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Effects of prey availability on Eurasian lynx (*Lynx lynx*) body mass and growth

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Abstract:

As vital rates in most species are affected by body mass, there is a general interest in understanding how different ecological conditions affect body mass. Here we tested for body mass differences between 1913 Eurasian lynx (*Lynx lynx*) with different ungulate availability in Norway and Sweden. Lynx were categorized living in either high roe deer (*Capreolus capreolus*) density areas (HR), low roe deer density areas (LR) or semi-domesticated reindeer (*Rangifer tarandus*) areas (R). We found significant difference between sexes and prey categories. The relationship between prey availability and asymptotic body mass was not consistent between sexes. For males, asymptotic body size was 21.73 ± 0.29 (SE), 20.85 ± 0.29 and 20.24 ± 0.22 in HR, LR and R areas respectively. Male lynx in HR areas were significantly larger than males in LR and R areas, but the latter two were not significantly different from each other. For females, asymptotic body size was 15.93 ± 0.2 , 15.86 ± 0.26 and 15.50 ± 0.17 in HR, LR and R areas respectively. Females in high and low roe deer density were not different from each other, but both were significantly larger than females in reindeer areas. The difference in body mass was larger between males than between females. This may be a result of females balancing growth and reproduction, with a greater reproductive effort in early life among females in HR areas. It can also be a result of that most animals were killed during mating season, when males increase activity and home range in search of mates, leaving them more prone to starvation in areas with low resource levels than females. Males outweighed females with approximately 30 – 35 %, grew faster and over an extended period. We argue that the male growth strategy and final size is the result of the benefits of larger body size in attainment and defence of home range and mates. We conclude that lynx in HR areas are in better conditions and the regular but low occurrence of roe deer in LR areas are a more favourable food base than provided by migrating and seasonal reindeer in R areas. The body mass difference could reflect differences in survival and fecundity and more conservative management decisions should be applied to lynx in LR and R areas.

Introduction:

Body size and growth can have important implications for the life history of an animal (Roff 1992; Stearns 1992). Body mass affects both survival and reproduction, and in general, heavier individuals within a population are expected to start breeding earlier, have more offspring, live longer, and have higher individual and offspring survival (Roff 1992; Stearns 1992). General life history theory predict a trade-off between growth and reproduction (Roff 1981; Stearns & Koella 1986; Roff 1992; Stearns 1992). Thus organisms suffering from slower growth in poorer conditions can delay their onset of first reproduction, favouring continued growth and eventually attainment of larger body size (Stearns & Crandall 1981; Stearns & Koella 1986). However, conditions experienced during body development can also have consequences for an organism's future fitness, and have lasting effects on the individual and/or the population (Gaillard et al. 1997; Lindstrom 1999; Gaillard et al. 2000; Beckerman et al. 2002; Lindstrom & Kokko 2002). Thus, differences in body mass can be important to address when dealing with the conservation and management of a species. In several mammalian groups, for example wild ungulates, the effect of body size on fecundity, primarily age at first reproduction, is well documented and often correlate with environmental variables such as climate, food availability and population density (Kingsley et al. 1988; Saether & Heim 1993; Sand et al. 1995; Langvatn et al. 1996; Sand 1996; Hilderbrand et al. 1999; Ferguson & McLoughlin 2000; Pistorius et al. 2001; Reimers et al. 2005). In carnivores, prey availability is one of the most common contributors to variation in demographic parameters (Fuller & Sievert 2001). Population dynamics, body size, growth, survival, litter size and age at first reproduction, both between and within populations are often affected by prey density (Mowat et al. 1996; White et al. 1996; Odonoghue et al. 1997; Fuller et al. 2003; Laundre et al. 2007; Yom-Tov et al. 2007). Of the four species of lynx, bobcat (*Lynx rufus*), Canadian lynx (*L. canadensis*), Iberian lynx (*L. pardina*) and Eurasian lynx (*L. lynx*), all except the larger Eurasian lynx prey mainly on small game species (Werdelin 1981). For instance, Canadian lynx show a dramatic dependence on snowshoe hare (*Lepus americanus*) density (Brand & Keith 1979). The Eurasian lynx differs from its smaller cousins in that their main prey is medium sized ungulates, and Eurasian lynx populations with access to ungulates often exhibit more stable

dynamics than those that do not (Jedrzejewski et al. 1993; Jedrzejewski et al. 1996), emphasizing the general importance of ungulates in Eurasian lynx demography.

The Eurasian lynx are distributed across most of Scandinavia, except the southernmost parts of Sweden and south-western parts of Norway. Here, the lynx prey on several species, including lagomorphs and tetraonids, but the main prey are roe deer (*Capreolus capreolus*) and semi-domestic reindeer (*Rangifer tarandus*) (Pedersen et al. 1999; Sunde et al. 2000; Odden et al. 2006). Lynx within reindeer herding ranges experience large seasonal variation in ungulate density. Reindeer are moved by herders between different grazing grounds throughout the year, which periodically “depletes” the ungulate prey base. In contrast roe deer do not migrate over long distances and are year round residents, which make them a more stable food source. But the densities vary spatially and some areas have very low densities. In eastern Finland, where ungulate prey for lynx are negligible, lynx prey on mountain hare (*Lepus timidus*) and brown hare (*Lepus capensis*) (Pulliainen 1981). In these areas, individual lynx are in worse condition and smaller than lynx in southern Finland with access to the introduced white-tailed deer (*Odocoileus virginianus*) and roe deer (Pulliainen et al. 1995). However the Scandinavian population consist of animals with a seasonal access to ungulates (Semi-domestic reindeer areas) and a year round access (roe deer areas) but with densities varying spatially, and it is hard to predict how this might affect body mass. How these varying ecological conditions affect the Scandinavian lynx population is of great interest, and here we examine the growth and body mass of lynx under different prevailing conditions. That is, we will examine lynx growth patterns and body size in high roe deer density areas (HR), low roe deer density areas (LR) and reindeer areas (R). Lynx tend to prefer lowlands inhabited by roe deer as supposed to alpine areas occupied by reindeer in regions where both prey species are available, which suggests the need of a stable year round prey (Sunde et al. 2000). If year round access is most important for determining lynx body mass and growth, lynx in roe deer areas should be larger, independent of densities. However, lynx are an efficient predator, both on small game and ungulates (Pedersen et al. 1999) and lynx in reindeer areas have on average more prey resources per predator than lynx in roe deer areas when reindeer are present (Danell et al. 2006). Given its abilities to switch between several prey species, a seasonal, but superabundant, ungulate prey availability may supply better

nutritional conditions than a stable but low density of roe deer. We predict that lynx living in HR areas are larger than any of the other two. Concerning the lynx living in low roe deer density and reindeer areas, we have two contrasting (alternative) predictions; If the low roe deer density areas provide better nutrition conditions than the seasonal reindeer areas, lynx in roe deer areas should be largest regardless of roe deer density. In contrast, if seasonal reindeer abundance provides a better food base than low density roe deer areas, we might expect larger body mass and faster growth by lynx living in reindeer areas.

Material and methods:

Most body mass data were obtained from carcasses obtained from the annual harvest in Norway and in Sweden. In Norway, hunting season takes place between 1st February and 30th April. The yearly quota is based on the previous year's population censuses and depredation losses on sheep and semi domestic reindeer. In Sweden, hunting season starts 10th January and ends 31st March. The yearly quota is also determined by population censuses. In both countries, hunters must report in any kill, with its body weight and where it is shot, and the carcass must be sent in to the management authorities for autopsy. We also included animals killed in traffic, found dead and killed as depredators in the analysis. Animals dying from diseases such as sarcoptic mange were removed from the dataset because this may effect condition and hence body mass of the animals.

In some cases, only body weight of the skinned animal was available. To be able to use these animals, we used animals with known total and skinned body weight to calculate a conversion factor using a regression, allowing us to estimate total body mass of skinned carcasses. In the Norwegian dataset, some carcasses were without skins and feet. Separate regressions were used on these carcasses to estimate total body weight. The regressions are presented in table 1. To estimate age, incremental lines in tooth cementum were used (Kvam 1984).

Regional prey categories:

Roe deer are distributed throughout Scandinavia. High densities of roe deer occur mainly in southern Sweden and Norway, and along the coast in central Norway. The reindeer areas in Scandinavia are large and cover 40% of the Scandinavian Peninsula, and are distributed from central Scandinavia and northwards. To determine which areas contained high densities of roe deer, hunting statistics averaged over 1997 -1999 were used. The use of hunting statistics serves as a sufficient tool to make a coarse division between areas with high and low prey densities, as research on other ungulates has shown (Solberg et al. 1999). The municipality where the individual lynx were killed was used to place them either in HR or LR areas. In Nord-Trøndelag some municipalities contained both reindeer areas and high densities of roe deer. In these areas lynx tend to prefer the lowlands, close to roe deer, as supposed to the alpine areas containing reindeer (Sunde et al. 2000). In addition, due to easy access by roads etc. and being in near vicinity of human development, the harvest is biased towards lynx in lowlands where lynx prey on roe deer (Sunde et al. 1998). Most importantly, lynx in these areas live with high densities of ungulates, both reindeer and roe deer, further advocating a placement in the HR category. Maps over reindeer areas were obtained from Norway (Reindeer Management Authority) and Sweden (Länsstyrelsen 2007). Municipalities containing reindeer areas were classified in the reindeer category, and hence, the lynx shot within them. As mentioned, municipalities with reindeer and a high roe deer density were placed in the HR-category. The southern range of the reindeer herding areas can contain low densities of roe deer, which was not taken into account when classifying the data. We are aware that lynx use very large territories that can typically span several municipalities (Herfindal et al. 2005), and some lynx have access to prey outside the municipality it is shot. However, we do believe that our classification method provides a functional classification for a study area as large as Scandinavia. .

Seasonal correction of body masses:

Time of death varied, but the vast majority were shot during the hunting season. To test and correct for seasonal variation in body mass, regressions for seasonal

variation in body mass were conducted for each age class, sex, and prey category. Most deaths occurred during February, and this was the month chosen to be the standard to which the others were regressed. Because of the rapid growth during their first year of life, juvenile (shot during first year of life) body mass was regressed using days as an explanatory variable. Juveniles were regressed to 14 February, the middle of the month when most animals were killed. It is important to note that animals with age 0, is in reality closer to age 1, as they are 8 months in February or 0.67 years. To determine the age in days and months, 1st June was set as date of birth, as parturition takes place in late May - early June (Tumanov 2000). Regressions were performed on lynx up to the third year of life. The lower sample size combined with few animals killed outside the hunting season in the older age classes, made no reasonable regressions possible. This is probably not a serious issue because the fast growth stage of the lynx were surpassed and the majority of animals were killed during the seasonally limited hunting season, which mean that most deaths occurred within a relative short time interval. Linear regression was used in all age classes and they are presented in table 2.

Growth pattern and body mass analysis:

The body masses were fitted to the von Bertalanffy growth equation of the form (Swenson et al. 2007):

$$w(a) = W[1 - e^{(-k_w(a-A_w))}]^3$$

Where $w(a)$ = body mass (kg) at age a (years), W = asymptotic body mass (kg), k_w = growth year constant (per year) and A_w = fitting constant (extrapolated age (years) at zero size). The curve was fitted using iterative Gauss-Newton algorithms. Independent curves were fitted for each sex in each prey category.

Individual growth curves were generated by a method introduced by Swenson et al. (2007). When analyzing body mass, age is an important factor to take into consideration. But the nonlinear relationship between age and body mass make such attempts difficult and problematic. Therefore, we modeled individual weights at a common age, based on body mass measurements in different ages assuming the

growth pattern follows the von Bertalanffy equation (see appendix for further information). This allowed us to evaluate body mass at a common age for the population as a whole, and we omitted age as an explanatory variable when constructing the linear model (figure 1.). This does not exclude age in the analysis, because it is indirectly included as a covariate as result of the modeling. We believe that this is a superior method as supposed to using age, age^2 or age^3 directly in a multivariate analysis, because a quadratic or cubic relationship between body mass and age are poor descriptors of body mass development in relation to the von Bertalanffy equation. Three years was set as the common age to be used in the analysis, as the variance and uncertainty was low at this age because of large sample sizes.

It is important to note that this approach does have its weaknesses. First, we assume that all individuals follow the same growth pattern as described by the von Bertalanffy equation, with different individual deviations from the mean, which is not necessary true. Second, the modeling neglects any senescence effect. We are aware that a nonlinear mixed effect model could have mitigated this, but we argue that our method is more pedagogical and easier to follow and interpret than a nonlinear mixed effect model. In addition, the large data material reduces the uncertainty in the growth curves, which makes the residuals approximately independent and well suitable for this approach.

A factorial ANOVA was used to test for differences between sex and prey category and the linear model included these variables and interactions: sex + prey-category + sex :prey-category. To test for further differences within sexes and between prey categories we used a one-way ANOVA with multiple comparisons by the Tukey's Honestly Significant Difference Method on males and females separately.

Results:

Body mass differences between sex and prey category:

A total of 1913 lynx body masses were used in the analysis with 679, 332 and 902 animals from the HR, LR and R areas respectively. There was a significant difference in body mass between sexes (Table 3, p-value = 0.00) and between individuals in areas with different prey availability (Table 3, p-value = 0.00). When body mass differences were tested for males, the one-way ANOVA and the multiple comparisons revealed significant differences between males in all prey categories (table 4, p-value = 0.00). As predicted, HR males were largest. Males living in LR areas were significantly smaller than HR males (p value=0.00). LR males were larger than R males but the difference was not significant (table 4, p-value= 0.087). The females showed significant different body masses between prey categories (table 5, p-value 0.004). The females in HR and LR areas were significantly larger than females in R areas but not from each other (table 5). For both sexes the largest lynx were those in HR areas, and the smallest in R areas. The observed interaction (table 3, sex:prey-category) show that the sexes are differently affected by prey availability (p-value = 0.00). The difference between females was not as pronounced as between males.

Asymptotic body mass and growth pattern

The von Bertalanffy growth curve provided a good fit with the data, and described the pattern well (figure 2. And figure 3.). The largest asymptotic body masses were from lynx living in HR areas, while the smallest were lynx in R areas for both sexes (Table 6). Notably, the differences between males are larger than between females. Based on the asymptotic body mass estimated by the von Bertalanffy equation, males outweighed females with approximately 30 – 35%; 36% in HR areas, 31% in LR areas and 30% in R areas. To compare growth pattern between the sexes and prey categories, the age at which 90% of asymptotic body mass is attained was set as the time achieving adult body mass. Since animals were in reality weighed when their 0.67, 1.67 2.67 etc. years of age, 0.67 was added. For males, adult body mass

was achieved at 2.13, 2.08, 1.91 years of age for HR, LR and R areas respectively. For females it was 1.77, 1.47, 1.84 years of age in HR, LR, and R areas respectively.

Discussion:

Effects of prey availability on body mass in lynx:

We found differences between all prey categories, but the results were different for the two sexes. For males, the largest lynx were as predicted those living in HR areas. The obvious explanation is that the seasonal stability and abundance of roe deer in these areas provides a superior food conditions than in the other areas. But in addition, lynx home range size correlates negatively with prey density (Herfindal et al. 2005). Lynx movement are governed by prey, and tend to increase with time since last kill (Schmidt 1999; Jedrzejewski et al. 2002). Lower prey density also affects the hunting effort, and lynx in low prey density use more time and energy on hunting (Schmidt 2008). The higher male body mass for males in HR areas probably reflect the relaxed home range requirements and the lower hunting effort needed to catch prey. We failed to find a significant difference between males living in areas with low roe deer density and males in reindeer areas. However, LR males are larger, and the difference is almost significant ($p = 0.087$). The lowering of both the mean body mass and sample size could be one reason for the non-significant difference. Males in R areas were the smallest, although non-significantly from the LR males. Lynx in reindeer areas showed a large variation in body mass and included both the largest and smallest males. This probably reflects the varying conditions these animals are sampled from, spanning from central Scandinavia to the North. Some parts of the reindeer area can also contain low densities of roe deer, leading to access to both prey species, and some lynx can have home ranges overlapping several seasonal grazing grounds, which provide a year round access to reindeer. The hunting season takes place during winter, and animals shot within winter ranges for reindeer can be large and in good condition, while those outside reindeer winter ranges rely on small game and experience conditions similar to the lynx in eastern Finland (Pulliainen et al. 1995). Studies have also shown that some individual reindeer can remain behind in areas after the majority of the herd has been moved, depending on weather conditions during the round-up and migration (Pedersen et al.

1999; Danell et al. 2006). Some years may leave more animals, while fewer remain in other years, placing the nutritional fate of the lynx in the hands of the herders.

For females, the results were somewhat different. HR females were not significantly different from LR females, in fact, they were overwhelmingly similar ($p = 0.99$), Females in R areas were significantly smaller than both LR and HR females, indicating better conditions in roe deer areas regardless of density. Several factors may explain the gender variation related to HR and LR areas. The effect of body mass on age at maturity is well documented in ungulates (Sæther & Heim 1993; Langvatn et al. 1996; Sæther et al. 1996; Sæther 1997). Green and Rothstein (1991) showed that heavier juvenile bison (*Bison bison*) females commenced reproduction earlier than lighter ones, but were smaller as adults. Female moose (*Alces alces*) that were smaller as yearlings, tend to delay maturity, favoring prolonged growth over reproduction and ultimately becoming larger than females that reproduced as yearlings (Sæther & Haagenrud 1985). Based on data obtained from radio-collared lynx in Scandinavia, a higher proportion of two year old females reproduced in high density roe deer areas (0.74 and 0.5) as supposed to reindeer and low density roe deer areas (0.23 and 0.33 respectively), leaving the mean number of cubs per two year old in HR areas (2.8) higher than in LR and R areas (0.8 and 0.5 respectively) (Scandlynx unpublished data). Female lynx with kittens have a higher level of activity than non-reproducing females (Schmidt 1999; Jedrzejewski et al. 2002) and smaller home ranges (Schmidt et al. 1997; Linnell et al. 2001) and suffer the energetic cost of lactating, which can be substantial (Oftedal & Gittleman 1989). Postponing reproduction by one year would reduce the allocation of resources spent on reproductive activities such as lactation and rearing the young, allowing them to be allocated to further growth. The evidently higher reproductive effort in HR females may be one reason for the similarity in body mass. Another possible explanation to the different effects of prey availability on sex is the fact that the hunting season takes place during the mating season. Male lynx have larger home ranges than females, overlapping one to several females (Jedrzejewski et al. 1996; Schmidt et al. 1997; Breitenmoser-Wursten et al. 2007), and they can expand their home ranges during the mating season (Schmidt et al. 1997) and increase their movement and activity (Schmidt 1999; Jedrzejewski et al. 2002), which in turn indicate a spacing pattern determined by chance of meeting females (Sandell 1989). Areas with low

prey density show a greater difference between male and female home range than in high density areas (Herfindal et al. 2005). Males in low prey density areas must use larger areas to cover several females, than males in areas with good prey availability, and while females in low density areas can concentrate their time on foraging, males suffer the cost of increased movement, have less time for foraging and possibly compete with other males over females, making them more prone to food stress. In contrast, females are more tolerant to lower prey densities, not confronted with the additional energetic cost of roaming larger areas in search for mates at the expense of prey search.

Body mass differences between sexes:

In a polygamous mating system, males compete for access to that of several females (Cluttonbrock 1989). In direct competition, larger body size is an advantage, resulting in a selection for faster and/or prolonged growth in males. (Andersson 1994).

Although the evidence is scarce for solitary carnivores, the benefit of larger body weight on male reproductive success is reported in both brown (*Ursus arctos*) and black bear (*Ursus americanus*) (Kovach & Powell 2003; Zedrosser et al. 2007). Our study shows that Eurasian lynx males grow faster and over a longer period than females, ultimately outweighing them with 30 – 35%. We believe the observed pattern is a result of selection for greater body size in males, leading to higher reproductive success. Different growth strategies could also explain why prey density affects the sexes differently. Environment is known to affect sex differently in other mammals (Saether & Haagenrud 1985; Festa-Bianchet et al. 2000; Solberg et al. 2004). Males are selected to maximize growth, while females can balance their energy between growth and reproduction if necessary.

Implication for population dynamics and management of the Eurasian lynx in Scandinavia:

The difference in body mass could imply different demographic patterns as a result of the ecological conditions. Studies of Canadian lynx show that variation in prey density affects body size (Yom-Tov et al. 2007) and reproduction rates, including age at maturity (Slough & Mowat 1996; Mowat & Slough 1998). Eurasian lynx in Poland

also lowered reproduction rates when deer densities declined (Okarma et al. 1997). The higher body mass observed in the HR areas reflects good condition, and lynx within them probably enjoy higher reproduction and survival rates (Roff 1992; Stearns 1992). Areas containing high densities of prey can also contain a higher density of lynx (Herfindal et al. 2005) Thus, regions with high roe deer density in Scandinavia can maintain populations at higher densities and individuals with higher fitness. This being said, it is important to realize that lynx densities in Scandinavia are also heavily influenced by human harvest. In the LR and R areas, the lower body mass in relation to HR areas suggest lower survival and reproductive output. Andr en (2002) documented lower reproduction rates in the lynx living in areas with reindeer or low roe deer density compared to the high density roe deer area. Both the larger home ranges and lower food abundance implies a potential cost. Although the difference was non – significant between males, the significant difference between females in LR and reindeer husbandry areas suggest that the year round access to roe deer provide a better nutritional base than reindeer that migrate. The seasonal movement of reindeer leaves lynx in these areas to conditions similar to that of lynx in eastern Finland and the Canadian lynx during some parts of their life cycle. The lower body mass indicate a greater cost of living with a migrating prey, as supposed to the regular but low food supply in LR areas. The temporally absence or low levels of reindeer are evidently more costly even though the resource level can be quite high when reindeer is present, and independent results suggest lower reproductive rates and survival in reindeer areas. In addition, we found a large variation in body mass in lynx from reindeer areas, especially from males. This can imply highly variable conditions in reindeer areas, both spatially and temporally. S aether et al. (in prep.) found 5 times higher environmental stochasticity in lynx in reindeer areas compared to lynx in roe deer areas. Higher environmental stochasticity reduces population growth rate (Lande et al. 2003) further arguing for lower survival and recruitment in these areas. The effects of ungulate prey availability on lynx body mass revealed by our study show that lynx do not manage to compensate for lower or seasonal access to ungulates by switching to other prey. Thus, ungulate prey density must be considered when deciding management regimes for the lynx. In Norway and Sweden, reindeer areas and areas containing low densities of roe deer should implement more conservative management terms such as lower hunting quotas.

Lynx in areas with high roe deer density however, could endure a greater exploitation and less conservative management practice.

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Table 1: Regressions on skinned carcasses, with and without feet, used to estimate total body mass. SW = Skinned weight (in kg), SFW = skinned and footless weight (in kg)

Material	Regression	R-squared	p- value
Skinned carcasses	$1.16 + 1.08 * SW$	0.94	0.00
Skinned footless carcasses	$3.09 + 1.30 * SFW$	0.75	0.00

Table 2. Regression used to correct body masses within a year. For carcasses in age 0, days were used and body masses were corrected to 14 February. For animals > 0, months were used, and body masses were corrected to February. X = age in days, Z = Month number

Prey category	Sex	Age	Regression	R - squared	p -value
HR	Male	0	$0.70 + X * 0.04$	0.49	0.00
HR	Male	1	$17.32 + Z * 0.11$	0.01	0.43
HR	Male	2			
HR	Female	0	$-0.83 + X * 0.04$	0.47	0.00
HR	Female	1	$13.30 + Z * 0.15$	0.02	0.29
HR	Female	2	$10.69 + Z * 0.49$	0.14	0.01
LR	Male	0	$-0.22 + X * 0.04$	0.49	0.00
LR	Male	1	$16.64 + Z * 0.14$	0.01	0.61
LR	Male	2			
LR	Female	0	$-0.20 + X * 0.04$	0.43	0.00
LR	Female	1			
LR	Female	2	$12.66 + Z * 0.44$	0.10	0.18
R	Male	0	$0.92 + X * 0.04$	0.16	0.00
R	Male	1	$15.88 + Z * 0.25$	0.02	0.16
R	Male	2	$15.48 + Z * 0.41$	0.03	0.07
R	Female	0	$0.43 + X * 0.04$	0.37	0.00
R	Female	1	$11.51 + Z * 0.3$	0.04	0.12
R	Female	2	$9.61 + Z * 0.6$	0.16	0.00

Table 3: Factorial ANOVA used to test for body mass differences between sex, prey category and the interaction.

Variables	Degrees of freedom	Sum of squares	Mean squares	F - value	p - value
Sex	1	11794.9	11794.9	1973.88	0.00
Prey category	2	332.2	166.1	27.8	0.00
Sex : Prey category	2	77.8	38.9	6.51	0.00
Residuals	1907	11395.2	6.0		

Table 4: One-way ANOVA and the multiple comparisons used to test for body mass differences between males in different prey categories.

	F -value	Difference	P - value
Prey category	25.66		0.00
HR - LR		0.82	0.00
HR - R		1.31	0.00
LR - R		0.49	0.087

Table5: One-way ANOVA and the multiple comparisons used to test for body mass differences between females in different prey categories.

	F -value	Difference	P - value
Prey category	5.57		0.004
HR - LR		- 0.02	0.995
HR - R		0.47	0.01
LR - R		0.49	0.04

Table 6: Asymptotic body mass and growth constant (K) of lynx from different prey categories.

Prey category	Sex	Asymptotic body mass (kg, mean \pm SE)	K \pm SE	N
HR	Male	21.73 \pm 0.29	1.19 \pm 0.10	356
HR	Female	15.93 \pm 0.20	1.36 \pm 0.19	323
LR	Male	20.85 \pm 0.29	1.24 \pm 0.14	186
LR	Female	15.86 \pm 0.26	1.80 \pm 0.44	146
R	Male	20.24 \pm 0.22	1.39 \pm 0.13	507
R	Female	15.50 \pm 0.17	1.25 \pm 0.15	395

Figure headings:

Fig. 1: An illustration of our modeling approach which allowed us to estimate all body masses at a common age, three. Age is indirectly incorporated in the linear model as a covariate. Solid line displays the general growth development for males in HR areas. The dashed lines shows individual growth curves for 4 males used to standardize body mass to age three. Circles show the age and body mass before modeling, squares body mass at age three. The modeling is based on one body mass measurement per age per individual. All curves were specific to sex and prey category.

Fig. 2: Body mass development for male lynx in different prey categories using the von Bertalanffy equation.

Fig. 3: Body mass development for female lynx in different prey categories using the von Bertalanffy equation

Fig. 1

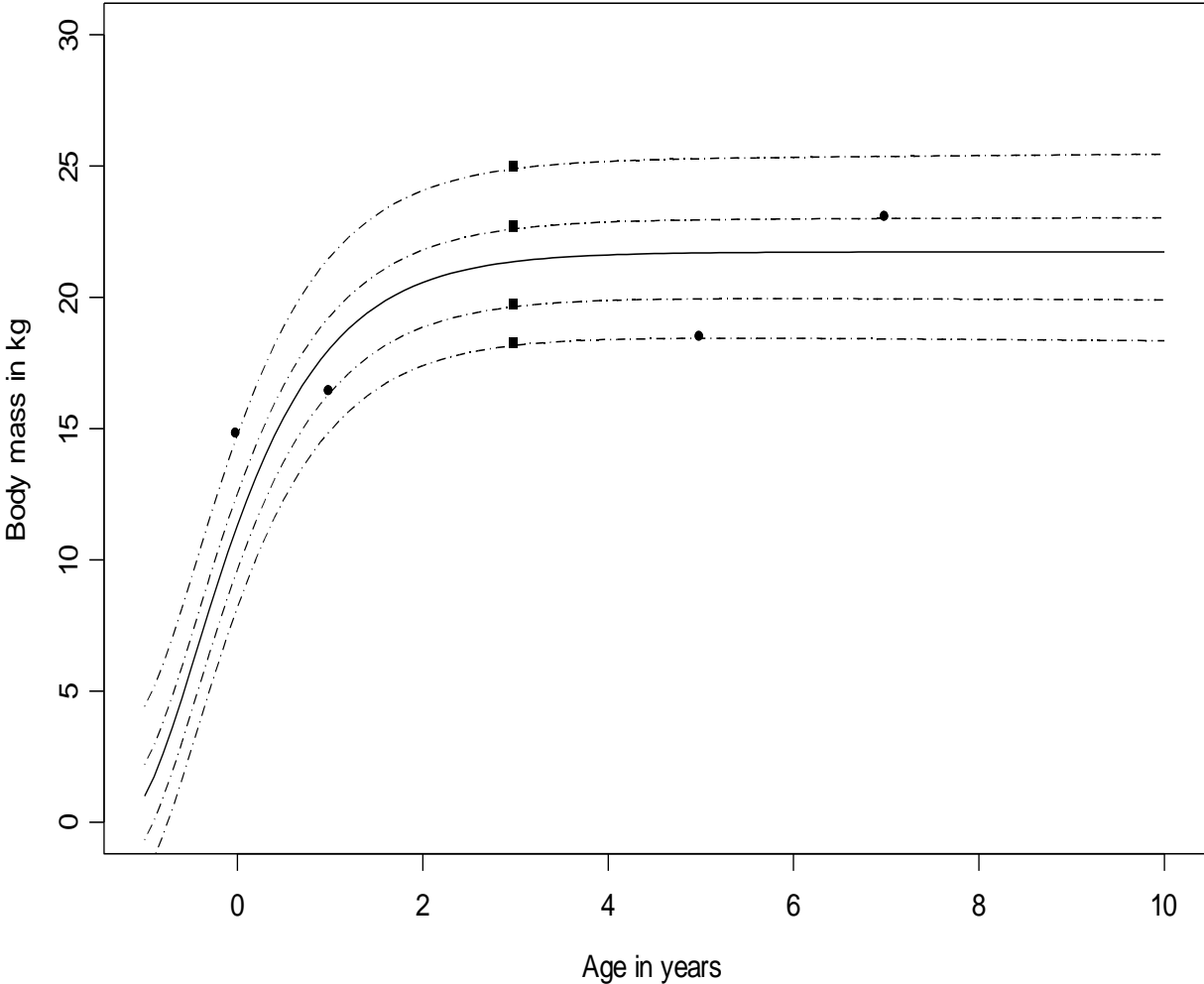


Fig. 2

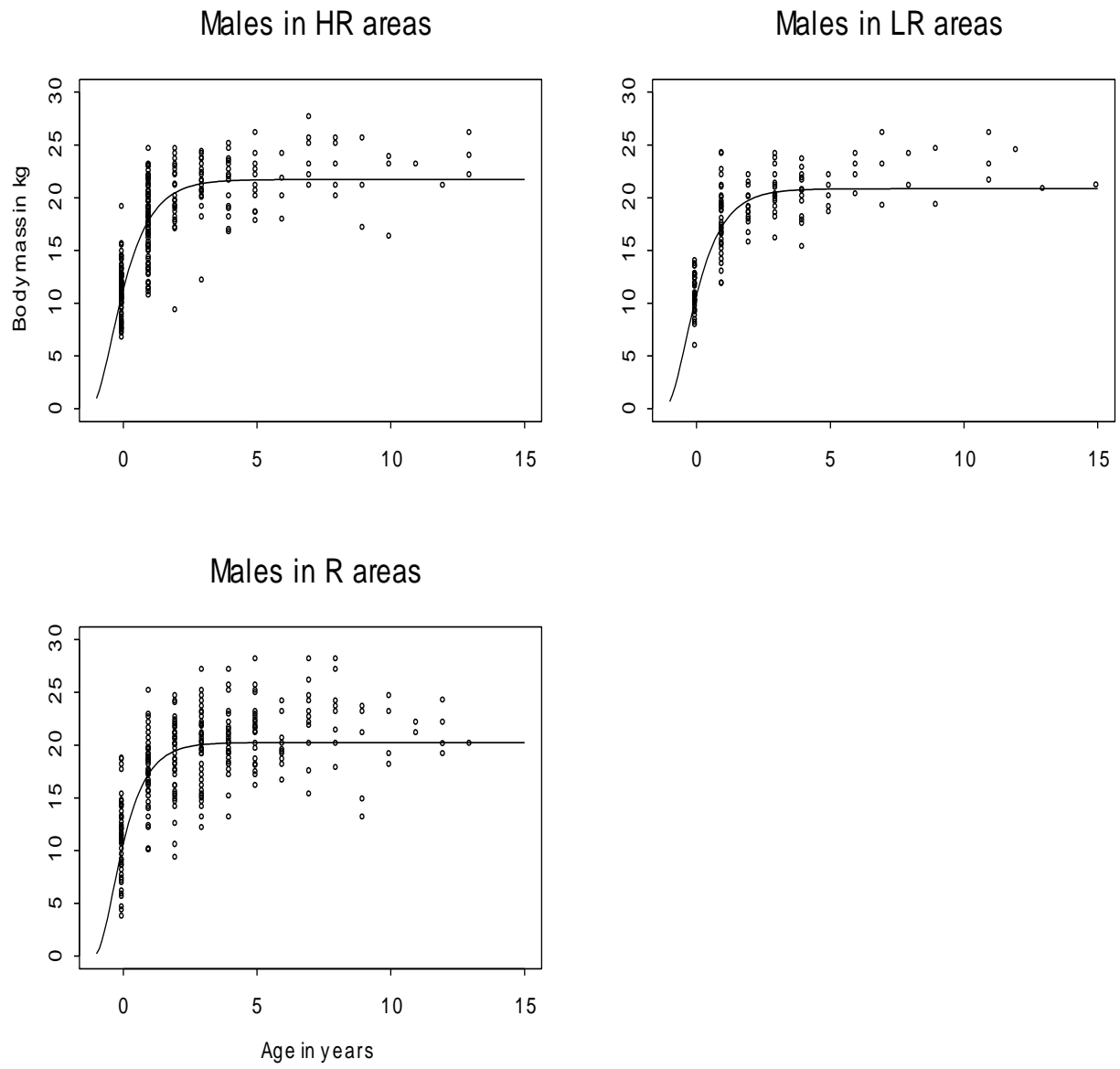
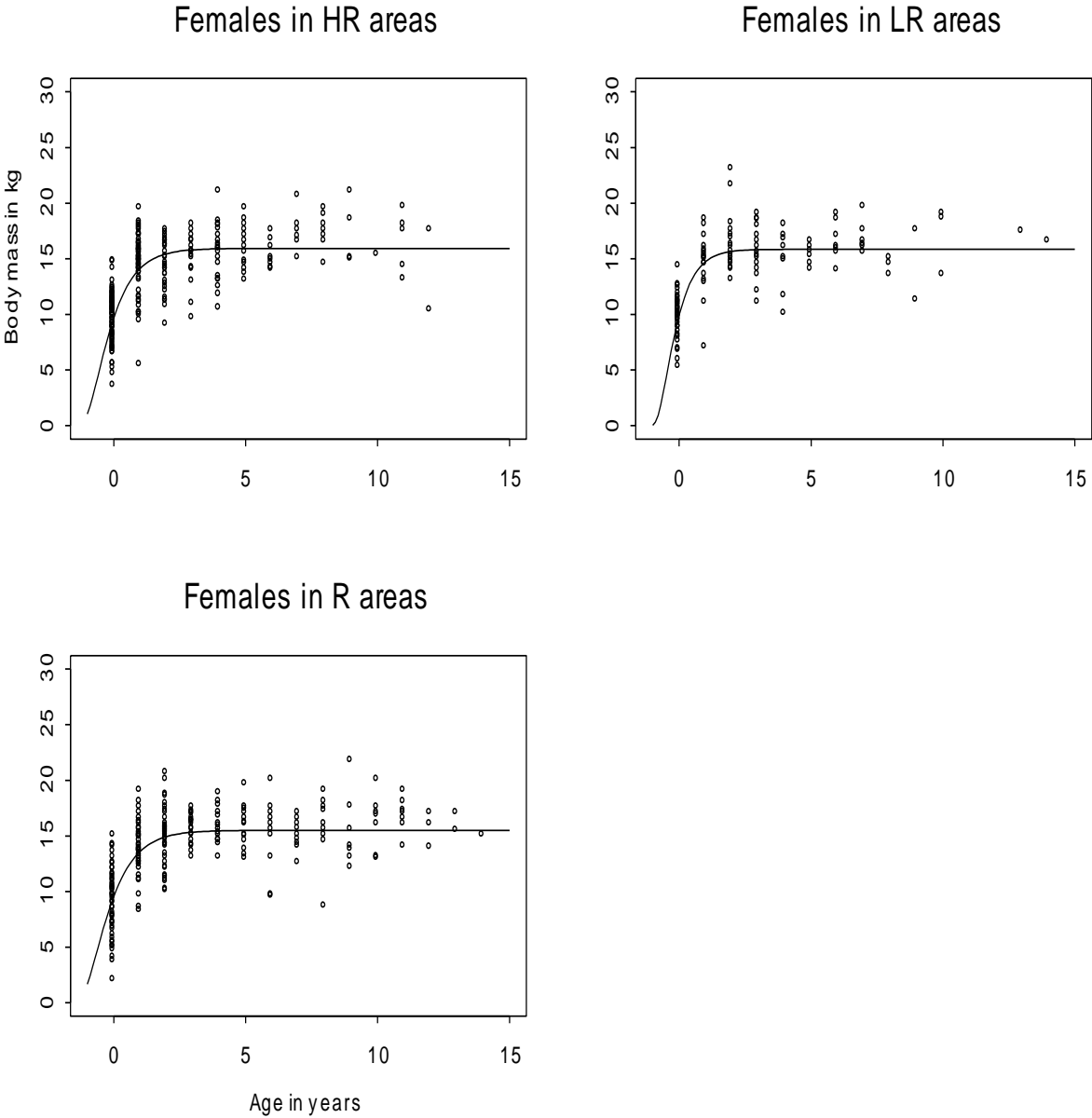


Fig. 3



Appendix 1

Here, the mathematics used to generate the individual growth curves is explained based on the von Bertalanffy equation for each prey category and sex. In the first equation:

$$1) X = \frac{V_t - \bar{V}_t}{\sqrt{\sigma^2(t)}}$$

X represents the scaled body mass deviation from the von Bertalanffy equation for one individual at age t . V_t is the observed body mass at age t and \bar{V}_t is the body mass predicted from the von Bertalanffy equation: $\bar{V}_t = W[1 - e^{(-k_w(t-A_w))}]^3$, based on the given sex and prey category. $\sigma^2(t)$ is a function of the form $at + b$ and models the distributions of the squared residuals, where a and b are constants and t is age. Note that any function describing the squared residuals well can be applied, the function we chose are the one that fit our data best:

In equation 1, the variance equals 1, hence, X describe the deviation from the von Bertalanffy growth curve at any age. The expected body mass, $V_{t_f}(X)$, for an individual with discrepancy X from \bar{V}_t at age t can be expressed as

$$V_{t_f}(X) = \bar{V}_t + \sqrt{\sigma^2(t)} \cdot X \rightarrow$$

$$2) V_{t_f}(X) = W \left[1 - e^{(-k_w(t_f - A_w))} \right]^3 + \frac{V_t - (W[1 - e^{(-k_w(t_0 - A_w))}]^3)}{\sqrt{at_0 + b}} \cdot \sqrt{at_f + b}$$

where W = asymptotic body mass, V_t = observed body mass, t_0 = age when mass was observed and t_f = final age in which all body masses are estimated.

The individual age corrected masses, $V_{t_f}(X)$, from equation 2 were used as the new response variable in the ANOVA analysis. This method model the effect of age on body mass before the construction of a linear model. Body masses are corrected for the effect of age according to the von Bertalanffy relationship an incorporated in to the model as a covariate. Individual curves, showing expected growth pattern using t as a variable, can be generated (fig. 1). A program was designed in S-plus 7.0 to do these tasks.