

Population cycles and changes in body size of the lynx in Alaska

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Abstract The lynx *Lynx canadensis* is a common predator in the boreal forests of North America. Its population fluctuates during a 9- to 11-year cycle in synchrony with the population size of its main prey, the snowshoe hare *Lepus americanus*. Using adult museum specimens, we studied changes in skull (and hence body) size of the lynx in Alaska during the second half of the 20th century. The population cycle in Alaska averaged 9 years, similar to that reported in the neighbouring Yukon. Using harvest data of lynx as an estimate of population size, we found that skull size was negatively related to population size. This relationship was strongest not for the population density in the year of death (X), but for year X-3, a carry-over effect from the first year (or years) of life, indicating that conditions during the fast-growth years are determining body size. We suggest that the density-dependent effect is probably due to changes in food supply, either resulting from the adverse effects of

competition or a possible diminished availability of food. Two skull parameters decreased significantly during the second half of the 20th century. We do not know the cause for the year effect and suggest that it might be due to a long-term change in the availability of prey. Canine size did not change during the study period, probably an indication that snowshoe hares maintained their status as the main prey of the lynx throughout the study period.

Keywords Lynx · *Lynx canadensis* · Density dependence · Body size · Population cycles · Alaska

Introduction

Temporal and spatial intraspecific variation in adult body size may be related to several factors, including nutrition and ambient temperature. Body size appears to be determined during the period of time that growing individuals have unhindered access to food of the highest quality (Geist 1987). In many birds and mammals, conditions experienced during early development affect growth and ultimately body size, as well as a range of related properties (Henry and Ulijaszek 1996; Lindstrom 1999). In humans, the prime determinants of this trend are considered to be improved nutrition and availability of public health services (Ulijaszek et al. 1998). Similar phenomena have been observed in animals. For example, in harbour porpoises (*Phocoena phocoena*), increased prey availability resulted in an increase in body length of calves and earlier sexual maturity of females (Read and Gaskin 1990). Variations in food availability drive variation in

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growth rate and body mass of juveniles, as has been demonstrated for fish (Jorgensen 1992), frogs (Galatti 1992), snakes (Madsen and Shine 2000), birds (Lepage et al. 1998; Larsson and Forslund 1991) and mammals (Bolton et al. 1982).

Food availability (and consequently body weight) may be influenced by several factors, including climate, as is the case with the water pythons *Liasis fuscus* in Australia where the abundance of their rat prey is determined by rainfall or population density (Madsen and Shine 2000). Population density was found to be negatively related to body size of either (or both) juvenile or adult animals, as in the red deer *Cervus elaphus* (Mysterud et al. 2001), the roe deer *Capreolus capreolus* (Toigo et al. 2006), the brown bear *Ursus arctos* (Zedrosser et al. 2006) and the great tit *Parus major* (Both 1998; Wilkin et al. 2006).

Global mean surface temperatures have increased, on average, by 0.6°C from the late 19th century to 1994 (Houghton et al. 2001). In high latitudes, the increase was greater than average, and minimum temperatures increased at about twice the rate of maximum temperatures (Houghton et al. 2001). In northwestern America, and particularly in Alaska, average warming since 1950 has been about 2°C and almost twice as much in the interior in winter (Parker et al. 1994; www.usgcrp.gov/usgcrp/Library/nationalassessment/overview). Global warming can affect the physiology, distribution, phenology and adaptation of plants and animals (reviewed by Hughes 2000) and affect animals in various ways (Millien et al. 2006). For those sensitive to ambient temperature, such as the woodrat *Neotoma albigula* in New Mexico (Smith et al. 1998) and four species of passerines in Israel (Yom-Tov 2001), it may cause a decrease in size as predicted by Bergmann's rule. However, increased temperature, especially during the winter, enables animals to divert energy from maintenance to growth, and there may be an increase in the length of the growing season, thus increasing primary production and consequently food availability. Individuals may in turn increase in body size, thus producing a trend contrary to Bergmann's rule, as found in the Japanese large field mouse *Apodemus speciosus* (Yom-Tov and Yom-Tov 2004) and the masked shrew *Sorex cinereus* in Alaska (Yom-Tov and Yom-Tov 2005).

Lynx (*Lynx canadensis*) populations in Alaska and much of Canada have been shown to fluctuate greatly over a 9- to 11-year cycle (Elton and Nicholson 1942). Long-term data on the Canadian lynx from eight Canadian provinces display large-scale spatial synchrony in population fluctuations (Ranta et al. 1997a, b). These population cycles are considered to be a di-

rect response to changes in hare *Lepus americanus* abundance through the number of offspring produced and their survival, as well as adult survival (O'Donoghue et al. 1997). This is due to the fact that hares compose as much as 83% of the lynx' diet (Tumilson 1987; O'Donoghue et al. 1997). Slough and Mowat (1996) and O'Donoghue et al. (1997), who studied wild, un-trapped populations of lynx in the Yukon, have shown that hare density affected lynx reproduction, kit survival, young recruitment, adult mortality, emigration and population density. Hence, it is reasonable to assume that lynx population density also affects its body size.

The aim of this study was to use museum specimens to determine whether the body size of the lynx in Alaska is related to its population density and whether it has changed over the second half of the 20th century due to climate warming. We assume that food resources available for growth are inversely related to population density of lynx and predicted that body size is negatively related to population density.

Materials and methods

Measurements were taken from the skulls of 555 (271 females, 284 males) lynx at the University of Alaska Museum of the North, in Fairbanks. A list of the specimens measured and their details (sex, longitude, latitude and year of collection) are provided in Appendix 1. The specimens were adults of known sex and with data on latitude, longitude and year of collection. Skulls of young specimens (in which there exist open sutures between the bones of the skulls) were not studied. Most of the specimens had been either donated by over 50 different trappers or collected by various scientists and staff of the Alaska Department of Fish and Game during the period 1953–2000. The collection effort had not been uniform throughout the study period, and no skulls had been deposited in the museum during the 1980s. Using digital calipers, four measurements were taken from each skull to an accuracy of 0.01 mm: greatest length (GTL) from the front of the premaxilla above the incisors to the back of the lamboidal crest, the maximal width of the zygomatic breadth (ZB), the minimal width of the inter-orbital constriction (IO) and antero-posterior diameter of the upper canine. In mammals, the three skull parameters (GTL, ZB and IO) are correlated with body weight and length (Creighton 1980; Johnston 1991), and in felids the size of the canine is generally associated with prey size (Ewer 1973). We also used principal component analysis (PCA) to combine the

information of the three skull measurements (GTL, ZB and IO) into a single variable.

Several authors have shown that cyclic fluctuation in lynx abundance is genuine, and that the pelt harvest does cycle in parallel to census data (summarized by Royama 1992). However, harvest data are influenced by several factors such as the number of trappers and their trapping effort, duration of the trapping season, weather and reporting accuracy. A calculated cycle based on such data is, by definition, a smoothing function that does not show extreme peaks and troughs, but rather a mean for the multi-annual cycle and, as such, may better represent population fluctuations. We used lynx harvest data for 1977–2003 (kindly provided by H. Golden, Alaska Fish and Game Department) as a proxy for lynx population size. The harvest data represent lynx that were trapped throughout Alaska during those years. In Alaska, all untanned lynx pelts are marked with a plastic locking tag (sealed) issued by the federal government as part of the CITES program. Anyone who harvests a lynx is supposed to have the pelt sealed within 30 days after the close of the season. Nearly everyone does, although a few individuals may tan the pelt themselves to use locally (H. Golden, personal communication). Commercial tanneries and fur auction houses are not allowed to accept any untanned lynx pelts that have not been sealed for processing (H. Golden, personal communication). Hence, the harvest data are expected to offer a fairly accurate representation of changes in the frequency of trapper encounters with lynx and, therefore, the actual number of lynx in Alaska.

Effects of food availability (and population size) on individual lynx are expected to occur mainly during the period of rapid growth, which in mammals (whose growth is asymptotic) is the year of birth. However, although we used only adult animals, we did not know their ages. We therefore tested the effect of the predicted population density in the year of collection (X) and each of the 4 years before it on the skull parameters.

The data were analysed using two approaches. With the first, we used multiple regressions to test whether latitude, longitude, sex, year of collection and predicted harvest (at year X-3) affected the four skull parameters and PC1 of all individuals. Predicted harvest is the number of lynx estimated by the calculated cycle to be trapped at year X-3. With the second approach, we used multiple regressions to examine the effects of harvest data and year of collection on yearly means of the residual skull data corrected for sex and longitude (parameters that were found to affect at least one skull parameter significantly). The second

approach was used in order to avoid the problem of varied sample sizes among years.

Results

Lynx harvest data were available for the years 1977–2003, for which we fitted a sinusoidal function

$$[\sin((\text{year} - 1974) \times 6 \times 3.1415/27 - 2.89) \times 727.5 + 2,176.8].$$

The frequency and phase of the sinusoidal function was that of the highest peak in the spectrum of the harvest data found using Fourier transformation. The relative year (1974) was found so that the sinusoidal function maximally matched the actual harvest data. This equation significantly fitted the actual harvest data ($R^2 = 0.301$, $P = 0.003$), and we used the predicted figures from the above equation as a proxy for population density for each of the years for which we had museum specimens. Our calculated population cycle was 9 years, which is very similar to that reported for the province of Yukon, Canada, which borders Alaska (Krebs et al. 2001). For the period 1950–2000, for which our calculated harvest data overlapped with those reported by Novak (1987; 1950–1981) and Statistics Canada (1970–2004), peak years were 1954, 1962, 1971, 1980, 1989 and 1998 in this study and 1955–1956, 1964–1965, 1973–1974, 1981–1982, 1989–1990 and 1998–2000 in the above sources, i.e., our calculated cycle in Alaska significantly matched that observed in Yukon ($F_{1,4} = 2753.7$, $R^2 = 0.999$, $P < 0.0001$). The observed Yukon peaks occurred, on average, 1.6 years later than those predicted for Alaska.

Preliminary examination showed that year X-3 had the most significant effect on all skull parameters (possibly indicating that the average age of our sample is 3 years), and in further tests we used the predicted harvest of this year as a proxy for population size (the percentage values for variation of residual PC1 explained by predicted harvest were 3.8, 9.1, 11.5, 22.2 and 9.9% for years X, X-1, X-2, X-3 and X-4, respectively, and only X-3 was significant at $P = 0.0086$).

The PCA clumped three morphological measurements (GTL, ZB and IO) into a single factor in each of the specimens used. The Eigenvalue was 2.587, and the proportion of variance explained by that factor (PC1) was 86.2%.

Table 1 represents the effects of sex, latitude, longitude and predicted population density in the year X-3 on skull size. All skull parameters were significantly larger in males than in females; year had a significant

Table 1 The effects of sex (dummy variable), year, latitude, longitude and predicted harvest in year X-3 on various skull parameters of the lynx. Coefficients (slopes) are marked b. Significant results are underlined. *GTL* greatest length of the

skull, *ZB* zygomatic breadth, *IO* the width of the interorbital constriction, *C* upper canine diameter, *PC1* the first principal component calculated from *GTL*, *ZB* and *IO*

	GTL	ZB	IO	Canine	PC1
Intercept	159.369	109.443	46.651	6.732	7.827
Sex, b	6.499	3.492	1.488	0.587	1.121
<i>P</i> value	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>
Year, b	-0.017	-0.012	-0.011	0.0004	-0.005
<i>P</i> value	0.0843	0.1435	0.0101	0.7521	0.0277
Latitude, b	0.003	-0.005	-0.042	0.003	-0.009
<i>P</i> value	0.9668	0.9316	0.1906	0.7758	0.5841
Longitude, b	0.029	0.046	0.053	-0.001	0.018
<i>P</i> value	0.4874	0.1565	0.0023	0.7996	0.0450
Harvest, b	-0.002	-0.002	-0.001	-0.0002	-0.001
<i>P</i> value	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>
<i>N</i>	550	550	548	477	548
<i>R</i> ²	0.544	0.403	0.316	0.379	0.477
Overall <i>P</i> value	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>	<u>≤0.0001</u>

negative effect, and longitude had a significant positive effect on *IO* and *PC1*; latitude had no effect on any skull parameter; and predicted harvest had a strong significant negative effect on all parameters. Since the aim of this study was to examine temporal effects on body size, we used the residuals of the four skull parameters and *PC1* corrected for sex and longitude against year of collection and predicted harvest in year X-3 for further analysis. The results indicated that both harvest and year had a significant effect on *PC1*, *GTL*, *ZB* and *IO*, but not on the canine size, and year of collection had a much weaker effect than did harvest (Table 2). The effect of population size (using predicted harvest alone as surrogate) is shown in Fig. 1, where it is plotted against residual *PC1* corrected for sex, longitude and year. Population size explained 22.2% of the variation in *PC1*.

Table 2 The effects of year and predicted harvest in year X-3 on residual skull parameters corrected for sex and longitude. Coefficients (slopes) are marked b. Significant results are underlined. *GTL* greatest length of the skull, *ZB* zygomatic breadth, *IO* the width of the interorbital constriction, *C* upper canine diameter, *PC1* the first principal component calculated from *GTL*, *ZB* and *IO*

	GTL	ZB	IO	Canine	PC1
Intercept, a	60.21	63.98	55.41	6.63	18.81
Year, b	-0.029	-0.031	-0.027	-0.003	-0.009
<i>P</i> value	0.050	0.028	0.0313	0.2572	0.0154
Harvest, b	-0.001	-0.001	-0.001	-0.00001	-0.0003
<i>P</i> value	0.0142	0.0098	0.0393	0.2972	≤0.0059
<i>N</i>	30	30	30	29	30
<i>R</i> ²	0.287	0.323	0.264	0.082	0.363
Overall <i>P</i> value	0.0103	≤0.0052	≤0.0160	0.3290	≤0.0023

Discussion

We found that skull (and hence body) size of the lynx in Alaska was significantly and negatively related to a measure of population density. It also slightly declined during the second half of the 20th century. We shall discuss the effect of population density first, as it has a stronger effect on body size than has year of collection.

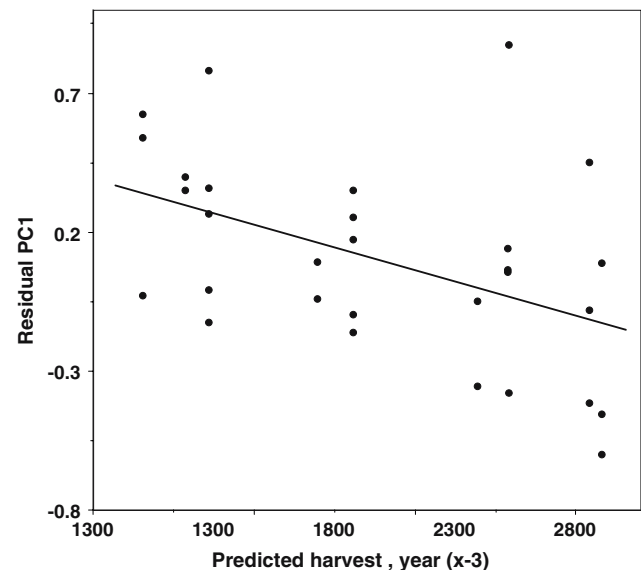


Fig. 1 The relationships between the residuals of *PC1* (corrected for sex, longitude and year of collection) and predicted harvest at year X-3. Predicted harvest is the number of lynx estimated by the calculated cycle to be trapped at year X-3. Res. *PC1* = 0.828–0.0003*(Harvest), *R*² = 0.222, *F*_{1,28} = 7.988, *P* = 0.0086

Body size and population density

It is well known that various life-history parameters are affected by population density (Newton 1998). Cyclic population fluctuations in voles and lemmings are characterised by a relatively repeatable pattern of change in body weight (Chitty Effect: Boonstra and Krebs 1979), with individuals from increasing populations typically larger than those in declining populations (Ergon et al. 2001). The causes of the above trends have been disputed (Keith and Windberg 1978; Hodges et al. 2006). Norrdah and Korpimäki (2002) suggested that the observed changes in voles are a result of the combined effect of changes in predation pressure and availability of food. Royama (1992), who analysed demographic data of the snowshoe hare in Canada, claimed that body-weight changes are governed by the quantity and quality of foods, which, in turn, depend on hare density. Similarly, birth weight of red deer fawns was density dependent (Nussey et al. 2005), as was body size in adult red deer (Mysterud et al. 2001), roe deer (Toigo et al. 2006), brown bear (Zedrosser et al. 2006) and barnacle goose (Larsson and Forslund 1991). Both (1998) showed experimentally that fledgling weight of great tits was related to population density, and a negative relationship between territory size and fledgling weight was found during a long-term study of great tits in Oxford (Wilkin et al. 2006). The authors of this latter study attributed this density-dependent relationship to reduced nestling provisioning in high-density areas in terms of food quantity and/or quality, and also to possible intraspecific interference. We suggest that the negative relationship between population density and body size found here is a result of food shortage during peak years and abundant food during trough years, as was suggested for the great tits in Oxford (Wilkin et al. 2006). However, since our results are only correlational, only an experimental study can support or refute our suggestion.

Skull size was best related to population density 3 years before death, and such a carry-over effect is known from other natural populations (Royama 1992). Although we do not know the ages of the lynx in our sample, this finding probably indicates that conditions during the growth period (rather than during adulthood) have an important effect on body size of the lynx. It is well known that prey availability affects various life history parameters (i.e., reproduction, kit survival, young recruitment, adult mortality, emigration and population density) of lynx (Slough and Mowat 1996). The above finding that lynx body size was negatively related to its population density is probably

due to variations in prey availability. Quality and quantity of food during the growth period have been shown to correlate with growth rate and body mass of juveniles of animals ranging from fish to mammals (Jorgensen 1992; Galatti 1992; Madsen and Shine 2000; Lepage et al. 1998; Larsson and Forslund 1991; Bolton et al. 1982); we suggest that this was also the case in this study.

In felids, the size of the canine is generally associated with prey size (Ewer 1973). We found that canine size did not change in accordance with population density, unlike other skull parameters. This is explained by the lynx continuing to rely chiefly on hares as their main prey, even during years of low hare populations. This dependence is considered to be the cause of the lynx cycle. However, only an experimental study could support or refute this assumption.

Body size and Bergmann's rule

We also found that two of the four skull parameters measured—ZB and IO—significantly declined during the study period; GTL was also seen to decrease, but not significantly so ($P = 0.05$) (Table 2). Similar recent declines in body size of birds and mammals have been observed in several countries. For example, Smith et al. (1998) demonstrated that the average body size of woodrat populations (*Neotoma albigula*) in New Mexico had decreased by approximately 15% within a decade. Similarly, four of the five passerine bird species studied by Yom-Tov (2001) in Israel decreased in body size during the second half of the 20th century in Israel. Body size decreases have also been observed among several species of British passerines studied continuously during the last three decades in England (Yom-Tov et al. 2006). All these declines were attributed to climate warming, in accordance with Bergmann's rule.

We do not know the cause of the observed, relatively small, decline in some skull parameters in the lynx, but suggest that it may reflect either a reaction to warming of the climate (conforming to Bergmann's rule) or a long-term decline of snowshoe hares. However, we have no data at present to support either suggestion.

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