Lynx Body Size in Norway is Related to its Main Prey (Roe Deer) Density, Climate, and Latitude

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Abstract We studied the effect of various factors on body size variation of the Eurasian lynx in Norway, using data from 374 lynx collected between 1960 and 1976 and whose locality of capture, year of birth, sex, and age were known. Body size of lynx in Norway was mainly affected by sex and age. Female skull size (and by implication body size) was also positively affected by the availability of its main prey (roe deer) and by latitude, and negatively by the North Atlantic Oscillation (NAO). Male size was not affected by any of the environmental factors examined. We interpret the effects of NAO and latitude on body size through their effect on the local climate and particularly snow conditions. We suggest that females are more sensitive to environmental factors than males.

Keywords Eurasian lynx · Norway · Roe deer · *Capreolus capreolus* · NAO · Latitude

INTRODUCTION

The lynx (*Lynx lynx*) is widely distributed in the boreal region of Northern Europe and Siberia, from Scandinavia to the Bering Straits (Kvam 1990; Nowell and Jackson 1995). Due to a relatively large population of lynx, Scandinavia is the most important area for this species in Western Europe and before the end of the nineteenth century it was relatively common in most parts of Norway north to the Arctic Circle. In Norway, a state bounty was paid for lynx from 1845 to 1980 (Central Bureau of Statistics of Norway 1978, 1979, 1980, 1981). The number of lynx taken decreased rapidly during the early part of the last century, and by the 1930s the lynx was almost extinct in southern Norway. However, it was still relatively

common in the county of Nord-Trøndelag in central Norway (Olstad 1945).

Following the abolition of lynx hunting in Sweden between 1928 and 1943 there was an apparent expansion of the lynx from central Norway and neighboring parts of Sweden into both southern and northern Norway. This expansion was probably assisted by the expansion of the roe deer (*Capreolus capreolus*) during the same period (Raiby 1968; Hagen 1969; Cederlund and Liberg 1995). From the 1970s lynx were found in most of the country (Fig. 1). The westernmost counties of Hordaland and Sogn og Fjordane, which had never previously any stable lynx population, are today the only counties in southern Norway where the lynx occurs sparsely.

Roe deer and semi-domestic reindeer (*Rangifer tarandus*) are the most important natural prey for the lynx in Norway, but they commonly feed also on mountain hare (*Lepus timidus*), tetraonids (*Tetraonidae*), and domestic sheep (Kvam 1990; Sunde and Kvam 1997; Sunde et al. 2000; Odden et al. 2006). The roe deer was widespread in the Scandinavian Peninsula in the Middle Ages, but decreased noticeably as early as the fourteenth century, probably due to hunting, grazing competition from sheep and cattle and a colder climate, especially during the eighteenth century. Roe deer hunting was not permitted in Norway before 1927. Roe deer were legally hunted in increasing numbers as far north as central Norway in the 1950s, and were found north of Saltpjället and the Svartisen glacier in the late 1960s (Central Bureau of Statistics of Norway 1971).

Body size of animals may vary temporally and spatially, and these variations have been related to several factors, including food availability, climate, and their interactions. Among mammals, body size is determined during the growth period (Geist 1987). Variations in food availability during the growth period thus affect variation in growth

Fig. 1 Norway and its districts. The reindeer husbandry area is marked in gray. Saltfjellet is mountain area

rate and body mass (Bolton et al. 1982). For example, body size of juveniles and/or adults was negatively related to population density in the red deer (*Cervus elaphus*; Mysterud et al. 2001), roe deer (Pettorelli et al. 2002), and brown bear *Ursus arctos* (Zedrosser et al. 2006). Yom-Tov et al. (2007) have shown that population density affected body size of the Canadian lynx (*Lynx canadensis*) in Alaska and suggested that this was due to food availability. Yom-Tov et al. (2010) showed that body size and mass of the European lynx in Sweden was affected by the availability of roe deer, its main prey, during its birth year. In Sweden, the lynx is smaller in the semi-domestic reindeer areas in comparison with lynx in southern Sweden, probably because reindeer are more difficult to hunt and have a more unpredictable occurrence than roe deer (Yom-Tov et al. 2010).

Food availability is often related to climate (reviewed by Madsen and Shine 2000). The North Atlantic Oscillation (NAO) is a climatic phenomenon in the North Atlantic Ocean of fluctuations in the difference in sea-level pressure between the Icelandic Low and the Azores High. NAO affects weather, including ambient temperature and precipitation, throughout the North Atlantic region. A high index year (positive NAO) leads to cool wet summers and mild wet winters in Europe. In contrast, when NAO is negative, European winters are cold. NAO affects ecological

ecosystems and animals (Post et al. 1999; Mysterud et al. 2003), and its ecological responses include changes in timing of reproduction, population dynamics, abundance, spatial distribution, and interspecific relationships such as competition and predator–prey relationships (reviewed by Ottersen et al. 2004). The arrival time of migratory birds in Iceland (Gunnarsson et al. 2006) and North America (Marra et al. 2005) can be predicted by using NAO. Recently, Hersteinsson et al. (2009) have shown that body size of the Arctic fox (*Vulpes lagopus*) was negatively related to winter NAO. Nilsen et al. (2009) who studied lynx in south-eastern Norway, used NAO as a proxy for weather conditions and found that, in the northern part of their study area, winter snow cover was positively correlated to NAO.

Haglund (1966) stated that the high success rate of lynx chasing reindeer in winter can be explained, at least partially, by the greater sinking depth of reindeer in the snow. Hunting success of Canadian lynx is related to snow conditions (Stenseth et al. 2004). A small reduction in speed of an escaping roe deer due to snow cover may affect the hunting success of lynx (Nilsen et al. 2009). Hence, it is logical to assume that when winter NAO is negative, hunting success of the lynx will be higher.

Geographical variation in body size is often related to ambient temperature in accordance with Bergmann's rule (Mayr 1965). There is a selective advantage to a higher body surface-to-volume ratio in warm areas, and conversely, to the reduced heat loss that accompanies a lowered surface-to-volume ratio in higher latitude climates (e.g., Mayr 1965).

The aim of this study was to examine the effects of prey availability (roe deer density and density of the semi-domestic reindeer), NAO and latitude on lynx body size in Norway.

MATERIALS AND METHODS

We examined the skulls of 374 adult (208 male, 166 female) lynxes collected by hunters, deposited through licensed culls or following accidental death, between 1960 and 1976 across Norway. Skulls of additional 43 juveniles were also available for analysis. Data on skinned body mass of 348 lynx were also available. Most of these skulls are deposited at the Bergen Museum, University of Bergen, the Natural History Museum, University of Oslo, and at the Norwegian Institute for Nature Research (NINA), Trondheim, Norway. We used only skulls with known year and locality of capture. Skull size is strongly affected by age and lynx continue to grow, albeit slowly, after their first year (Andersen and Wiig 1984; Wiig and Andersen 1986; Tumilson 1987). Age was determined from skull criteria (i.e., bone fusion) and annual growth layers of a canine

tooth (Kvam 1983, 1984). Year of birth was determined by subtracting age (in years) from the year of capture.

Various skull measurements have been used as indicators of lynx size (e.g., Kvam 1984; Andersen and Wiig 1984; Wiig and Andersen 1986). In the present analysis, we used three skull measurements (taken by calipers to accuracy of 0.1 mm): namely, the maximal length of the skull (GTL), breadth between the zygomatic arches (ZB), and the breadth between the mastoid processes (MAS). Lynx grow very fast during their first year, but skull size continues to increase, albeit at a much slower rate, also in older specimens (Andersen and Wiig 1984; Wiig and Andersen 1986). In this study, we used skulls of animals 1 year of age and older.

We used principal component analysis (PCA) to combine the data on the three lynx skull measurements (GTL, ZB, and MAS, normalized by using the formula $10^{X/100}$, where X is the dependent factor) into a single variable.

No actual estimates of local roe deer density or availability exist in Norway. However, the harvest of wild animals is reported annually to the Central Bureau of Statistics by municipal game boards throughout Norway. We used reported municipality roe deer bag size per km² forest area (as forested habitat near farmland is the preferred habitat of roe deer) in that municipality as a coarse proxy to which determine spatial and temporal variation in roe deer availability. This approach has been used by several researchers: Mysterud et al. (2001) in Norwegian red deer, Grøten et al. (2005), Mysterud and Østbye (2006), and Nilsen et al. (2009) in Norwegian roe deer, Zannèse et al. (2006) in French roe deer, and Yom-Tov et al. (2010) in the Swedish roe deer.

Information on density of semi-domestic reindeer was estimated from the information provided by the Norwegian reindeer management authorities (<http://www.reindrift.no/>, Anonymous 2003, 2009). Almost all municipalities in the four northernmost counties in Norway (Nord-Trøndelag, Nordland, Troms, and Finnmark) have semi-domestic reindeer. In addition, semi-domestic reindeer are found in some municipalities in more southerly counties (Møre og Romsdal, Oppland, Hedmark, and Sør-Trøndelag). The semi-domestic reindeer is managed in defined reindeer areas with fixed borders. One reindeer area might partly cover several municipalities and one municipality might be partly covered by several reindeer areas. The estimated density of reindeers within a municipality was therefore based on estimated combined density within all reindeer areas that were partly within a municipality. Reliable numbers for the years the lynx were hunted do not exist (Anonymous 2003). Therefore, we have used reindeer number for the production year that ended in March 1999. There was no apparent increase in the total number of semi-domestic reindeer during the period 1980–1999 for

areas south of Finnmark county (south of 69.5°N). As most of the samples in the present study were taken south of this county, we believe the densities we have used here provide the best approximation of density for the years when the lynx were born. The total number of semi-domestic reindeer in Norway was about 188,000 in 1999 and 252,000 in 2008 (Anonymous 2009). Wild reindeer are only found in some alpine areas in Southern Norway and are not regarded as significant prey for the lynx, which is a typical forest-dwelling species.

Monthly NAO data were obtained from the Climate Research Unit database at the University of East Anglia (<http://www.cru.uea.ac.uk/cru/data/nao.htm>). Mean summer (June, July, and August), spring (March, April, and June) NAO for the birth year was calculated from the monthly means, and winter NAO as the monthly mean for January, February of birth year and December of the previous year. Consequently, winter NAO refers to the period of just prior to mating and pregnancy. Preliminary analyses indicated that only winter NAO was significantly related to PC1, and this parameter was used in further analyses.

We examined the effects of age, latitude, NAO, roe deer density and density of semi-domestic reindeer according to the municipality in which the lynx was killed, on PC1, separately for females and males, by fitting a general linear model (GLM) using Statistica (ver. 8, StatSoft), and selected the best model (i.e., subset of predictors) using the Akaike's Information Criterion (AIC; Burnham and Anderson 2001; 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 (2001). Level of support for an AIC_c value was evaluated by ΔAIC_c (i.e., $\text{AIC}_c = \text{AIC}_i - \text{AIC}_{\min}$) and Akaike weights (Burnham and Anderson 2001). An Akaike weight is the relative likelihood of the model given the data. Models with ΔAIC_c values of 0–2 provide similar support (Burnham and Anderson 2001).

Reindeer density data have some limitations. We used numbers of semi-domestic reindeer from 1999 and not from the years when the lynx were born. The semi-domesticated reindeer are herded by the Saami people who are nomadic, and their reported reindeer numbers are not necessarily those that occur in a particular county at the time of report. In addition, the herders try to protect their reindeer from predation, and the intensity of this differs between herds. Hence, the calculated reindeer density alone is not an accurate measure of their availability to the lynx. In spite of these shortcomings, we used this factor in our analyses in case they have some significant effect on lynx size.

RESULTS

The PCA clumped three normalized morphological measurements (GTL, ZB, and MAS) into a single factor in each of the specimens used. Eigenvalue was 2.6896, and the proportion of variance explained by that factor (PC1) was 89.655%. As expected, there was a highly significant relationship between PC1 and carcass body weight ($R^2 = 0.5257$, $F_{1,293} = 324.8017$, $p < 0.0001$).

Annual and February NAO indices were negatively related to snow depth in March, the month when snow depth is normally maximal (Annual NAO: $R^2 = 0.0937$, $F_{1,409} = 42.2724$, $p < 0.0001$; February NAO: $R^2 = 0.0740$, $F_{1,409} = 32.6883$, $p < 0.0001$).

Roe deer density was negatively related to latitude ($R^2 = 0.3726$, $F_{2,413} = 122.6569$, $p < 0.0001$), and there were no reports of roe deer harvest north of latitude 66°N (Fig. 2).

AIC selected two (for females) and four (for males) models for PC1 variation that obtained similar support (Δ AIC values smaller than 2). All models included age as well as one or more of the other variables (Table 1). In further analyses, we selected the model that explained the highest proportion of the variation in PC1.

For females, the model that explained the highest proportion of variation included all five factors examined (Table 1). PC1 was significantly and negatively related to NAO (Fig. 3a), and positively related to age, roe deer density (Fig. 3b), and latitude (Fig. 3c), but not to density of reindeer ($R^2 = 0.3759$, $F_{5,108} = 13.0134$, $p < 0.0001$; Table 2). For males, the model that explained the highest proportion of the variation included three of the five examined factors: namely, age, latitude, and NAO. PC1

was positively related to age but not to any of the other factors examined ($R^2 = 0.1668$, $F_{5,166} = 11.0785$, $p < 0.0001$; Table 2).

In order to compare our results to those obtained by Yom-Tov et al. (2010) for the lynx in neighboring Sweden, we ran a multiple regression examining the effect of the above five parameters (age, winter NAO, latitude, roe deer density, and reindeer density) and sex on our Norwegian lynx sample. We found that these factors explained 62.5% of the variation in PC1 ($R^2 = 0.6250$, $F_{6,296} = 80.5588$, $p < 0.0001$).

DISCUSSION

We found that, in addition to the strong and well-known effect of age, female (but not male) lynx size was significantly affected by the environmental factors examined. Among females, PC1 (and thus body size) was significantly and negatively related to NAO, and PC1 was also significantly and positively related to latitude and roe deer density.

It is well known that conditions experienced during early development, particularly food quantity and quality, affect growth, and ultimately adult body size (Bolton et al. 1982; Lindström 1999; Yom-Tov et al. 2006; Hersteinsson et al. 2009). Yom-Tov et al. (2010) have shown that this is the case also for the lynx in Sweden, where roe deer density at birth year affects body size. 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. Hence, our results add to the growing body of evidence showing the effect of environmental conditions during the period of fast growth (first year of life) on body size.

The fact that females reacted differently than males to the examined environmental parameters requires an explanation, and the answer may be as follows. Our results indicate that females, being the smaller sex and the sole providers for the young, find it more difficult to obtain sufficient food for both maintenance and the cubs and, due to this, they are sensitive to fluctuations in food availability and weather (Schmidt et al. 1997). Schmidt (2008) found that adult females reacted more strongly to the food shortage than did males and subadult females and emphasized that prey depletion may have a particularly strong effect on lynx conservation through affecting reproducing females. This is in accordance to Sandell (1989) who predicted that females' reproductive strategy in solitary carnivores is shaped by reliance on food resources, while that of males relies on distribution of females. The main food of the lynx in Norway is the roe deer, whose body mass (between 16 and 35 kg; Macdonald and Barrett 1993) is about equal or larger than that of an average female lynx,

Fig. 2 The relationship between roe deer density and latitude. Density = $0.4941 - 0.0074 * \text{Latitude} + 0.0009 * (\text{Latitude} - 65.0913)^2$; $R^2 = 0.3726$, $F_{2,413} = 122.6569$, $p < 0.0001$

Table 1 Effect of age, latitude, roe deer density, winter North Atlantic Oscillation (NAO), and density of reindeer, on PC1 (skull size) of the lynx in Norway

Variables selected					<i>K</i>	AIC	Δ AIC	<i>p</i>	<i>R</i> ²
Females									
Age	Latitude	Roe deer	NAO		4	282.29	0.00	<0.0001	0.3684
Age	Latitude	Roe deer	NAO	Reindeer	5	283.19	0.900	<0.0001	0.3760
Variables selected					<i>K</i>	AIC	Δ AIC	<i>p</i>	<i>R</i> ²
Males									
Age	Latitude				2	457.56	0.00	<0.0001	0.1849
Age	Latitude	NAO			3	458.71	1.15	<0.0001	0.1902
Age	Latitude	Roe deer			3	458.85	1.29	<0.0001	0.1894
Age	Latitude	Reindeer			3	459.49	1.93	<0.0001	0.1860

The best two (females) and four (males) models, selected by the Akaike information criterion (AIC), are presented. *K* is the number of parameters in the model, Δ AIC is the difference between the AIC of each model and the best model (i.e., lowest AIC)

and females may find it more difficult than males to hunt this prey. However, Sunde and Kvam (1997) did not find any evidence that body weight was related to prey choice in lynx, but suggested that the difference in prey choice between the sexes is caused by different ranging behavior. Hersteinsson et al. (2009) examined the effect of several environmental factors on mandible size and body mass of the Arctic fox in Iceland, and found that these factors explained a higher proportion of the variation among females than among males. We have no experimental proofs for the above hypothesis, and suggest that this question will be examined experimentally by testing body condition of females and males during winter.

Abiotic factors such as climate might be quite important in shaping prey dynamics even in simple predator–prey systems (Vucetich and Peterson 2004). In our study, female body size was negatively related to winter NAO during the year of birth. In this context, it is interesting that Nilsen et al. (2009) reported that hunting success of the lynx in southeastern Norway was related to NAO, and that NAO was associated with increased snow depth. We also found that annual and February NAO were significantly and negatively associated with snow depth in March. Thus, the effect of NAO on body size was indirect, and affected body size through its effect on prey availability for the lynx.

Since lynx are born in spring and do not experience the conditions during the winter of their birth year, these results are best explained as a carry-over effect of the mother on the body condition on her offspring. Similar carry-over results were reported for the Arctic fox in Iceland (Hersteinsson et al. 2009), where female size was negatively related to winter NAO at birth year. They interpreted these results as females, in being the smaller sex, are also more sensitive to the nutritional state of their mothers. It has been shown that the mother's condition is

positively related to that of her young (Clutton-Brock et al. 1982), as well-fed mothers may provide more nutrients to their embryos and richer milk to their cubs, and among carnivores they are probably better hunters than the more emaciated ones. Following this view, Hersteinsson et al. (2009) suggested that the link between female size and winter NAO is that the mother's condition influence her cubs in utero, and that females, being the smaller sex, are more sensitive to the nutritional state of their mothers.

Our results indicate that female body size was related to roe deer density through its effect on climate conditions (with NAO as proxy). Nilsen et al. (2009) showed that hunting success of the lynx reached an asymptotic level at relatively low prey density (about 2 deer/km²; their Fig. 2). However, roe deer density during the period of our study (1960–1979) was by an order of magnitude lower than during the study period of Nilsen et al. (2009) (1995–2007), and the highest density for our sample was 0.17 deer/km². In addition, Nilsen et al. (2009) showed that the consumption rate of prey by females with dependent kittens was much higher than that of solitary individuals. In other words, the condition of females with kittens is much more dependent on prey availability than the condition of solitary males.

The Effect of Latitude

We found that latitude had a significant effect on female PC1. This effect of latitude may be explained as a Bergmannian reaction to ambient temperature, with females being more sensitive to environmental conditions than males. Bergmannian trend in body size was also detected among otters (*Lutra lutra*) in Norway, and was interpreted as a reaction to ambient temperature (Yom-Tov et al. 2006). However, in Sweden, the size of lynx increases with

Fig. 3 Partial regression plots for female PC1 as a function of (a) North Atlantic Oscillation (NAO; slope = -1.3861 , $p = 0.0039$); (b) Roe deer density index (slope = -1.4071 , $p = 0.0243$), and (c) Latitude (slope = -1.3898 , $p = 0.0039$) as a function of summer NAO

Table 2 Results of multiple regressions examining the effect of factors that were included in the best AIC models (those that explained most of the variation among the selected models), on PC1 (skull size) of the lynx in Norway

Term	Estimate	<i>t</i> Value	<i>p</i>
Females			
Intercept	-11.8200	-3.44	0.0008
Age	0.1954	7.16	<0.0001
Latitude	0.1473	2.84	0.0053
Roe deer density	8.9116	2.37	0.0195
NAO, winter	-0.2351	-2.99	0.0035
Reindeer density	0.1681	1.14	0.2554
Males			
Intercept	-3.0403	-1.21	0.2276
Age	0.1796	5.43	<0.0001
Latitude	0.0555	1.43	0.1532
NAO, winter	0.0575	0.80	0.4225

latitude within the reindeer area (north of latitude 63°N ; Yom-Tov et al. 2010) and was interpreted as a reaction to an increase in reindeer mean density toward the north rather than an effect of climate. Based on available statistics for 1999 (Anonymous 2003) this was not the case for our study area in Norway.

Another possible explanation is related to the history of recolonization of Scandinavia by lynx. It seems that this size pattern was already established during the period of rapid expansion of lynx in Norway. The lynx in our study were born in the period from 1952 to 1976. According to Heggberget and Myrberget (1980), the lynx expanded further southward and westward in 1970s in relation to the 1960s, while the distribution in northern Norway was little changed. This information was based on data from the municipality Game Boards, which also noted an increase in lynx density in most municipalities in northern Norway during that period.

Kurtén (1968) suggested that the post-glacial recolonization history of Scandinavian lynx might have followed two different routes: One might have followed a land bridge from Denmark while the other might have come from the east through Finland. Hellborg et al. (2002) studied genetic variation in northern European lynx. Two important patterns were seen: a distinct differentiation

between Scandinavian and more eastern populations, and a structuring consistent with isolation by distance along a north–south gradient within Scandinavia. The variation they detected was not consistent with the hypothesis of different recolonization histories in north and south Scandinavia. Rather, they consider it likely that strong genetic drift during the population bottlenecks in Scandinavia in recent centuries may have contributed to the genetic differentiation detected. Rueness et al. (2003) studied the genetic population structure in Scandinavian lynx and suggested the existence of at least three subpopulations, and that these subpopulations might have originated from more than one core area. We suggest that such a different origin of lynxes in northern Norway may also have affected the size variation of the lynx and that this is not only related to food availability.

A third explanation, and in our opinion the most plausible, is that latitude affected body size as a proxy for climate. Ambient temperature decreases with latitude, and with it snow cover increases. For example, in our sample, snow cover in March, the month with heaviest snow cover, is significantly related to latitude ($R^2 = 0.0386$, $F_{1,409} = 16.4022$, $p < 0.0001$). The fact that only a small proportion of the variation in snow cover is explained by latitude is due to other factors that affect snow cover, including altitude, wind velocity, exposure to solar radiation, slope direction, and topography. We suggest that an increase in latitude affects body size in the same way that NAO affects it, i.e., by increasing hunting success of the lynx.

Comparison Between Norwegian and Swedish Lynx

The parameters examined here explained a very similar proportion of the variation in PC1 to that found for the lynx in Sweden (62.5% in Norway; 63% in Sweden; Yom-Tov et al. 2010). Most of the variation explained in both studies is attributed to sex and age. However, comparison of the rest of the explained variation is less straightforward, because the roe deer indices used in the two studies may differ from one another. First, the roe deer harvest index is determined by several factors that may differ between the two countries. For example, hunting pressure (i.e., number of hunters days per area) and terrain may have been different, and there might also have been differences in the reliability of the hunters' reports provided to the authorities. Second, differing from with the Swedish study, NAO was used as an independent parameter in our study. Nevertheless, the fact that a similar proportion of the variation in body size was explained in the two studies may attest to the possibility that food availability and factors affecting it (such as NAO) as important in determining body size.

In both studies, nonetheless, a considerable proportion (about 37%) of the variation in body size remains unexplained, and we can only speculate regarding the responsible factors. It may be due to such factors as the rough nature of the measures of prey availability used by us (see above for details), lynx population density, inter-specific competition between lynx and other predators, age structure of roe deer population at various sites, availability of alternative prey (i.e., sheep), or persecution by humans.

Female body size (as represented by PC1) in both countries was significantly related to roe deer density as well as to abiotic environmental parameters. However, body size male lynx in Norway was not related to any of the examined environmental parameters. We suggest that the most likely factor is prey availability, which is probably scarcer in Sweden in comparison to Norway (particularly its central districts), where both reindeer and roe deer are available. Yom-Tov et al. (2010) have shown that body size of the lynx in Sweden is smallest in central Sweden (between latitudes 63 and 64°N) and increases toward south and north of these latitudes. They related this trend to an increase in roe deer density toward the south, and reindeer density toward the north. This pattern of prey availability should make lynx life easier in Norway than in most districts in Sweden, where in most areas only one of the two species is available as food resource. However, since roe deer density data in the two countries were estimated differently, and at present a comparison is difficult. Thus, only further studies may clarify this issue.

In summary, our study shows that body size of female lynx is more sensitive to conditions that prevail during the year of birth, such as prey density, NAO, and latitude than that of males. We suggest that the effect of the abiotic parameters examined (latitude and NAO) is through their effect on food availability. Our results add to the growing body of evidence showing that geographical and temporal variation in body size is related mainly to food conditions during the period of growth.

We can conclude that the relationships between body size on the one hand, and prey availability and climate on the other, are complex. We may rephrase Nilsen et al.'s (2009, p. 749) statement to say that a purely prey-dependent functional response model is not sufficient to explain the variation in lynx body size, and that additional factors are needed in order to obtain a reliable understanding of the factors that shape it.

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