio Chi-square statistics. Kit weights were compared between years and female age classes with Student's  $t$ -tests. Mean dates of birth were compared among years with a Kruskal-Wallis test and between yearling and adult females with Mann-Whitney U-tests.

We assumed that non-stationary females did not reproduce. We were unable to determine, though, if these females had not been pregnant or had lost their litters early pre- or postpartum. The proportion of monitored females with litters in June therefore represents a minimum estimate of birth rate.

Survival of kits to the following 30 March was determined from recaptures and by snowtracking adult females whose litters we had censused earlier (Mowat et al. 1996b). The sex ratios of age classes and age structure of lynx born in the refugium that emigrated were compared with parity with likelihood ratio Chi-square statistics.

#### **Lynx Carcass Analysis**

We obtained lynx carcasses from trappers on 60 RTCs within a 100 km radius of the study area in YT and BC, November 1986-March 1994, to assess the age structure, sex ratio, and reproductive rate of lynx in the adjoining harvested subpopulation. Reproductive tracts of females were examined for recent placental scars (Mowat et al. 1996a). Lower canines were aged from cementum annuli as described earlier for incisors.

Pregnancy rates, sex ratios and proportions in age classes were compared between years, and pregnancy rates were compared between age classes with likelihood-ratio Chi-square statistics. Annual litter sizes and mean age of adults were compared among years with ANOVA, and litter sizes of age classes were compared with Student's  $t$ -tests.

Annual age structures of the trapped and untrapped subpopulations were compared with likelihood-ratio Chi-square statistics and mean age of adults were compared with Student's  $t$ -tests.

## **RESULTS**

### **Snowshoe Hare Abundance**

We sampled fecal pellets on 360 quadrats in 1987-89, and on 480 quadrats in 1990-94. Estimated snowshoe hare densities differed significantly among years ( $F = 168.0$ , 7, 3471 df,  $P < 0.001$ ). The Tukey grouping of hare densities (Table 1; 1991 > 1990 > 1992 > 1989 > 1987, 1988, 1993, 1994; HSD,  $P < 0.05$ ) demonstrates the hare population cycle. Mean snowshoe hare density estimates increased from 0.8 hares/ha in June 1987 to a peak of 7.5 hares/ha in 1991 (Table 1). Densities declined to 1.3 hares/ha in 1993.

#### **Lynx Live-capture**

Annual capture efficiency increased from 451 trap nights/capture in 1986-87 to 66 trap nights/capture in 1990-91, after which it decreased substantially (Table 2).

One hundred sixty-one lynx (104M:57F) were live-captured 246 times during the 8 trapping sessions (Table 2). One hundred three of these (58M:45F) were radiocollared. Thirteen lynx (4 kits, 2 yrl and 7 ad) died from capture-related injuries, 7 when first captured. An additional 174 of 185 kittens from 39 litters were eartagged between 1 June and 1 July. Fifty-one eartagged kits were subsequently recaptured during live-trapping sessions (30 kits) or by trappers (21 kits). Fates of 70 lynx were resolved by 15 May, 1994. A further 29 radiocollared lynx, 39 winter eartagged lynx, and 123 summer eartagged kits were censored from survival analyses.

#### **Lynx Population Dynamics**

##### Home Range---

We found significant variation in home range size among years for adult male ( $F = 3.28$ , 7, 38 df,  $P = 0.008$ ) and adult female lynx ( $F = 20.6$ , 7, 43 df,  $P < 0.001$ ), but not for yearling males ( $F = 0.29$ , 3, 10 df,  $P = 0.83$ ) or yearling females ( $F = 1.96$ , 3, 9 df,  $P = 0.19$ ). Mean annual home ranges varied from 11.2-33.4 km<sup>2</sup> for adult females and 20.7-53.3 km<sup>2</sup> for adult males between

1986-87 and 1991-92. In 1992-93, the mean annual home ranges of males increased greatly to 119.2 km<sup>2</sup>, and in 1993-94 the ranges increased to 266.2 km<sup>2</sup> for males and 507.1 km<sup>2</sup> for females (Table 3). Mean adult home range sizes were larger in 1993-94 than in all other years (except 1992-93 for M) (HSD,  $P < 0.05$ ). Yearling ranges were 9.9-53.5 km<sup>2</sup> for males and 10.8-40.6 km<sup>2</sup> for females. Male kit ranges were 10.2-66.6 km<sup>2</sup> in 1989-90. Adult intersexual comparisons showed significant differences in 1989-90 ( $t = 4.06$ , 7 df,  $P = 0.005$ ), 1990-91 ( $t = 5.64$ , 22 df,  $P < 0.001$ ) and 1991-92 ( $t = 4.57$ , 20 df,  $P < 0.001$ ), when male ranges were larger. Yearling males had larger home ranges than yearling females in 1990-91 ( $t = 3.05$ , 10 df,  $P = 0.01$ ). Home range size did not vary with snowshoe hare density (ad M,  $r = -0.34$ ,  $n = 8$ ,  $P = 0.41$ , ad F,  $r = -0.32$ ,  $n = 8$ ,  $P = 0.44$ ).

#### Density.--

The lynx population increased from a density of 2.7/100 km<sup>2</sup> on 1 March, 1987 to 44.9/100 km<sup>2</sup> in 1991 at a mean annual finite rate of increase ( $\lambda$ ) of 2.03 (Table 4). The density increased in 1991-92 despite a declining hare population. The lynx decline began in 1993 ( $\lambda = 0.01$ ). The 1994 density of 2.0 lynx/100 km<sup>2</sup> was similar to that first observed in 1987.

Sex ratios of adults and yearlings did not differ from unity in any year ( $P > 0.05$ ). Yearlings dominated the age classes in 1990 ( $\chi^2 = 11.5$ ,  $P = 0.003$ ).

The mean age of adults differed among years ( $F = 17.55$ , 7, 417 df,  $P < 0.001$ ), decreasing from 6.7 years in 1987 to 3.0 years in 1994. The mean age in 1987-89 was greater than that in 1991-94, and the mean age in 1990 was greater than that in 1992-93 (HSD,  $P < 0.05$ ).

At the study's conclusion on 15 May, 1994, 2 of 3 remaining lynx had been born on the study area, including a 6-year-old male offspring of one of the original females, and a 5-year-old male.

#### Emigration and Mortality.--

At least 74 eartagged or radiocollared lynx emigrated from the study area. Emigration rates increased annually between 1989-90 and 1992-93 ( $P < 0.05$ ). (Table 5). Emigration took place throughout the year, but was lowest September-October (1%,  $n = 1$ ), and highest March-June, (51%,  $n = 38$ ). Fifty-eight percent ( $n = 43$ ) of emigrants were males, however this ratio and sex ratios of the age classes (7M:3F, 21M:9F, and 15M:19F for kits, yrl and ad, respectively) did not differ from parity ( $P > 0.05$ ). Forty-six percent of emigrants were adults  $\leq$  5-years of age, 40.5% were yearlings and 13.5% were kits ( $\chi^2 = 8.2$ , 2 df,  $P = 0.02$ ).

Thirty-three radiocollared emigrants were radio-tracked 10-145 km from the study area. Most of these were censored from survival analyses ( $n = 24$ ) and 2 died of natural causes. Twelve other radiocollared lynx (16%) were trapped 10-870 km away. Another 8 emigrants (eartagged only) were trapped, 2 were shot, and 1 was hit by a vehicle; these mortalities occurred between 10 and 1100 km from the study area. At least 17 lynx (radiocollared or eartagged) (14M:3F) traveled more than 100 km, 11 of these 500 km (8:3), and 2 1000 km (2:0) (Fig. 1).

Minimum daily travel distances of 8 radiocollared lynx that emigrated  $>100$  km averaged  $4.2 \pm 7.4$  km/day (0.3-23.6 km/day). A yearling female had the highest rate of movement for individuals traveling  $>500$  km, moving 840 km in 157-248 days at a rate of 3.4-5.4 km/day. The harvest pattern of emigrants (Fig. 1) reflected the concentration of trapping effort near the main highways.

Annual natural mortality rates were  $\leq 10.5\%$  the first 6 years of study, including the first 2 years of hare decline in 1990-91 and 1991-92 (Table 5). Natural mortality was 60% in 1992-93, significantly greater than the rate of the previous year ( $P < 0.05$ ). Causes of natural mortality were determined in 8 of 17 cases: starvation ( $n = 3$ ), cannibalism ( $n = 3$ ), and predation by wolverine ( $n = 2$ ). Fourteen lynx died as adults, 2 as yearlings and 1 as a kit. Seven resident lynx, 4 adult males and 3 female kits, were trapped within 5 km of the study area.

Ninety-two per cent (23 of 25) of known emigrant deaths were human-caused, primarily by trappers ( $n = 22$ ). The deaths of 60% of these occurred more than 100 km from the study area. At least 16% ( $n = 12$ ) of all radiocollared emigrants and 15% ( $n = 6$ ) of winter eartagged lynx were trapped.

All winter eartagged lynx were assumed to have emigrated if not recaptured, since natural mortality rates of resident kits and yearlings in late winter were negligible.

#### Immigration and Recruitment.--

Known immigrants to the refugium ( $n = 82$ ) were 50% adult males, 19.5% yearling males, 22% adult females, and 8.5% yearling females. These proportions were male biased ( $\chi^2 = 6.54$ , 1 df,  $P = 0.011$ ) and adult biased ( $\chi^2 = 8.39$ , 1 df,  $P = 0.004$ ). Immigration rates exceeded emigration rates during 2 years of population growth (Table 5: 1987-88 and 1989-90).

Adult female birthrates were 100% in 1987, 1989-91, and 1994; 50% in 1988, and 0% in 1992 and 1993 (Table 6). All yearlings produced litters in 1989-90, but none had litters in 1991-92. Some uncollared yearlings reproduced in 1989-91 as determined by snowtracking (Mowat et al. 1996b).

Adult litter sizes, were typically 3-4 kits in low hare years ( $\bar{x} = 3.5$ ,  $n = 2$ ) and as high as 7 kits when hares were abundant ( $\bar{x} = 5.3$ ,  $n = 17$ ), but did not vary among years ( $F = 1.09$ , 3, 28 df,  $P = 0.37$ ). The mean yearling litter size of 4.2 ( $n = 5$ ) in 1990 was not significantly different from the mean adult litter size that year ( $t = 1.27$ , 15 df,  $P = 0.22$ ).

Twenty-seven of 28 monitored females reproduced and had litters in mid-June during the hare population increase. All adults ( $n = 17$ ) but no yearlings ( $n = 7$ ) reproduced in 1991. All 15 females (14 ad, 1 yrl) did not have litters by mid-June the following 2 years. The lone female monitored in 1994 had a litter of 4.

Overall sex ratios of kittens were equal for adult (79M:68F) ( $\chi^2 = 0.41$ ,  $n = 147$ , 1 df,  $P = 0.52$ ) and yearling females (10:11) ( $\chi^2 = 0.024$ ,  $n = 21$ , 1 df,  $P = 0.88$ ). The mean weight of litters from adult females did not differ between 1990 ( $648 \pm 108$  g,  $n = 11$  litters) and 1991 ( $698 \pm 136$  g,  $n = 15$ ) ( $t = 1.00$ , 24 df,  $P = 0.33$ ). Yearling litters ( $261 \pm 53$  g,  $n = 6$ ) weighed less than adults in 1990 ( $t = 8.17$ , 15 df,  $P < 0.001$ ).

The mean date of birth for litters of adult females was 24 May ( $\pm 6.6$  days [SD]), ranging from 12 May-7 June. The mean date of birth for 5 yearlings monitored in 1990 was 16 June  $\pm 7.3$  days (10-28 June), 23 days later than the mean for adults that year (24 May  $\pm 6.0$  days) (Mann-Whitney  $U = 0.00$ ,  $P = 0.002$ ).

Mean dates of birth of litters of adult females did not differ among years (Kruskal-Wallis  $H = 3.92$ ,  $P = 0.27$ ).

The survival of kits of adult females increased from 0% in 1986-87 to 68% in 1988-89 and remained high until the second year of snowshoe hare decline. The survival of kits of yearling females was negligible except in 1990-91

(26%). Kits of 2 study area adult females killed in December were not observed again and presumably died (Mowat et al. 1996b).

Forty-six radiocollared lynx born on the study area dispersed, while 49 remained. Twenty-two percent (7M:3F) dispersed as kits, 46% (18M:8F) as yearlings, and 11% each as 2- (1M:5F) or 3-year-olds (5F) ( $\chi^2 = 5.05$ , 2 df,  $P = 0.082$ ). The yearling sex ratio was equal ( $\chi^2 = 2.01$ , 1 df,  $P = 0.16$ ). The youngest recorded dispersal was that of a male kit on 18 March (1991) at 10 months of age. The youngest dispersal of a female kit was 6 April (1992).

#### **Lynx Carcass Analysis**

We collected 888 lynx carcasses from trappers during the 8 winter trapping seasons (1 Nov-10 March), representing 79% of the lynx harvest from the collection area, as determined from mandatory pelt sealing records (H. Slama, Yukon Dep. Renewable Resour., unpubl. data).

Only one-half of the RTCs in the carcass collection area were trapped annually. The overall lynx harvest level for the area was 0.2 lynx/100 km<sup>2</sup> (1993-94) to 1.7 lynx/100 km<sup>2</sup> (1991-92). The harvest level was 3-15% of the density estimates for the refugium, being greatest in 1986-87 and 1992-93 when the lynx population was low. The harvest level exceeded the estimated density of lynx in the refugium on 1 RTC in 1986-87 (164%) and 1993-94 (196%), and on 2 RTCs in 1992-93 (140% and 186%). The more heavily harvested RTCs tended to be more accessible and near the trapper's permanent residence, where trapping was convenient throughout the season.

#### Reproduction.--

Pregnancy rates peaked in 1990-91 for adults and yearlings, remained high for adults in 1991-92, then declined sharply (Table 7). There were no significant differences in rates among years or between adults and yearlings

within years ( $\chi^2 > 0.05$ ). In utero litter sizes differed among years for adult females ( $F = 3.11$ , 6, 111 df,  $P = 0.008$ ; 1993-94 removed). Litter sizes in 1989-90 and 1990-91 were larger than that in 1986-87 (HSD,  $P > 0.05$ ). Yearling female litter sizes did not differ among years ( $F = 3.57$ , 4, 72 df,  $P = 0.01$ ). Adult and yearling litter sizes did not differ ( $t = 1.89$ , 193 df,  $P = 0.06$ ). The maximum recent placental scar count was 8 ( $n = 2$ ) in 1989-90.

#### Sex Ratio and Age Structure.--

Yearling sex ratios were male biased from 1989-90 to 1991-92 ( $P < 0.05$ ) (Table 8), however annual kit and adult sex ratios were even ( $P > 0.05$ ). The mean age of trapped lynx declined as the population increased. The annual proportion of kits increased in 1987-88 ( $\chi^2 = 7.67$ , 2 df,  $P = 0.02$ ), followed by an increase in yearlings in 1988-89 ( $\chi^2 = 19.5$ , 2 df,  $P < 0.001$ ). The proportions of yearlings and kits decreased in 1992-93 ( $\chi^2 = 78.3$ , 2 df,  $P < 0.001$ ). The mean age of adults varied among years ( $F = 36.3$ , 7, 112 df,  $P < 0.001$ ), with 1986-87 and 1987-88 samples older than the rest (HSD,  $P < 0.05$ ).

Comparisons of annual age structure of the harvest (Table 8) with that of the refugium lynx population (Table 4) showed no differences in 1987, 1988, 1993, or 1994, but were significantly different in 1989-92 ( $P \leq 0.001$ ), when the refugium population had a higher proportion of kits and a lower proportion of yearlings. The mean age of adults was lower in the carcass sample than in the refugium in 1987 ( $t = 2.04$ , 37 df,  $P = 0.048$ ), and higher in 1989 ( $t = 2.88$ , 22 df,  $P = 0.009$ ).

The harvested sample was composed of 36% fewer kits, 40% more yearlings and 4% fewer adults than were present on the study area (Table 9). However the capture bias of the refugium population over the same period (i.e., the Nov. 1 - Mar. 10 trapping season) was 12% fewer kits, 15% more yearlings, and 3% fewer

adults. Capture bias to April 14, the last date of live-trapping, was even lower.

## DISCUSSION

The peak lynx density of 44.9 lynx/100 km<sup>2</sup> was higher than any previously reported (10/100 km<sup>2</sup>, Brand et al. 1976; 20/ 100 km<sup>2</sup>, Parker et al. 1983; 10-20 or more/100 km<sup>2</sup> in 1973-73, 2.3/100km<sup>2</sup> in 1981, Bailey et al. 1986; 5.9-14.5/100 km<sup>2</sup>, D. Banville, Qué. Minist. du Loisir, de la Chasse, et de la Pêche, unpubl. data). 1986; 30/100 km<sup>2</sup>, Poole 1994). Most of these estimates were at peak hare densities, however Parker et al.'s (1983) estimate followed 2 years of hare decline (from 10 hares/ha in good habitats to 1.7/ha the summer after the lynx density estimate was made), and therefore is a minimal estimate. Bailey et al.'s (1986) 1981 estimate was in for heavily trapped area. In addition, the study areas cited above ,except that of Bailey et al. (1986), and "zone B" of Banville (op. cit.) were ≤ 135 km<sup>2</sup> and were surrounded by trapped areas that may have contained few refugia as sources of immigrants. The extreme high lynx density in our refugium may indicate the presence of good lynx habitat, or it may reflect the potential for lynx population growth within a refugium from trapping that has sources of immigrants from other refugia. Although Poole (1994) characterized his study area as untrapped and good habitat, the cyclic low lynx density before his study began may have been lower than ours due to trapping pressure (K. Poole, pers. commun.). Regional trapping pressure in NT (10-12% of estimated population) was similar to that in our study (3-15% of population).

Cyclic low lynx densities (2.7/100 km<sup>2</sup> in 1987, and 2.0/100 km<sup>2</sup> in 1994) were similar to others reported for concurrent low hare densities (2.3/100 km<sup>2</sup>: Brand et al. 1976, Koehler 1990, Poole 1994).

The lynx population expanded from a core of residents, doubling each of 4 successive years. The population growth rate was a result of a high percentage of breeding adults, large litters, high kit survival, low mortality, and immigration rates which balanced or exceeded losses to emigration. The lynx population continued to grow during the first year of hare decline, with successful recruitment of young produced by adult females, and then was reduced by 90% in 1 year. The decline was due to dispersal, natural mortality, and a collapse in recruitment and immigration. The conservation of the low density core lynx population for  $\leq 5$  years of low and initially recovering hare populations was probably responsible for the observed speed and amplitude of recovery of the lynx population. Immigrants from other refugia and the presence of good habitat also played important roles. Modeling of hare populations has shown that the amplitude of the hare population cycle would be greater with refugia from lynx predation (McNair 1986, Akçakaya 1992).

Maximum snowshoe hare density estimates of 7.5 hares/ha in 1991 (95% confidence interval; 5.3-10.4 hares/ha) were within the range of values reported for the northern boreal forest (5-17 hares/ha: Keith 1990:139) and during studies of lynx population dynamics (Brand et al. 1976, Ward and Krebs 1985). The peak hare density in the fall of 1990 was higher than that measured by the yearly averaging technique in June 1991, since the hare decline began in November 1990 (Slough and Mowat, unpubl. data). Minimal estimated densities during the cyclic low (0.8 hares/ha, 0.6-1.0), however, were higher than most (0.34, Brand et al. 1976; 0.02/ha, Krebs et al. 1986; 0.2/ha, Ward and Krebs, 1985; 0.4, Poole 1994).

Lynx home ranges reported here were similar to most others reported (Hatler 1988; Noiseux and Doucet, Qué. Minist. du Loisir, de la Chasse, et de la Pêche, unpubl. data; Koehler 1990; Poole 1994). There was no trend of

decreasing home range size of lynx with increasing hare density as suggested by Ward and Krebs (1985) and Poole (1994). Instead, ranges were relatively stable throughout. The large home ranges of 1992-94 were, however, a response to decreasing hare densities. A small proportion of the lynx population may maintain large home ranges at any hare density. Male adults and yearlings had a tendency throughout the study to range over areas 6 times greater than average for males (2 of 6 in 1988-89, 3 of 10 in 1989-90, 2 of 19 in 1990-91, and 2 of 6 in 1992-93, and 5 of 5 lynx in 1993-94). This type of extended home range was described as nomadic behavior by Ward and Krebs (1985). Our lynx were not nomadic, as they repeatedly revisited the extremities of their ranges.

Ward and Krebs were limited to ground telemetry and admitted to having trouble regularly locating nomadic lynx. Larger home ranges have also been reported for lynx in marginal habitats (Brainerd 1985, Mont.; Carbyn and Patriquin 1983, Manit.; Mech 1980, Minn.; Brittell et al. 1989, Wash.) and for a heavily exploited lynx population at peak hare densities (Bailey et al. 1986, Alas.).

Yearling females contributed little to population growth with a maximum contribution of recruited kits/female 33% that of adults in the peak hare year.

Data from reproductive tracts alone (Brand and Keith 1979, O'Connor 1984) produce overestimates of recruitment from yearling females into a population because many yearlings become pregnant and implant fetuses, but few of these fetuses survive. The late birthdate of kits of yearling females, along with the inexperience of yearlings at raising young, probably contributed to their higher mortality rate. Carcass analyses verified the changes to lynx reproduction observed on the study area, but the breeding success of yearling females was exaggerated by the pre- and postpartum loss of young.

The natural mortality of lynx is reportedly low when hare abundance is increasing or high (Ward and Krebs 1985, Poole 1994, this study). The high

trapping mortality rates of lynx found in other studies (Brand et al. 1976, Ward and Krebs 1985) are probably additive to natural mortality rates, except in the second or third year of hare decline when natural mortality removes a high proportion of the population (this study, Poole 1994, O'Donoghue et al. 1995). There have been several other documented cases of starvation (Ward and Krebs 1985, Poole 1994, O'Donoghue et al. 1995), predation (cougar [Felis concolor], Koehler et al. 1979; wolves, Iurgenson 1955 and O'Donoghue et al. 1995; wolverine and coyote, *ibid.*), and cannibalism (Elsley 1954, Nellis et al. 1972, Brittell et al. 1989, Poole 1994, O'Donoghue et al. 1995) of lynx.

Our study documented a relatively balanced exchange between trapped and untrapped subpopulations, but immigration exceeded emigration during the population growth phase, and emigration was greater during the decline. Emigrants were predominantly yearlings and adults of both sexes. Immigrants were predominantly adult males. Population turnover rates of territorial species in optimal habitats is believed to be less than in suboptimal habitats (Winker et al. 1995). Turnover rates observed in our study may be minimal for lynx populations if the high lynx densities were habitat related.

The low trapping intensity of the surrounding region and the existence of other refugia probably contributed to the source of immigrants to the refugium.

Pulliam (1988) argued that reproductive surpluses from source populations may maintain populations in sink habitats, where reproduction fails to keep pace with mortality, particularly for animals with active habitat selection. Again, due to low trapping mortality in the region, there were probably few sinks, other than in marginal habitats.

At least 16% of emigrant lynx were trapped, some  $\leq 1100$  km from the study area. Trappers sometimes failed to see eartags, especially the smaller tags used on kits (T. Hunter, pers. commun.) and some trappers may not have reported

the capture of marked animals. These factors, along with tag loss (estimated at 0.2% over 1 year, Mowat 1993), suggest that dispersal movements and trapping mortality of lynx were more extensive than our data have shown. Long distance movements of lynx (>100 km), once reported as anomalies (Nellis and Wetmore 1969, Mech 1977), are considered characteristic (Ward and Krebs 1985, Brittell et al. 1989, O'Donoghue et al. 1995). Many of our study area lynx that emigrated probably survived in refugia in at least 5 northwestern jurisdictions (Alas., Yukon Territ., B.C., Northwest Territ., and Alta.). Evidence was given by 2 males, one tagged as a kit in June 1991 and trapped Dec 1994, 650 km west in AK, and another tagged as a kit in June 1990 and trapped Jan 1996, 550 km east in NT. Both lynx had survived the 1992-94 hare population low and may have survived longer in untrapped areas.

The snowshoe hare population cycle has been shown to be in phase across Canada with population changes occurring in concentric waves, emanating from several population centers (Smith 1983). The locations of population centers may change between cycles. Lynx dispersal patterns could act as a synchronizing element of the cycle (Butler 1953, Lack 1954).

Trapping was the main observed source of mortality for dispersing lynx since our main source of information was trapper returns and not radiotelemetry. Study area lynx were also vulnerable to trapping  $\leq 5$  km from the area's boundary. Seven residents were captured in 2 seasons of light trapping effort on a single RTC adjacent to the study area. Trapping near the boundary of the area would have captured all males in 1992-93 and all residents in 1993-94. The dependence of a harvested population on immigration from refugia has been shown for bobcats (Felis rufus) (Bailey 1981, Knick 1990).

The age and sex of harvested lynx are reportedly biased due to age and sex related differences in behavior and temporal differences in behavior within

sex or age class (Brand and Keith 1979, Quinn and Thompson 1985). An analysis of new captures of lynx during this study, analogous to removal trapping, has shown that biases observed in carcass samples (from populations of unknown composition) may have been overstated. We found only a slight underrepresentation of kits and overrepresentation of yearlings. The tendency for males to disperse further than females would increase their vulnerability to trapping and cause sex-biased trapping mortality as reported by Quinn and Thompson (1985). Van Zyll de Jong (1963) noted a predominance of male yearlings in a harvested sample in unfavorable habitat. A carcass collection from a previously unharvested lynx population in Québec was comprised of an even sex ratio, with 16% kits and 11% yearlings (Noiseux and Doucet, Qué. Minist. du Loisir, de la Chasse, et de la Pêche, unpubl. data), typical of an increasing population rather than a harvest-biased sample. The long season in YT would also eliminate any harvest bias caused by temporal changes to age or sex trapping vulnerability. For example, the proportion of kits in a trapped sample tends to increase markedly after December (Quinn and Thompson 1985, Slough and Mowat, unpubl. data).

Trap vulnerability of lynx also varies with hare density and availability. During the first full winter of hare decline (1991-92), 2.5 times the effort was required to capture a lynx as compared to the previous year at similar lynx densities. A decrease in trap vulnerability was also observed by many YT trappers (J. Fraser, Yukon Trappers Assoc., pers. commun.).

Poole (1994) attributed this phenomenon to high hare vulnerability to predation during a hare crash, as hypothesized by Keith (1990), reducing the lynx's need to investigate traps. Recaptures declined at a much higher rate than new captures; therefore decreased trap vulnerability may also be due to learned trap avoidance. Furthermore, most lynx were attracted to scent, rather

than edible baits, suggesting a reduced need for scent marking. The pattern of trap avoidance did not continue in 1992-93, when lynx (average wt 2 kg less than the previous winter; Slough and Mowat, unpubl. data) came readily to bait; however, it recurred in 1993-94, when both hare and lynx densities were low. The tendency for healthy lynx to avoid traps during the hare decline and initial low population phase may help protect individuals during dispersal and population establishment. The harvest of nutritionally stressed lynx that are highly vulnerable during at least 1 year of the hare population crash is probably compensatory to natural mortality.

The harvested sample consisted of 36% fewer kits and 40% more yearlings than the refugium population between 1988-89 and 1991-92. Although in part an artifact of age-related trapping bias, the harvest age structure was the result of the annual removal of adults from RTCs throughout the population cycle. Vacant ranges were available for colonization by yearlings; yearling females recruit fewer kits than adult females. Mean ages of adults of both subpopulations decreased throughout the study. The mean age of adults from the carcass collection did not differ from that of the refugium population, except in 1986-87 when they were younger, and 1988-89 when they were older. These data show that older residents continued to survive on RTCs, as they did in the refugium, throughout the study period. Adult lynx survived on RTCs due to low trapping effort, the existence of refugia on RTCs, and lynx management training given trappers (Slough et al. 1987). Lynx management also benefits from incentives inherent in the RTC tenure system which limits numbers of trappers and eliminates competition for the resource. Knick (1990) attributed a predominantly yearling population of bobcats in a harvested area to the high harvest mortality, low reproduction, and yearling immigrants that filled vacant ranges. Lembeck and Gould (1979) found that adult bobcats averaged 3 years

older in unharvested versus harvested areas. We attributed the male-biased sex ratios of yearlings in the 1990-91 and 1991-92 carcass samples to the greater mobility and hence trap vulnerability of dispersing male lynx.

At least 8 lynx (4M:4F) were resident during 4 or more years of the 8-year study. A female, 9 years old when first captured in January 1987, died in early 1992 at age 14 years, 11 months (4 months older than a record reported by Chubbs and Phillips [1993]). Twelve of the lynx (5M:7F) had been born at or before the previous hare peak (1981), and 13 (10M:3F) were born during the 1982-85 hare low. Two of 3 residents in 1993-94 were produced on the area between 1988 and 1990. These observations satisfy 2 predictions of Breitenmoser et al.'s (1993) core population hypothesis, that (1) territories occupied by residents at the cyclic low are maintained throughout the cycle, and (2) during the decline phase, offspring of both sexes may remain in or near parental ranges. Poole (1994) did not observe the survival of core residents in his NT study area, indicating that lynx habitat was not as good as in our concurrent study. We also observed young females residing and reproducing in or near their mothers ranges throughout the hare cycle (Slough and Mowat, unpubl. data) as predicted by Breitenmoser et al. (1993).

#### **MANAGEMENT IMPLICATIONS**

The Snafu Lake lynx refugium, 301 km<sup>2</sup> of high quality habitat surrounded by RTCs containing additional refugia, may not be large enough to conserve lynx if the RTCs were trapped intensively to the refugium boundary. The home ranges of many resident lynx occasionally extended to areas where trapping was permitted. A higher proportion of residents is vulnerable during nomadism (Ward and Krebs 1985, Poole 1994), or as we observed, when home ranges expand following a hare crash. A buffer zone around a protected population must be considered when designing refugia. Some of the inaccessible lynx range in YT,

NT, and northern BC is, by default, saturated with refugia. In addition, YT trappers are educated in the utility of refugia for managing lynx and other species, and are motivated to conserve through the endowment of long-term trapping RTCs (Slough et al. 1987). Joshi and Gadgil (1991) related the practice of many prescientific societies to use refugia for both the conservation and sustainable use of biological resources. A form of ownership of the resource by the users (e.g., tenured harvesting rights) contributed greatly to the success of these resource management systems. Areas with high accessibility, unlimited trapper entry, or small RTCs may experience high trapping pressure and low conservation incentives (Todd 1985, Bailey et al. 1986). Managers should consider legislating regularly spaced refugia in these cases.

We estimate that the minimum effective size for a refugium in high quality habitat is 500 km<sup>2</sup> in years of home range stability. All study lynx were vulnerable to trapping in 1993-94, the third year of hare decline, and all males were vulnerable the second year of lynx decline, when they extended home ranges beyond the refugium boundary. Changes to the trapping regime such as area-specific quotas in limited entry areas (i.e., RTCs), or season restrictions could be used to temporarily increase the effective refugium size at this time. Harvest quotas assigned to individual trappers are meaningless in unlimited entry areas, especially when pelt prices are high. A round shape would minimize the effect of border trapping.

The persistence of sink populations (i.e., in trapped areas) may be as much or more influenced by the proximity of source habitats (i.e., refugia) than by habitat quality within the sink (Pulliam 1988). The ideal dispersion of refugia is highly dependent on species-specific dispersal distances (Knick 1990). Regular spacing of lynx refugia 50 km apart in continuous habitat would

protect 15% of all habitat, and provide opportunities for dispersers to colonize other refugia as well as vacant areas of suitable habitat on trapped areas. Larger refugia could be spaced  $\leq 100$  km apart, given the propensity of lynx to disperse that distance. Refugia should also be high quality habitats such as snowshoe hare refugia; areas with dense cover (Keith and Windberg 1978, Wolff 1980).

The chronology of a tracking strategy may vary among geographic areas, among hare cycles of varying duration or amplitude, or among consecutive cycles in successional habitats. Our refugium lynx population peaked 1 year after the snowshoe hare peak; however, lynx recruitment dropped 2 years after the hare peak, not 3-4 years after as documented by Brand and Keith (1979). In our case the tracking strategy of Caughley (1977) should be implemented 3 years following the hare peak, not 4-5 years after. Poole (1994) reported no lag effect of declining hare numbers on lynx reproduction. When natural mortality is high, and probably compensated by trapping mortality, during the second and third year of hare decline in this study, there is no need to curtail harvest in a tracking strategy.

We recommend population monitoring with lynx pelt measurements to estimate recruitment, or carcass collections to obtain sex and age ratios and reproductive data. These data will aid in the fine tuning of refugium or tracking harvest strategies, or strategies employing seasons or quotas. Brand and Keith (1979) recommended an examination of annual fur harvests to detect the lynx harvest peak and plan ahead for lynx harvest curtailment. However, fur harvests may be influenced by factors independent of furbearer population levels such as pelt values, weather, economic conditions and present harvest restrictions (Slough et al. 1987). The methods used by Strickland (1994) for monitoring harvest rates of American martens (Martes americana) and fishers (M.

pennanti), and Knick (1990) for monitoring bobcats, with sex and age ratios of harvested animals, should have relevance to lynx as well. However, techniques requiring biological submissions are impractical when few carcasses or pelts are available due to low harvests during low population phases or trapping closures. The use of hare fecal pellet sampling (Krebs et al. 1987) or snow-track counts of hare or lynx (Thompson et al. 1989) may be more useful at these times.

We recommend that season restrictions be enacted in the early winter to avoid removing females from dependent family groups. Timing of the harvest season has been shown to produce additive mortality by removing more adult females in early winter (Quinn and Thompson 1985), leading to the increased mortality of dependent kits (Parker 1981, Brainerd 1985, Bailey et al. 1986, this study). In fact there is no evidence that orphaned kits survive.

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Table 1. Mean snowshoe hare density estimates for the preceding 12 months (hares/ha) from fecal pellet counts, Snafu Lake study area, Yukon Territory, June 1987-June 1994. Means with the same letter are not different (Tukey's Studentized Range Test,  $P > 0.05$ ).

Year	1987	1988	1989	1990	1991	1992	1993	1994
$\bar{x}$ Density	0.8	1.0	2.8	5.7	7.5	4.7	1.3	1.1
UCL	1.0	1.3	3.4	7.7	10.4	6.3	1.6	1.3
LCL	0.6	0.8	2.1	4.2	5.3	3.5	1.0	0.8
Tukey grouping	E	E	D	B	A	C	E	E

Table 2. Trapping success for lynx in the Snafu Lake study area, Yukon Territory, December 1986-April 1994.

Trapping period	New captures	Recaptures	Trap nights/ capture
1986-87	6	0	451
1987-88	8	7	412
1988-89	10	8	318
1989-90	41	14	76
1990-91	57	41	66
1991-92	34	9	153
1992-93	3	6	607
1993-94	2	0	2139
Total	161	85	167

Table 3. Mean annual (16 May-15 May) home range size (95% min. convex polygon) of lynx in the Snafu Lake study area, Yukon Territory, 1988-87 to 1993-94.

Year	Age	n	$\bar{x}$ no. locations	Size <sup>a</sup> (km <sup>2</sup> )	SD	Range
1986-87						
F	Ad	2	28	12.8	0.7	12.3-13.3
M	Ad	4	26	20.7	12.7	11.6-39.3
1987-88						
F	Ad	2	49	10.9	7.2	5.8-16.0
M	Ad	3	57	25.7	11.2	17.4-38.4
1988-89						
F	Ad	1	30	33.4		
M	Yrl	1	21	9.9		
M	Ad	5	31	53.3	40.2	18.6-108.8
1989-90						
F	Yrl	2	58	17.0	3.5	14.5-19.4
M	Yrl	3	34	47.7	33.6	10.4-75.7
F	Ad	4	58	20.3	9.2	8.0-27.4
M	Ad	7	47	48.4	26.0	18.7-90.7
M	Kit	4	23	35.7	28.9	10.2-66.6
1990-91						
F	Yrl	5	39	10.8	11.7	3.3-31.1

M	Yrl	8	27	53.5	60.6	18.2-197.6
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F	Ad	13	45	12.8	4.0	5.7-20.5
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M	Ad	12	31	44.4	23.1	15.8-97.4
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1991-92

F	Yrl	5	41	38.0	26.6	7.3-74.1
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M	Yrl	2	44	27.5	1.1	26.7-28.2
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F	Ad	15	45	11.2	4.7	3.0-23.7
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M	Ad	7	46	30.3	17.6	16.2-63.3
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1992-93

F	Yrl	1	26	40.6		
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F	Ad	10	31	22.7	7.1	10.4-32.6
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M	Ad	6	29	119.2	188.8	16.5-498.2
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1993-94

F	Ad	4	37	507.1	297.2	139.1-774.6
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M	Ad	2	41	266.2	105.5	191.6-340.8
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<sup>a</sup> Arithmetic mean recalculated after excluding each fix (Kenward 1990).

Table 4. Annual lynx population estimates and age composition on 1 March, on the 301 km<sup>2</sup> Snafu Lake study area, Yukon Territory, 1987-94.

Year	MNA <sup>a</sup>	Estimated Total	$\lambda$	Lynx/ 100 km <sup>2</sup>	Population Composition (%)						$\bar{x}$ adult age $\pm$ SD
					Kit n	Yearling n	Adult n	%	%	%	
1987	6	8	-	2.7	0	0	0	100.0	8	6.7 $\pm$ 1.6	
1988	13	17	2.13	5.6	23.5	4	5.9	1	70.6	12	5.7 $\pm$ 1.7
1989	18	32	1.88	10.6	53.1	17	3.1	1	43.8	14	4.7 $\pm$ 1.8
1990	53	73	2.28	24.3	47.9	35	27.4	20	24.7	18	5.2 $\pm$ 3.4
1991	80	134	1.84	44.5	49.3	66	18.7	25	32.1	43	4.1 $\pm$ 3.0
1992	63	135	1.01	44.9	55.6	75	17.8	24	26.7	36	3.6 $\pm$ 2.7
1993	10	13	0.01	4.3	0	0	0	0	100.0	13	3.0 $\pm$ 1.3
1994	3	6	0.46	2.0	0	0	0	0	100.0	6	3.0

<sup>a</sup> Min. no. alive based on captures.

Table 5. Annual mortality, emigration and immigration rates (%) ( $n$ ) for lynx on the Snafu Lake study area, Yukon Territory, 31 January 1987-15 May 1994. Mortality and emigration were calculated for radiocollared lynx after Pollock et al. (1989). Immigration was estimated from the % of the 1 March population not present the previous year.

Year	Max. no. at risk	Natural mortality	Trapping mortality	Total mortality	Emigration	Immigration
1986-87	6	0	0	0	16.7(1)	unk.(-)
1987-88	11	10.0(1)	0	10.0(1)	0	37.5(6)
1988-89	17	0	0	0	31.6(4)	20.7(6)
1989-90	42	0	10.0(2)	10.0(2)	10.9(2)	23.8(15)
1990-91	53	10.5(5)	13.0(5)	22.2(10)	32.8(16)	34.3(37)
1991-92	43	5.4(2)	0	5.4(2)	55.0(27)	12.0(13)
1992-93	30	60.0(8)	0	60.0(8)	79.2(21)	50.0(4)
1993-94	5	25.0(1)	0	25.0(1)	52.0(3)	16.7(1)

Table 6. Reproductive success and kit survival to 1 March on the Snafu Lake study area, Yukon Territory, May 1987-June 1994.

Year	Age class	Pregnancy rate (%)	Litter size	Est. births	Kit survival rate (%)
1986-87	Ad	unk.	unk.	≥2	0
1987-88	Ad	100(2)	3.5 ± 0.7	18	22.2
1988-89	Ad	50(2)	(3.5) <sup>a</sup>	25	68.0
1989-90	Ad	100(4)	5.3 ± 1.2	42	83.3
	Yrl	0(2)	(4.2) <sup>a</sup>	25	unk.
1990-91	Ad	100(13)	5.3 ± 1.6	85	63.5
	Yrl	100(5)	4.2 ± 0.8	46	26.1
1991-92	Ad	84(19)	4.9 ± 1.1	98	75.5
	Yrl	0(7)	0	12	(0.08) <sup>a</sup>
1992-93	Ad	0(9)	0	0	-
	Yrl	0(1)	0	0	-
1993-94	Ad	0(5)	0	0	-

<sup>a</sup> Estimated from snow-tracking data.

Table 7. Lynx pregnancy rates (%) and in utero litter size from carcass collections, southcentral Yukon Territory and northwestern British Columbia, November 1986-March 1994.

Year	Adult pregnancy rate	$\bar{n}$	$\bar{x}$ litter size $\pm$ SD	$\bar{n}$	Yearling pregnancy rate	$\bar{n}$	$\bar{x}$ litter size $\pm$ SD	$\bar{n}$
1986-87	70.6	17	2.7 $\pm$ 0.9	12	-	0	-	0
1987-88	83.3	18	3.8 $\pm$ 1.6	15	100.0	2	3.5 $\pm$ 2.2	2
1988-89	75.0	8	3.2 $\pm$ 0.8	6	50.0	8	2.3 $\pm$ 1.3	4
1989-90	81.3	16	4.7 $\pm$ 2.0	13	68.2	22	4.1 $\pm$ 1.8	15
1990-91	93.1	29	4.6 $\pm$ 1.5	27	70.0	30	4.4 $\pm$ 1.2	21
1991-92	75.6	45	4.0 $\pm$ 1.5	34	47.9	73	3.4 $\pm$ 1.3	35
1992-93	37.9	29	4.0 $\pm$ 1.6	11	0	1	-	0
1993-94	33.3	3	1.0	1	-	0	-	0

Table 8. Annual proportion of lynx age (%) and sex classes (%F) from carcass collections, southcentral Yukon Territory and northwestern British Columbia, November 1986-March 1994.

Year	Sex ratio (%F)			Age structure						
	Kits	Yearlings	Adults	Kits	$\bar{n}$	Yearlings	$\bar{n}$	Adults	$\bar{n}$	$\bar{x}$ Adult age $\pm$ SD
1986-87	60.6	-	51.5	13.2	5	-	0	86.8	33	5.7 $\pm$ 1.0
1987-88	54.6	50.0	62.1	25.0	11	9.1	4	65.9	29	6.7 $\pm$ 1.5
1988-89	37.5	32.0	44.4	15.7	8	49.0	25	35.3	18	7.3 $\pm$ 2.3
1989-90	44.4	31.1	44.7	24.0	36	50.0	75	26.0	39	5.1 $\pm$ 3.6
1990-91	52.5	26.2	52.5	19.6	42	53.7	115	28.5	57	3.9 $\pm$ 2.8
1991-92	48.2	43.9	52.2	17.4	55	54.2	173	28.5	91	3.0 $\pm$ 2.4
1992-93	100.0	12.5	50.0	1.5	1	12.3	8	86.2	56	2.8 $\pm$ 1.6
1993-94	-	0	50.0	0	0	14.3	1	85.7	6	2.8 $\pm$ 0.4
Combined	49.0	35.0	51.4	17.8	158	45.2	401	37.1	329	

Table 9. Age structure (%) of the lynx carcass sample, new lynx live-captures in the refugium, and the refugium population, 1986-87 to 1993-94 data combined.

	Kits	Yearlings	Adults
Carcass sample	17.8 (158)	45.2 (401)	37.0 (329)
(1 Nov 1-10 Mar)			
Refugium captures	41.4 (36)	20.7 (18)	37.9 (33)
(30 Nov-10 Mar)			
Refugium captures	47.8 (77)	15.5 (25)	36.6 (59)
(30 Nov-14 Apr)			
Refugium	53.5 (197)	5.7 (21)	40.8 (150)
Population			

Fig. 1. Lynx study area and final locations of lynx emigrants more than 100 km from the study area, November 1, 1987-May 15, 1994. All lynx were trapped except A (determined from radiotelemetry) and B (killed by a vehicle). Current lynx range from Quinn and Parker (1987). Main highways are shown on map and inset.