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Body size in the Eurasian lynx in Sweden: dependence on prey availability

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Abstract The Eurasian lynx (*Lynx lynx)* is a common predator of both roe deer (*Capreolus capreolus*) and reindeer (*Rangifer tarandus*) in Sweden. We investigated the influence of prey availability, latitude, sex, and age on body size and body mass variation of the Eurasian lynx in Sweden, using data from 243 specimens whose locality of capture, year of capture, sex, and age were known. We found that both body size and body mass of the lynx in Sweden are mainly affected by the lynx sex and age but also by the availability of prey during the first year of life. Body size and body mass of lynx as well as the density of roe deer increased from Central Sweden to South. Furthermore, body size and body mass of lynx increased from Central Sweden to North (i.e. within the reindeer husbandry area). Lynx body size was slightly smaller within the reindeer husbandry area (approximately north of latitudes 62°–63°N) compared to outside, probably because reindeer are more difficult prey to hunt, as well as being migratory and thus an unpredictable prey for the Eurasian lynx compared to the non-migratory roe deer. Our results support a growing body of evidence showing that food availability at growth has a major effect on body size of animals.

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Introduction

Changes in resource availability affect most life-history traits of vertebrates (Fowler 1987; Stearns 1992). Body mass or body size is affected by food availability (Ulijaszek et al. 1998; Yom-Tov et al. 2006, 2007), and it is usually a good proxy for individual performance (Clutton-Brock 1991). As a general rule, the heaviest individuals survive better at all ages (Gaillard et al. 1997, 2000), and these individuals also produce more offspring over their life span than lighter individuals (Albon et al. 1983; Hewison 1996). Moors (1980) and King (1989) claimed that a large body size is an advantage for a male in the competition for females, especially among polygamous carnivores (King 1989). There is generally a consistent inverse relationship between body mass and population density (Skogland 1983; Hewison et al. 2002), and birth weight is in turn related to adult body mass (Dooney and Gunn 1981; Albon et al. 1987; Clutton-Brock et al. 1987). Thus, the level of resource availability during early growth can determine adult body mass and, hence, the survival and subsequent reproductive rate of individuals (Albon et al. 1987; Skogland 1990; Rose et al. 1998; Gaillard et al. 2003 for a review on deer).

Food availability (and consequently body mass) may be influenced by several factors, including climate, as is the case with the water python *Liasis fuscus* in Australia, where the abundance of their main prey (the dusky rat *Rattus colletti*) is determined by rainfall (Madsen and Shine 2000). Body size of juveniles and/or adults was negatively related

to population density in the red deer *Cervus elaphus* (Mysterud et al. 2001a, b), roe deer *Capreolus capreolus* (Pettorelli et al. 2002), brown bear *Ursus arctos* (Zedrosser et al. 2006) and great tit *Parus major* (Both 1998; Wilkin et al. 2006). Recently, Yom-Tov et al. (2007) have shown that body size of the Canadian lynx *Lynx canadensis* in Alaska varies in accordance with the cycles of population density of the snowshoe hare *Lepus americanus* during the period of growth of the lynx. In Norway, where food conditions for the otter *Lutra lutra* have improved due to fish farming, otter body size was shown to be related to fish farming production during the otter's year of birth (Yom-Tov et al. 2006).

The Eurasian lynx *Lynx lynx* is widely distributed in the Palearctic, where it is an important predator on a wide range of mammals, birds and other animals (Haglund 1966; Aanes et al. 1998; Jedrzejewski and Jedrzejewska 1998; Matyushkin and Vaisfeld 2003). In the Yukon, Canada, prey availability has affected Canadian lynx reproduction, kit survival, young recruitment, adult mortality, emigration, and population density (Slough and Mowat 1996; O'Donoghue et al. 1997). During the first half of the twentieth century, lynx numbers in Scandinavia were decimated, but the removal of bounties during the second half of the twentieth century and some level of protection have enabled its recovery, and at present, there are reproductive lynx populations in most of Sweden and Norway (Liberg and Andrén 2006). Concomitant with the increase in lynx populations there has been a rise in conflicts involving predation of the semi-domestic reindeer *Rangifer tarandus* (Pedersen et al. 1999), as well as some domestic sheep *Ovis aries* (Odden et al. 2002) and wild roe deer *Capreolus capreolus* (Haglund 1966; Aanes et al. 1998). The reindeer-herding Sámi people traditionally live by following the semi-domesticated reindeer between their summer grazing land in the mountains and winter grazing land in the forests, and subsist on their meat, skins, milk, and antlers. In the reindeer husbandry area, i.e. the three northernmost counties in Sweden (approximately 40% of Sweden north of latitudes 62°–63°N) semi-domestic reindeer make up 70–80% of the lynx diet (Pedersen et al. 1999). Outside the reindeer husbandry area, i.e. approximately the southern half of Sweden (south of latitudes 62°-63°N), roe deer make up 60–95% of the lynx diet (Haglund 1966; Aanes et al. 1998). The recent increase in lynx numbers in Sweden has coincided with the decline in the roe deer bag (i.e. number of deer hunted; Liberg and Andrén 2006).

The aim of this study was to investigate the effect of roe deer and reindeer density on skull and body size of the Eurasian lynx over a geographical gradient of prey availability in Sweden. As the lynx should be considered as an income breeder (sensu Jönsson 1997), relying on current resource intake for survival, reproduction, growth, and individual

adult body mass probably varies very little over years since they do not store large fat reserves to compensate for changes in per capita food availability. During their growth period, all predatory animals are highly sensitive to changes in environmental conditions and prey availability, and we therefore predict that (1) the lynx during the first year in life should show marked among-year variation in body size (using skull size as a proxy) and body mass in relation to resource availability, i.e. roe deer and reindeer; and (2) that the effect of roe deer density would disappear within the reindeer husbandry area (approximately north of latitudes 62°–63°N), where the migratory and unpredictable reindeer become the main prey for lynx. We tested these predictions using data from lynx shot in Sweden that had been aged, weighed and measured, and analysed in relation to a proxy for prey availability during the first year of life.

Materials and methods

Skulls of 243 (106 females, 137 males) Eurasian lynx collected between 1987 and 2006 were measured at the Swedish Museum of Natural History (NRM), Stockholm, Sweden. Of these, 124 were from outside the reindeer husbandry area and 119 from within it (Table 1). The total sample size for lynx body mass was slightly smaller (231).

The specimens were adults of known sex and with data on latitude, longitude, and year of collection. Specimens younger than 1 year (open sutures between the bones of the skulls) were not measured. Although for body size and body mass, animals younger than 1 year could be considered as the most sensitive age class in relation to prey availability, we did not use this age class from the analysis. This was mainly due to very low sample size (eight animals) and the fact that cubs at this stage are undergoing such a rapid growth spurt that their age is probably much more important for the actual body size and body mass than food availability. Age (in 1-year intervals) was determined by counting annual rings in cross sections of the canine teeth, a method that can determine age to within an accuracy of 1 year (Matson 1981; http://www.matsonslab.com/html/Techniques/CementumAging/CementumAging.htm#Standardized). Most lynx in this study (in all but five cases) had been hunted

Table 1 Sex and age distribution of the lynx sample size by reindeer husbandry area

Age (years)	Reindeer area		Outside reindeer area	
	Male	Female	Male	Female
1	16	13	17	13
2	24	10	13	9
3 and above	31	25	36	36

under licenses issued by the Swedish Environmental Protection Agency. Most of the carcasses were weighed either in the laboratory or by the hunters, but on different scales. Using digital callipers, three 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), and the minimal width of the interorbital constriction (IO). In mammals, the three skull parameters (GTL, ZB, and IO) are correlated with body weight and length (Creighton 1980; Johnston 1991). A list of the measured specimens will be provided on request.

No actual estimates of local roe deer density or availability exist in Sweden over the large geographical scale at which this study was preformed. However, we used reported roe deer bag size per km^2 as a coarse proxy to determine spatial and temporal variation in roe deer availability. The bag records collected during the 6-month hunting period each year were assigned to such coarse spatial scales (from 1997 approximately 300–1,500 km^2, i.e. at the level of hunting districts or prior to that at the county level, >5,000 km^2) in order to reduce possible fine-scaled local changes or differences in hunting behavior between years. This approach was used by Mysterud et al. (2001a, b) in Norwegian red deer, Grøten et al. (2005), Mysterud and Østbye (2006) and Nilsen et al. (2009) in Norwegian roe deer and Zannèse et al. (2006) in French roe deer. To support the viability of this proxy, we assume that hunting effort is constant between years and areas. We consider this valid for the following reasons: first, Grøten et al. (2005) reported a very good concordance between bag records of roe deer and three other independent indexes of roe deer abundance. Andrén and Liberg (2008) also found a good concordance between pellets groups counts of roe deer and bag records of roe deer ($r = 0.85$, $df = 42$, $P < 0.0001$). Further, in Sweden, there is an open hunting season for roe deer, of roughly 6 months with no bag limits, which has not changed since the 1980s and local bag records were collected using the same reporting system every year by the Swedish Hunters Association for Hunting and Wildlife Management, ensuring consistency between years and areas. This means that we used hunting bag size (number of killed roe deer per km^2 in a certain year) in the district where each lynx was killed, to an index of roe deer density at the birth year (RAB; Fig. 1). Bag size values ranged between 0 and 25 at latitudes 67°N and 60.35°N, respectively. Thus, although bag record is a crude index of roe deer abundance, we argue that the large spatial variation in bag record (1–2 orders of magnitude) depicts a true variation in roe deer abundance. Prey density index values were used for the district from which each lynx was collected, but it should be noted that lynx males collected after their first year may well have travelled 100–200 km away from
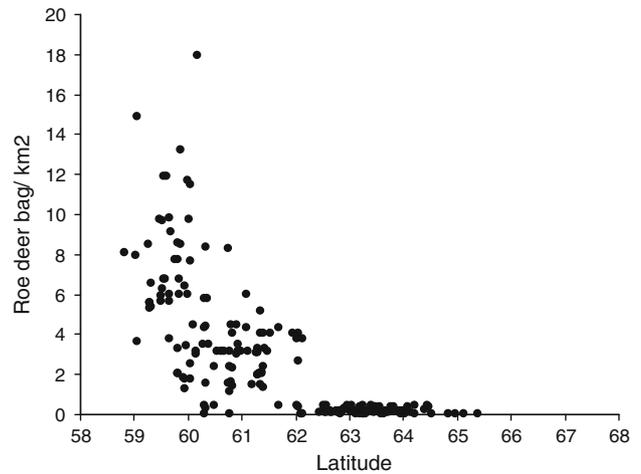
Fig. 1 Roe deer density (shot roe deer/km^2) in relation to latitude. The reindeer husbandry area is approximately north of the latitudes 62°–63°N

the district in which they were born, whereas lynx female usually disperse less than 100 km (Liberg and Andrén 2006). However, roe deer density is geographically continuous and neighboring districts have similar densities. Long distance dispersal will weakened the relationship between body size and availability of prey during the first year of life.

The reindeer husbandry areas cover approximately 40% of Sweden. The area is divided into 51 reindeer-herding districts, and we had data on the number of reindeer per reindeer-herding district (official statistics from the Swedish Board of Agriculture). However, the reindeer migrate from their summer mountainous ranges in the northwest to their forest winter ranges in the southeast, usually 100–300 km apart. The lynx are found throughout Sweden and are permanent residents that do not follow the reindeer migration (Danell et al. 2006). Therefore, we discarded the data of reindeer availability as a continuous measure. Instead, we used presence/absence of reindeer (REIN), i.e. whether the lynx was collected from within the reindeer husbandry area or not. The total reindeer population after the slaughter in December has varied between 220,000 and 260,000 during the last 10 years and the number of reindeer within a reindeer-herding district is mainly influenced by the slaughter (official statistics from the Swedish Board of Agriculture). Within the reindeer husbandry area, going from south to north, the number of reindeer within Jämtland County (49,400 km^2) has been around 45,000 for the last 10 years; around 55,000 reindeer within Västerbotten County (55,400 km^2); and around 140,000 reindeer within Norrbotten County (99,900 km^2). Thus, the density of reindeer increases northwards and the mean densities (assuming a sedentary reindeer population and an even distribution) within these

counties have been 0.9 reindeer/km^2, 1.0 reindeer/km^2 and 1.4 reindeer/km^2, respectively.

We used principal component analysis (PCA) to combine the data on the three lynx skull measurements (GTL, ZB, and IO, normalized by using the formula $10^{X/100}$, where X is the dependent factor) into a single variable. Our analysis aimed to explain the variance in body size (PC1) and body mass as a function of a series of independent variables: presence/absence of reindeer (REIN), sex (categorical variables), as well as age, latitude (LAT) and longitude (to control for possible bio-geographical gradients), and the proxy for population density of roe deer (RAB), as continuous variables. We examined the effects of these variables on both body size (PC1) and body mass by fitting general linear models (GLM) using R 2.4.1 statistical software (R Development Core Team; Ihaka and Gentleman 1996). Sex and age were included in all models, thus, the effects of these two variables were not formally evaluated. We selected the best model (out of 28 models) using the Akaike's Information Criterion (AIC; Burnham and Anderson 2002; Johnson and Omland 2004). This approach weighs all the possible subsets (i.e. models) by the amount of the variance explained and model complexity (i.e. the number of explanatory variables; K). When $n/K < 40$, the AIC values were corrected for small sample size (AIC$_c$) using the equation in Burnham and Anderson (2002). Level of support for an AIC$_c$ value was evaluated by ΔAIC$_c$ (i.e. ΔAIC$_c$ = AIC$_c$ − AIC$_{min}$; Burnham and Anderson 2002). Models with ΔAIC$_c$ values of 0–2 provide similar support (Burnham and Anderson 2002).

Results

Body size index and body mass

The PCA clumped three normalized morphological measurements (GTL, ZB, and IO) into a single factor for each of the specimens used. Eigenvalue was 2.5914, and the proportion of variance explained by that factor (PC1) was 86.4%. Body mass was normally distributed (Shapiro–Wilk W Test: $P = 0.14$ and 0.26 for males and females, respectively). All three skull parameters as well as PC1 were significantly related to body mass (GTL: $P < 0.0001$, $R^2 = 0.61$; ZB: $P < 0.0001$, $R^2 = 0.66$; IO: $P < 0.0001$, $R^2 = 0.49$; PC1: $P < 0.0001$, $R^2 = 0.70$). Males had significantly larger PC1 ($t_{106,137} = 16.58$, $P < 0.0001$) and were heavier ($t_{99,132} = 14.86$, $P < 0.0001$) than females.

Independent variables

Preliminary examination revealed that longitude was not related to either PC1 or body mass, and it was removed

from further analysis. Further, tolerance (i.e. $1 − R^2$), which is a measure of colinearity between the independent variables, was low for the relationships between latitude and RAB (0.27). The low tolerance implies high correlation among the independent variables. Hence, latitude (LAT) and roe deer density (RAB) were not included in the same models.

Body size, prey density, and latitude

PC1 (body size): The AIC model selection showed that all four predictors (SEX, AGE, RAB, and REIN; Table 2) comprised the best model for PC1 variation. The two models including the interaction SEX and AGE or not were almost similar (ΔAIC$_c$ = 0.33; Table 2). Following Burnham and Anderson (2002) rules of thumb of parsimoniousness, we selected the model without the interaction term. PC1 (body size) increased with an increase in RAB (Table 3; Figs. 2, 3). The slope between body size (PC1) and roe deer density (RAB) was slightly steeper within the reindeer husbandry area as compared to outside, as shown by the interaction term RAB*REIN (Tables 2, 3; compare Figs. 2, 3, note the different scales of roe deer density in the two figures).

The best model including latitude (LAT) also included REIN and the interaction REIN and LAT (Table 3). The interaction term shows that the effect of latitude were different outside (decreasing body size with latitude) and within

Table 2 Effect of SEX, AGE, RAB (roe deer density), REIN (outside or within the reindeer husbandry area) and LAT (latitude) on PC1 (body size) of the lynx in Sweden

Variables included	df	AIC$_c$	ΔAIC$_c$
SEX + AGE + SEX*AGE + RAB + REIN + RAB*REIN	6	451.49	0
SEX + AGE + RAB + REIN + RAB*REIN	5	451.81	0.33
SEX + AGE + REIN + LAT + REIN*LAT	5	457.33	5.84
SEX + AGE + SEX*AGE + REIN + LAT + REIN*LAT	6	457.82	6.33
SEX + AGE + RAB + REIN	4	458.84	7.36
SEX + AGE + SEX*AGE + RAB + REIN	5	458.64	7.50
SEX + AGE + SEX*AGE	3	480.63	29.1
SEX + AGE	2	482.02	30.5
SEX	1	533.87	82.4
AGE	1	672.69	221.2
"NULL"	0	674.29	242.8

The best six models out of 28 models (all with SEX and AGE included), selected by the Akaike information criterion (AIC), are presented. ΔAIC$_c$ is the difference between the AIC each model to the best model (i.e. lowest AIC$_c$). The selected models including RAB (roe deer density) or LAT (latitude), respectively, are in bold. We have also included the models with only SEX and AGE, as well as the null-model (i.e. without any independent variables) for comparison
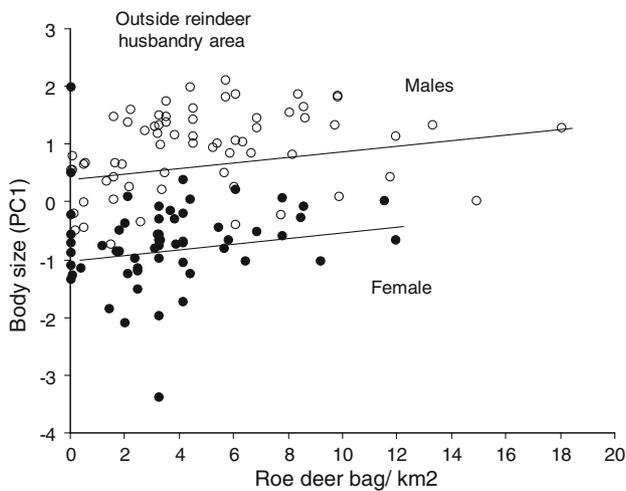
Table 3 Results of a multiple regression calculating the effects of SEX, AGE, RAB (roe deer density), REIN (outside or within the reindeer husbandry area) and LAT (latitude) on PC1 (body size) of the lynx in Sweden

Term	Estimate	t value	Partial P
Model 1			
Intercept	−1.12	10.6	<0.0001
SEX[a]	1.41	17.75	<0.0001
AGE	0.093	6.68	<0.0001
RAB	0.040	2.48	0.014
REIN[b]	−0.39	3.24	0.001
RAB*REIN[b]	1.14	3.01	0.003
Model 2			
Intercept	5.54	1.81	0.07
SEX[a]	1.45	17.98	<0.0001
AGE	0.11	7.81	<0.0001
REIN[b]	−14.9	3.13	0.002
LAT	−0.11	2.15	0.03
REIN[b]*LAT	0.23	3.06	0.002

Model 1: $F_{5,236} = 86.97$, $R^2 = 0.64$, $P < 0.0001$ and Model 2: $F_{5,236} = 83.74$, $R^2 = 0.63$, $P < 0.0001$
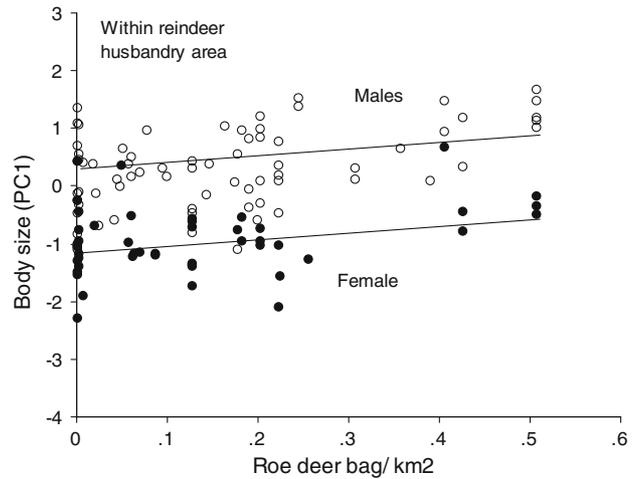
[a] SEX coded as females = 0 and males = 1

[b] REIN coded as south of the reindeer husbandry area = 0 and within the reindeer husbandry area = 1
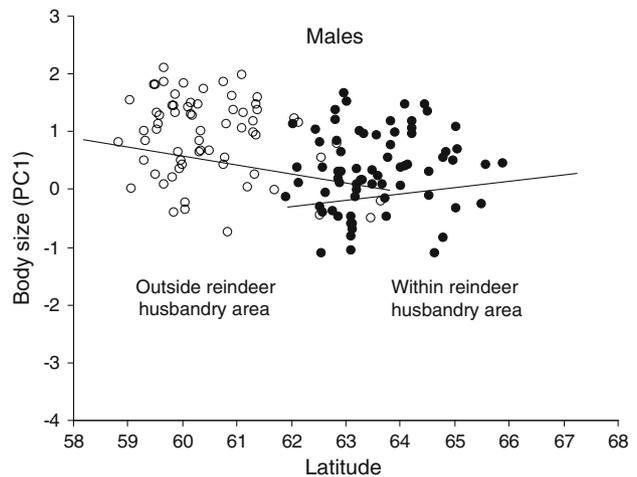

Fig. 3 Eurasian lynx body size (PC1 of three skull measurements) in relation to roe deer density (shot roe deer/km^2) in the year of birth (RAB) within the reindeer husbandry area (REIN = 1). Note the different scales for roe deer bag/km^2 in Figs. 2, 3. *Open circles* indicate males (SEX = 1) and *black dots* indicate females (SEX = 0). The *lines* are based on the equations given in Table 3 (Model 1), with AGE = 3. Equation: PC1 = −1.12 + 1.41 × SEX (if female = 0; if male = 1) + 0.093 × 3 + 0.040 × RAB − 0.39 × 1 + 1.14 × RAB × 1

Fig. 2 Eurasian lynx body size (PC1 of three skull measurements) in relation to roe deer density (shot roe deer/km^2) in the year of birth (RAB) outside the reindeer husbandry area (REIN = 0). Note the different scales for roe deer bag/km^2 in Figs. 2, 3. *Open circles* indicate males (SEX = 1) and *black dots* indicate females (SEX = 0). The *lines* are based on the equations given in Table 3 (Model 1), with AGE = 3. Equation: PC1 = −1.12 + 1.41 × SEX (if female = 0; if male = 1) + 0.093 × 3 + 0.040 × RAB − 0.39 × 0 + 1.14 × RAB × 0

Fig. 4 Eurasian lynx body size (PC1 of three skull measurements) in relation to latitude for males (SEX = 1). The reindeer husbandry area is approximately north of the latitudes 62°−63°N. *Open circles* indicate males outside the reindeer husbandry area (REIN = 0) and *black* indicate males within the reindeer husbandry area (REIN = 1). The *lines* are based on the equations given in Table 3 (Model 2), with AGE = 3. Equation: PC1 = 5.54 + 1.45 × 1 + 0.11 × 3 − 14.9 × REIN (if outside = 0; if within = 1) − 0.11 × LAT + 0.23 × REIN (if outside = 0; if within = 1) × LAT

(increasing body size with latitude) the reindeer husbandry area (Figs. 4, 5). The model including LAT was weaker than the model including RAB (ΔAIC$_c$ > 4; Table 2).
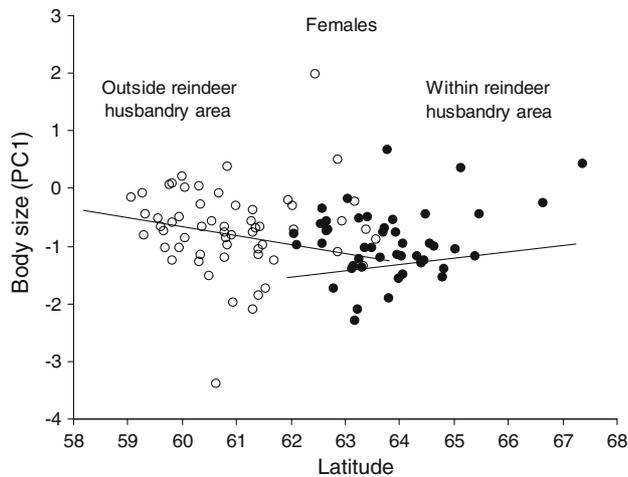
Body mass, prey density, and latitude

Body mass: The AIC model selection showed that all four predictors (SEX, AGE, REIN, LAT and the interaction REIN and LAT; Table 4) comprised the best model for

Fig. 5 Eurasian lynx body size (PC1 of three skull measurements) in relation to latitude for females (SEX = 0). The reindeer husbandry area is approximately north of the latitudes 62°–63°N. *Open circles* indicate females outside the reindeer husbandry area (REIN = 0) and *black dots* indicate females within the reindeer husbandry area (REIN = 1). The *lines* are based on the equations given in Table 3 (Model 2), with AGE = 3. Equation: PC1 = 5.54 + 1.45 × 0 + 0.11 × 3 − 14.9 × REIN (if outside = 0; if within = 1) − 0.11 × LAT + 0.23 × REIN (if outside = 0; if within = 1) × LAT

body mass variation. The interaction term shows that the effect of latitude were different outside (decreasing body mass with latitude) and within (increasing body mass with latitude) the reindeer husbandry area. The best model including RAB also included REIN, but not the interaction term (Table 4). The partial effect of RAB was not significant, while the partial effect of REIN was significant (Table 5).

Discussion

The findings of this study indicate a strong effect of sex and age on both body size (PC1) and body mass, as males are larger than females and both sexes grow for several years after birth. However, while sex and age effects on body size and mass should be considered as a trivial finding and here treated rather as constants, we found that both body size (skull size, PC1) and body mass of the Eurasian lynx were also affected by our indices of prey density [roe deer bag (RAB) and the presence/absence of reindeer (REIN); Tables 2, 4]. This conclusion is also justified by following Burnham and Anderson (2002) rules of thumb of parsimoniousness, as less complex models having ΔAIC within 1–2 of the best model have substantial support and should receive consideration in making inference. We therefore found support for our prediction; i.e. that adult body size and body mass of the Eurasian lynx in Sweden are influenced by our proxy for food availability.

Table 4 Effect of SEX, AGE, RAB (roe deer density), REIN (outside or within the reindeer husbandry area) and LAT (latitude) on body mass of the lynx in Sweden

Variables included	df	AIC$_c$	ΔAIC$_c$
SEX + AGE + REIN + LAT + REIN*LAT	5	1,042.62	0
SEX + AGE + SEX*AGE + REIN + LAT + REIN*LAT	6	1,042.66	0.04
SEX + AGE + SEX*AGE + REIN	4	1,049.08	6.46
SEX + AGE + SEX*AGE + RAB + REIN	5	1,049.21	6.59
SEX + AGE + REIN	3	1,049.31	6.69
SEX + AGE + SEX*AGE + RAB + REIN + RAB*REIN	7	1,049.59	6.97
SEX + AGE + SEX*AGE	3	1,065.80	23.2
SEX + AGE	2	1,066.82	24.2
SEX	1	1,111.41	68.8
AGE	1	1,232.22	189.6
"NULL"	0	1,249.81	207.2

The best six models out of 28 models (all with SEX and AGE included), selected by the Akaike information criterion (AIC), are presented. ΔAIC$_c$ is the difference between the AIC each model to the best model (i.e. lowest AIC$_c$). The selected models including RAB (roe deer density) or LAT (latitude), respectively, are in bold. We have also included the models with only SEX and AGE, as well as the null-model (i.e. without any independent variables) for comparison

Table 5 : Results of a multiple regression calculating the effects of SEX, AGE, RAB (roe deer density), REIN (outside or within the reindeer husbandry area) and LAT (latitude) on body mass of the lynx in Sweden. Model 1: $F_{5,225} = 70.40$, $R^2 = 0.60$, $P < 0.0001$ and Model 2: $F_{5,225} = 67.16$, $R^2 = 0.59$, $P < 0.0001$

Term	Estimate	t value	Partial P
Model 1			
Intercept	42.22	3.78	0.0002
SEX[a]	5.08	16.62	<0.0001
AGE	0.37	7.32	<0.0001
REIN[b]	−63.83	3.26	0.001
LAT	−0.46	2.49	0.012
REIN[b]*LAT	1.00	3.21	0.002
Model 2			
Intercept	14.66	33.31	<0.0001
SEX[a]	4.41	8.78	<0.0001
AGE	0.25	2.92	0.004
SEX*AGE	0.18	1.65	0.10
RAB	0.073	1.39	0.16
REIN[b]	−1.02	2.66	0.008

[a] SEX coded as females = 0 and males = 1

[b] REIN coded as south of the reindeer husbandry area = 0 and within the reindeer husbandry area = 1

It is well known that conditions experienced during early development affect growth and ultimately adult body size in many birds and mammals (Geist 1987; Henry and Ulijaszek 1996; Lindström 1999). It has been shown that growth rate and body mass of animals ranging from fish to mammals are related to quality and quantity of food during the growth period (Jorgensen 1992; Galatti 1992; Madsen and Shine 2000; Lepage et al. 1998; Larsson and Forslund 1991; Bolton et al. 1982; Yom-Tov et al. 2006) and we suggest that this is the case in this study too. Yom-Tov et al. (2007) showed that body size of the Canadian lynx in Alaska is related to its population density in the year of growth, and contended that this effect is due to food availability. When lynx population density was high, food availability decreased, and body size of lynx born in those years was smaller.

The smaller proportion explained for body mass (59 and 60%, respectively; Table 5) is probably due to the fact that this parameter depends on many factors, among them time and size of latest meal, defecation, blood loss after the animal was shot, and the fact that the carcasses were weighed using different scales and by different people.

The roe deer is most abundant in southern Scandinavia, outside the reindeer husbandry area south of latitude 62°N, and its density increases from north to south, while reindeer do not occur south of this latitude. In the roe deer area, the lynx body size and mass decrease within the roe deer area in parallel with the decrease in its prey availability (towards latitude 62°N, Tables 3, 5; Figs. 1, 2). However, the relationship between lynx body size and prey availability is more complex within the reindeer husbandry area. The lynx body size in the reindeer area increased with latitude (Tables 3, 5; Figs. 4, 5), maybe because on a broad scale there is a small increase in reindeer mean density towards the north. Further, the effect of increased roe deer density is somewhat stronger (i.e. slightly steeper slope) in the reindeer husbandry area than in the roe deer area, but the range in roe deer density is smaller within the reindeer area (0–0.5 shot roe deer/km^2; Fig. 3) as compared to the roe deer area (0–18 shot roe deer/km^2; Fig. 2). Thus, we did not find support for our second prediction that the effect of roe deer density on lynx body size should disappear within the reindeer husbandry area, where reindeer become the main prey. Although reindeer is the main prey for lynx within the reindeer area, an additional prey even at low density seems to affect the body size in lynx.

We found that the lynx body size is on average slightly larger outside the reindeer husbandry area than within it, as the term REIN was negative (Tables 3, 5, REIN was coded as south of the reindeer husbandry area = 0 and within the reindeer husbandry area = 1). Data from the two study areas of intensive lynx research (Andrén et al. 2002; Danell et al. 2006), located in northern Sweden (67°N) and in

southern Sweden (60°N), support this conclusion. The mean reindeer density (assuming a sedentary reindeer population and an even distribution) was about 1.4 reindeer/km^2, whereas the roe deer density in the southern study area was 3–4/km^2 (Danell et al. 2006). The adult body mass (60–65 kg) of a reindeer is about twice that of an adult roe deer (20–30 kg). Therefore, the total available prey biomass is roughly the same within the northern area (67°N) as it is in the study area in southern Sweden (60°N). However, reindeer are migratory while the lynx are resident (Danell et al. 2006). Furthermore, reindeer are larger than roe deer and thus harder to prey upon and their availability as prey may depend on several factors, among them population density, and the amount and hardness of the snow. Eurasian lynx density is higher in southern than in northern Sweden (Liberg and Andrén 2006). The smaller lynx body size inside the reindeer husbandry area in northern Sweden is possibly an indication that the reindeer is a harder prey to catch (for a 3-year-old male the predicted PC1 is 0.179 and 0.889 and body mass is 19.3 and 20.9 kg inside (RAB = 0) and outside (RAB = 8), respectively; Model 1 in Table 3 and Model 2 in Table 5). Reproduction in the lynx shows the same pattern, with lower reproduction in northern (67°N) compared to southern Sweden (60°N) (Andrén et al. 2002).

In this study, we used reindeer availability as a categorical variable, as reindeer are migratory between their summer ranges in the mountains and winter ranges in the forest, usually 100–300 km apart, while the Eurasian lynx are resident. Therefore, a detailed description of the number of reindeer in a reindeer-herding district is not a good estimate of the available resources for Eurasian lynx. However, on a broad scale there is a small increase in mean reindeer density (assuming a sedentary reindeer population and an even distribution) with latitude within Sweden, from 0.9 reindeer/km^2 in the southernmost county within the reindeer husbandry area (Jämtland) to 1.4 reindeer/km^2 within the northernmost county (Norrbotten).

Lynx body size seems to be affected by both roe deer density at birth (RAB) and presence/absence of reindeer (REIN). From the perspective of the two opposite distributional patterns of the two prey species this most likely shapes the two opposing trends in lynx size in Sweden: i.e. lynx become larger towards the south with increasing roe deer densities, but also towards the north where reindeer are available. Thus, the lynx in central Sweden at about latitudes 62°–63°N are the smallest in the country, where prey availability is most scarce (Figs. 4, 5).

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