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Body mass dynamic in Eurasian lynx *Lynx lynx* kittens during lactation

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Body mass changes of Eurasian lynx *Lynx lynx* Linnaeus, 1758 kittens during the first four months of their life were studied in 1989–1999 in captivity. Four hundred thirteen records of body mass from 63 lynx kittens were analysed. The body mass of lynx kittens up to four months of age increased as a linear function with age. Daily growth rate (in grams) was minimal when the kittens were switching from milk to solid food at the age 41–60 days and was maximal at the age 61–80 days. Body mass dynamic and daily growth rates of kittens depended on the husbandry conditions of adult animals (or probably on their subspecies) and litter size, but did not depend on the sex of the kittens. Specific spontaneous fights during kittens' ontogenesis showed the trend to affect kittens' body mass dynamic and daily growth rate on some stages of kittens' development.

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Introduction

Although the Eurasian lynx *Lynx lynx* Linnaeus, 1758 is one of the most widespread and best-studied felines in the world (Nowell and Jackson 1996), some aspects of its biology are little known, including the postnatal development of lynx kittens. Data from the wild are usually unavailable to scientists, excluding some rare examples (Heptner and Sludskii 1972, Kaczensky 1991, Kvam 1991). The physical development of lynx kittens in captivity has been described by many authors as lynx reproduce well in zoos (Lindemann 1955, Stoyanova and Svarinskaya 1964, Andreevskaya 1964, Kunc 1970, Heptner and Sludskii 1972, Sulc *et al.* 1979, Stehlik 1980, 1984, 2000, Shilo and Leonova 1986, Hucht-Ciorgia 1988, Kaczensky 1991, Tumanov 2000). However, data on body mass changes of kittens have been published so far either for short time periods (Heptner and Sludskii 1972, Golubeva and Leonova 1986) or for only a few individuals (Kunc 1970, Sulc *et al.* 1979), so that statistical analyses were difficult. Usually only raw data were published (Stoyanova and Svarinskaya 1964, Kunc 1970, Sulc *et al.* 1979, Golubeva and Leonova 1986, Hucht-Ciorgia 1988). As a result it has not been possible to analyse the influence of litter size and sex of kittens on their body mass development. It is not possible to pool data from different studies, because the lynx demonstrates wide geographical variation in body size: lynx from

Yakutia *L. l. wrangeli* are almost twice as heavy as animals from European Russia *L. l. lynx* (Heptner and Sludskii 1972). These differences might affect the development of body mass in kittens. Other factors that may affect body mass changes in captive-bred kittens include average annual temperature and, most important, daily food ration.

The behavioural development of lynx has been studied less than their physical development and the results are often contradictory (Lindemann 1955, Stehlik 1980, 1984, Naidenko 1997). Some behavioural traits of lynx (eg, duration of lactation, weaning period, fighting between siblings (Sokolov *et al.* 1994)) may affect or be affected by the kittens' body mass development.

The aim of this study was to analyse the main factors influencing the development of body mass in lynx kittens during lactation, including subspecies/husbandry conditions, litter size and sex of kittens. I also wanted to compare the body mass development in litters, where siblings fought with each other (Sokolov *et al.* 1994, Naidenko 2000), with body mass dynamic in other litters.

Material and methods

This study was conducted in 1989–1999 at the Tchernogolovka Experimental Station of the A. N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences and partly in Saltikovskii fur farm. The station is situated 50 km north-east of Moscow and fur farm is located 30 km apart. Both, the station and fur farm are surrounded by natural mixed forest dominated by spruce *Picea alba*, pine *Pinus silvestris* and birch *Betula pendula*. This kind of forest is a typical habitat of lynx in Russia (Matjushkin 1978).

The lynx kept at Tchernogolovka station originate from European Russia and western Siberia. The animals bred at the Saltikovskii fur farm originate from the northern Altai region. The lynx inhabiting this region are exceptionally large and some authors have recognized them as another subspecies *L. l. wardi* (Heptner and Sludskii 1972).

In total, 54 kittens from 25 litters were weighed 377 times at the experimental station "Tchernogolovka" and 9 kittens from 4 litters were weighed 36 times at the Saltikovski Fur Farm. There were 7 litters with 1 kitten each, 16 litters with 2 kittens (in one litter only one kitten was weighed), and 6 triplets (in two litters data on only two kittens were available) at the station. The weighs of some kittens were missing for various reasons. The sex ratio of weighed kittens was close to 1:1 (29 males : 25 females). At the Saltikovskii Fur Farm there were 3 litters with 2 kittens and 1 litter with 3 kittens. The sex ratio was 1:2 (3 males and 6 females). More data concerning lynx reproduction at the Tchernogolovka Station and at the Saltikovskii Fur Farm have been published earlier (Naidenko 1997, Naidenko and Erofeeva 2004).

Lynx females with their kittens lived in two kinds of enclosures: six treeless enclosures (74 m^2 each) and one large enclosure (0.75 ha), which was a fenced part of the natural forest. Wild lynx were recorded near the station until 1992. The daily ration of food for each lynx female with kittens consisted of 1.5 kg of beef or chicken with 0.3 kg of various other foods (eg, fish, eggs, curd, beef and pork liver and heart, dry milk, vitamins). When the kittens reached 2 months of age, each family group started to get an additional 0.5 kg of meat each day. Further details of lynx husbandry conditions at the station were described earlier (Sokolov *et al.* 1994, 1995, Naidenko 2001).

Development of body mass in lynx kittens was recorded in 1989–1999. They were weighed from the 1st day of their life until they reached 129 days of age (but usually from the 5th day to avoid disturbing the female). Kittens were weighed in closed plastic or wooden boxes with an accuracy of 5 g. Because kittens were not tamed and actively avoided humans, weighing was stopped, if it was likely that the kittens may get injured during the experimental procedures. From three months of age, kittens were able to move very fast and regularly climbed up the trees and walls of the enclosures. The average time interval between two successive weighs of the same kitten was 9.3 days (SD = 8.2, n = 276). On average each kitten was weighed 7.0 times (SD = 6.0, n = 54; or 10.4 ± 5.3, n = 32, if excluding kittens for whom weighs were not regular).

The body mass of kittens at the Saltikovskii Fur Farm was determined for those born in 1990. Each of the nine kittens was weighed 4 times during 23 days (the average time interval between weighs was 7.7 ± 0.5 days, n = 27). The average age of the first weigh of these kittens was 42.0 ± 4.2 days, and of the last weigh – 65.0 ± 4.2 days.

It was not possible to weigh all of the lynx kittens at exactly the same age (because it was too difficult to separate them from their mothers in the enclosures) and to record their body mass changes for the whole period from the 1st to the 129th day. Kittens were weighed with different frequency (from once per two days to once per 10 days) and during different periods of their life (some kittens were weighed from the first day of life up to four months, other up to 1.5–2 months of age and the third group from 45–50 days of age. However, because of the unique character of the data all weigh records were analysed. I calculated a regression equation using all records with the Statistica software. The ANCOVA-test was used to estimate the effect of different fixed factors ("husbandry conditions", "litter size", "sex" and "fights observations") on the kittens' body mass (dependent variable), with age of kittens used as "covariate" and "individuality" as a random factor. For growth rate analyses during the different periods of ontogenesis the ANOVA test for repeated measurements was used. "Litter size", "sex" and "fights observation" were considered as the fixed factors. Ninety five percent confidence limits were calculated appropriately in all cases. Factor "husbandry condi-

tions" means an origin of kittens from either Tchernogolovka station or Saltikovskii fur farm. Because of a possibility that the lynx kept at these two breeding centres may belong to different subspecies, I will further regard this factor as "husbandry conditions/subspecies". During kittens ontogenesis spontaneous fights between littermates may occur (Sokolov *et al.* 1994) that may affect kittens' social relations (Naidenko *et al.* 2004). I consider these fights may influence the kittens' body mass too, although I am aware that not all fights could be observed. To acknowledge it, I call this factor "fights observations" instead of "fights occurrence".

The first four months of kittens' life include the very important changes in kittens' diet. Till the age of 42 days kittens were only fed with milk. After that they started to take solid food and since the age of two months meat became their main food, although lactation lasted up to 3–4 months (Naidenko 1997). Thus, the analyses of kittens' body mass dynamic were conducted separately for three periods: 2–42, 44–59 and 61–130 days. Analyses of kittens' daily growth rate was conducted for four periods (till 20 days, 21–40, 41–60 and 61–80 days). Changes in body weight were estimated in grams. However, the same body mass changes (for example, 25 g/day) mean different for a newborn kitten (body mass 300 g) and for a kitten 4-months old (5 kg).

Results

Kittens body mass changes

Only one newborn lynx kitten (a female) was weighed after she was abandoned by her mother. This kitten did not have siblings and weighed 298 g. In another case the body mass of a male kitten in the uterus (his mother did not give birth and died) was 285 g. He had two siblings, but their bodies had started to decompose (resulting in the mother's death) and it was not possible to estimate their body masses.

The body mass of lynx kittens increased as a linear function with age ($y = 0.906 + 0.034x$, $n = 413$, $p < 0.001$, where y is the body mass in kilograms and x is the age in days) during the first four months of life (Fig. 1). This function corresponds with a daily gain of 34 g during the first four months of kittens' life. The regression equations for Tchernogolovka station for litters with different number of kittens were: single: $y = 0.956 + 0.043x$, $n = 64$, $p < 0.001$, twins: $y = 0.905 + 0.034x$, $n = 212$, $p < 0.001$ and triplets: $y = 0.915 + 0.033x$, $n = 101$, $p < 0.001$.

The ANCOVA-test showed that only two factors out of four affected significantly kittens body mass dynamic: "husbandry conditions/subspecies" ($F = 11820$, df = 1, $p < 0.001$) and litter size ($F = 5.05$, df = 2, $p < 0.05$). Both other factors (sex and "fights observation") did not affect kittens' body mass dynamic ($F = 0.40$, df = 1, ns and $F = 1.66$, df = 1, ns, respectively).

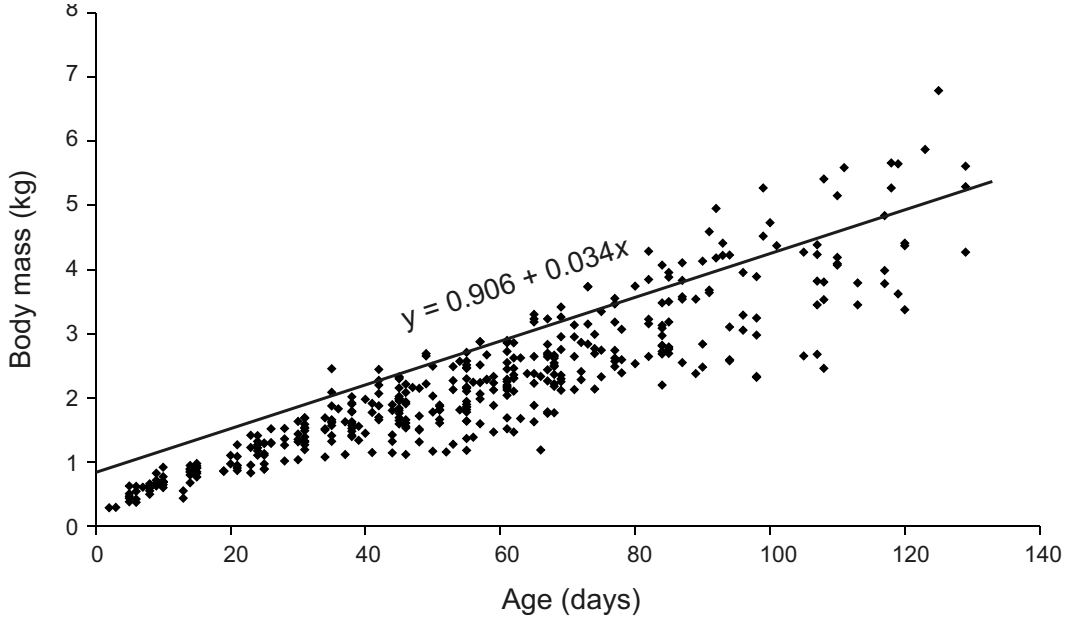

Fig. 1. Lynx kittens' body mass dynamic during the first four months of their development (line shows the regression equation for all data set, $n = 413$).

For all three recognised periods (2–42, 44–59 and 61–130 days) the effect of four factors was similar, however some differences were noted. For the first period, "husbandry conditions/subspecies" was only a factor affecting kittens body mass (F = 71582, df = 1, $p < 0.001$). There was a slight trend for "fights observations" to affect kittens' body mass dynamic during this period (F = 2.70, df = 1, p = 0.11), although the fights were described in older kittens. The effect of litter size and sex was not significant during this period (F = 0.11, df = 2, ns and F = 0.57, df = 1, ns, respectively).

However, already during the second period (age of 44–59 days) the effect of litter size and "husbandry conditions/subspecies" on kittens body mass were highly significant (F = 6.44, df = 2, $p < 0.01$ and F = 12004.8, df = 1, $p < 0.001$, respectively). Sex and "fights observation" did not affect kittens body mass dynamic during this period (F = 0.0, df = 1, ns and F = 0.35, df = 1, ns).

When kittens switched to solid food the effect of "husbandry conditions/subspecies" and litter size were important (F = 10489, df = 1, $p < 0.001$ and F = 3.33, df = 2, $p<0.001$, respectively). Sex of kittens and "fights observation" did not affect body mass dynamic during this period (F = 0.46, df = 1, ns and F = 1.04, df = 1, ns).

Sexual differences in kitten body mass dynamic may be obscured by the effect of other factors (eg, inter-litter differences). The analysis of kitten body mass was conducted in litters with siblings of different sexes. However, no differences in body mass of kittens were found at the age of ten days (Wilcoxon pair-matched test T = 16, n = 9, ns). When kittens became older usually males were heavier than females, but the sample size was too small for statistical comparison. Only five litters with kittens of different sex were measured (in four litters males were heavier than females).

Daily growth rate of lynx kittens.

The average daily growth rate of kittens varied significantly among the four distinguished periods from 21.5 to 46.5 g (the range: 9.0–94.4 g). It was largest at the age of 61–80 days and smallest at the age of 41–60 days (Fig. 2). This index was intermediate during the earlier stages of kittens' development. The average daily growth rate was significantly lower in kittens 41–60 days old than in kittens at the age < 20 and 61–80 days (Fig. 2; Wilcoxon pair-matched test T = 13, n = 15, $p < 0.01$ and T = 15, n = 15, $p < 0.05$, respectively).

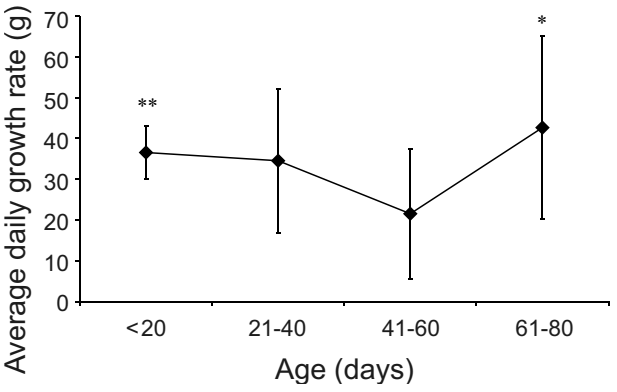

Fig. 2. Average daily growth rate (in grams) ± SD for lynx kittens during the four time intervals of their development. Only kittens weighed regularly during 80 days were included in analyses (n = 15). Asterisks show significant difference by Wilcoxon pair-matched test with the growth rate at the age 41–60 days ($p < 0.05$ and $p < 0.01$).

Repeated measures ANOVA used for changes in daily growth rate of kittens did not show significant effect of factors "litter size", "fights observation" and "sex". However, "fights observation" was found slightly, but not significantly affecting kittens growth rate (F = 3.69, df = 1, p = 0.08). Another important factor – age of kittens appeared to affect significantly kittens "growth rate" (F = 3.67, df = 3, $p < 0.05$).

The effect of the factor "age" was also proved by the ANOVA repeated measures test during the analyses of factors "litter size" and "sex" (F = 4.36, df = 3, $p < 0.05$). However, "litter size" and "sex" did not influence significantly kittens growth rate during these periods (F = 1.90, df = 2, ns and F = 0.00, df = 1, ns; for their interactions F = 0.91, df = 2, ns).

Discussion

Lynx reproduce usually once per year (Shilo and Leonova 1986, Kvam 1991), but sometimes females are able to have a second litter, if the

kittens from the first litter die at or soon after birth (Stoyanova and Svarinskaya 1964, Stehlik 1980, Valyus and Raudelene 1988). However, kittens from second litters are weaker and usually die before winter (Stoyanova and Svarinskaya 1964). As some seasonal differences have been observed for such litters I should mention that all litters considered here came out from the usual mating period (Naidenko and Erofeeva 2004). That allows to compare these data with the previously published results.

Development of body mass in lynx kittens

The body masses of two newborn kittens recorded during this study fall in the range known from previous studies (220 to 360 g; Rymareva 1933, Stoyanova and Svarinskaya 1964, Sulc *et al.* 1979, Stehlik 1980, 2000, Bondarenko and Topchii 1986, Golubeva and Leonova 1986, Yudina and Yudin 1990, Kvam 1991, Tumanov 2000). A study by Lindemann (1955) reported a body mass of newborn kitten's as around 69 g, but it is probably erroneous. Most likely, this value concerns the European wildcat *Felis silvestris silvestris*, as it is comparable to the average body mass of newborn kittens of this species found by Hemmer (1979) and much less than body masses of newborn Canadian lynx *Lynx canadensis* (197–211 g, Saunders 1964) and bobcats *Lynx rufus* (280–340 g, Lariviere and Walton 1997). The body masses of newborn kittens varied by approximately 1.6 times as the ratio of maximum to minimum masses, but including Lindemann's data, this ratio reaches 4.4, which would be highest in felines (Hemmer 1979).

The development of body mass in lynx kittens determined during this research was very similar to that found in Novosibirsk and Ostrava Zoos (Kunc 1970, Golubeva and Leonova 1986). However, kittens' body mass at Riga Zoo was lower than in my study before 3 months of age (Stoyanova and Svarinskaya 1964). The lynx kittens were significantly heavier at the Saltikovskii fur farm than at the Tchernogolovka station at the same age. Factor "husbandry conditions/subspecies" affected kittens' body mass dynamic highly significantly. Kittens of the largest lynx subspecies *L. l. wrangeli* from Wuppertal Zoo were also heavier than kittens of the same age at our station (Hucht-Ciorgia 1988). Perhaps lynx kittens' body masses during the first weeks of life depend on the body masses of their mothers as in domestic cats *Felis silvestris catus* (Deag *et al.* 1987). However, husbandry conditions may likely affect body mass development at a later stage. For example, adult lynx in Riga Zoo were fed a minimum of 1690 kcal (1.3 kg of beef) per lynx each day (Stoyanova and Svarinskaya 1964) and in Novosibirsk Zoo a mean of 2464 kcal was given per animal and 3156 kcal for each female with kittens (Golubeva and Leonova 1986). At the Tchernogolovka Station each lynx had more than 2000 kcal per day and each female with kittens received 2550 kcal daily. In contrast the individual lynx at the Saltikovskii fur farm consumed 2400 kcal daily and females with kittens got food *ab libitum*. This comparison shows that differences in kittens' weight among particular breeding centres could be associated with calorific content of the daily food ration. Lynx kittens of the largest subspecies *L. l. wrangeli* were significantly different from each other in body mass development at Wuppertal and Novosibirsk Zoos (Golubeva and Leonova 1986, Hucht-Ciorgia 1988). Probably food availability has a greater influence on body mass development of kittens than their genetic traits. It can be only confirmed by studying body mass development of the different lynx subspecies kept under similar controlled captive conditions.

The effect of sex on the development of body mass in lynx kittens

Lynx adult males are significantly heavier than adult females (Heptner and Sludskii 1972, Malafeev *et al.* 1986, Naidenko 1997). However, there was no effect of sex neither on kittens' body mass dynamics up to four months of age, nor on their daily growth rate during the first 80 days of their life at our station. Stehlik (1980) showed that newborn lynx males were slightly heavier than females in Ostrava Zoo (mean body masses 303 g and 272 g, respectively). I did not

find the differences in females and males body mass or growth rate between kittens of 5–10 days old. Possibly inter-sexual differences in body mass appear later than 9 months old, because no significant differences in body mass have been observed in wild lynx of 7–9 months old (Nikitenko and Kozlo 1965, Malafeev *et al.* 1986). In Iberian lynx inter-sexual differences in body mass were recorded only for animals more than 2 years old (Beltran and Delibes 1993).

The effect of litter size on body mass dynamics in lynx kittens

I expected the body masses of lynx kittens to be negatively correlated with litter size as described for some other mammals (Deag *et al.* 1987, Mendl 1988, but see also Nelson *et al.* 1969). In house cats the growth rate of kittens in larger litters is usually lower than in smaller ones during the whole lactation period (Deag *et al.* 1987, Mendl 1988). In my study, the litter size influenced significantly lynx kittens' body mass dynamic during the first four months of their postnatal ontogenesis. However, it concerned mainly the period, when the kittens switched to solid food. Among the kittens, which take only mother's milk, litter size did not have the significant effect on their body mass dynamic.

In some mammals significant differences in body mass occurred only in litters that exceeded the mean litter size for given species (for a review see Mendl 1988). The mean litter size in lynx consists usually of 2 to 2.4 kittens (Stehlik 1980, Kaczenski 1991, Breitenmoser *et al.* 1993, Kucherenko 1996, Naidenko and Erofeeva 2004). Indeed, in my study the kittens from triplets increased their body mass more slowly than single and twins. It might be expected that in very large litters (4–5 kittens), the development of body mass would be significantly different until at least 2 months of age, when the kittens are weaned, or even longer if prey abundance is limited. It may greatly affect their survival at all stages of development, as kittens are likely to be weaker in larger litters. Because litter size is crucial at the age 40–130 days (and probably later), when kittens started to rely on solid food , the availability of prey may be particularly important for normal development of kittens in large litters. In fact, lynx females with 3 kittens were rarely recorded during winter in the wild (Rukovskii 1977, Jędrzejewski *et al.* 1996, Kucherenko 1996).

Other factors affecting lynx body mass dynamics

The remarkable decrease in the kittens' daily growth rate found during this study seems to be clearly related to shortage of food. Similar decrease of the growth rate during the second month of the kittens' life was also calculated from the data on lynx kitten body mass in Riga and Prague Zoos (Stoyanova and Svarinskaya 1964, Sulc *et al.* 1979). The lynx kittens first tried to eat solid food at the age of 43–47 days at the Tchernogolovka station (Naidenko 1997), but milk was still the main source of food for kittens till the age of 55 days old. That's exactly during this period, when a decrease in growth rate for all kittens was recorded. Consequently, if kittens were experiencing a problem with shortage of mother's milk at this time, this problem would be exacerbated in larger litters, even though energy outputs of females with large litters was usually higher than those with small litters (Oftedal 1984). Daily energy requirements of the young increase with increasing body mass and at some point in time the females may be unable to satisfy the kittens' requirements by increasing energy output. At this stage the young are forced to seek solid food or reduce growth rates (Gittlemann and Oftedal 1987). The growth rate of lynx kittens increased again after the age of 60 days when they started to eat meat and it increased more in larger litters. Discontinuities in growth were also described for domestic cat kittens at weaning (Bateson and Young 1981, Deag *et al.* 1987), where it was recorded for 86 % of litters. The sharpness of the discontinuity in the growth rates of domestic kittens was significantly positively correlated with the number of living kittens in litters at this period (Deag *et al.* 1987). Therefore, the peak of growth rate in lynx kittens after 60 days of age was also probably a response to changes in diet at this period.

Fights between lynx kittens 45–61 days old were described in almost half of litters with two and three kittens (Sokolov *et al.* 1994, Naidenko 2000). These fights started spontaneously in litters where aggression between kittens had not been observed before. Sex of kittens and availability of solid food did not affect the frequency of these fights. Sibling aggression was recorded more frequently in litters with slightly heavier kittens. The factor "fights observation" showed a slight tendency to affect kittens body mass dynamic and daily growth rate. However, this tendency was noted only before fight period (< 42 days) and not after it. Possibly, the effect of fights may be partly messed because of 1) some cases/fights could be missed and/or 2) they affected differently on body mass dynamic of the fight winners and losers. The aggressor was in all but one case heavier than the second kitten (Sokolov *et al.* 1994, Naidenko 1997) in litters with 2 and 3 kittens. Thus, it could be supposed that aggressor kittens are better developed in comparison with their littermates. The result of a fight is the formation of a dominance hierarchy in the litter (Naidenko *et al.* 2004), so possibly that the most dominant kitten will be able to monopolise food resources.

Conclusions

My study showed that the dynamics of lynx kittens' body mass is mainly dependent on litter size and subspecies/husbandry conditions. Sex of the kittens did not affect body mass development during lactation. The age 41–60 days was a most vulnerable period during kittens' development, when they shifted to solid food. Availability of food during this period may be particularly crucial for their survival in the wild.

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References

Andreevskaya V. S. 1964. [Some data on reproduction and postnatal development of felines in Leningrad Zoo]. [In: I i II Konferentsiya Zoopoarkov, Riga, 1961–1962]. Riga: 21–25. [In Russian]

Bateson P. and Young M. 1981. Separation from the mothers and the development of play in cats. Animal Behaviour 29: 173–180.

Beltran J. F. and Delibes M. 1993. Physical charachteristics of Iberian lynxes (*Lynx pardinus*) from Doñana, southwestern Spain. Journal of Mammalogy 74: 852–862.

Bondarenko T. G. and Topchii V. N. 1986. [Lynx – the perspective species for the fur-farming]. [In: Pervoe vsesoyuznoe soveshchanie po problemam zookulturi. V. E. Sokolov, ed]. RU Centra Rosagropromnopt, Moscow 2: 179–180 [In Russian]

Breitenmoser U., Kavczensky P., Dotterer M., Breitenmoser-Würsten C., Capt S., Bernhart F. and Liberek M. 1993. Spatial organization and recruitment of lynx (*Lynx lynx*) in a reintroduced population in the Swiss Jura Mountains. Journal of Zoology, London 231: 449–464.

Deag J. M., Lawrence C. E. and Manning A. 1987. The consequences of differences in litter size for the nursing cat and her kittens. Journal of Zoology, London 213: 153–179.

Gittleman J. L. and Oftedal O. T. 1987. Comparative growth and lactation energetic in Carnivores. Symposia of the Zoological Society of London 57: 41–77.

Golubeva L. F. and Leonova O. V. 1986. [Husbandry, growth and development of some representatives of felinae family in Novosibirsk Zoo]. [In: Soderzhanie i razvedenie dikikh zhivotnikh. A. F. Kovshar', ed]. Kainar, Alma-Ata: 54–63. [In Russian]

Hemmer H. 1979. Gestation period and postnatal development in felids. Carnivore 11: 90–100.

Heptner V. G. and Sludskii A. A. 1972. [Mammals of the Soviet Union. V. 2. P. 2. Carnivores (Hyaenas and felids)]. Vyschaya shkola, Moscow: 1–551. [In Russian]

Hucht-Ciorgia I. 1988. Studien zur Biologie des Luchses: Jagdverhalten, Beuteausnutzung, innerartliche Kommunikation und an den Spuren faßbare Körpermerkmale. PhD thesis, Justus-Liebeg-Universität, Gießen: 1–177.

Jędrzejewski W., Jędrzejewska B., Okarma H., Schmidt K., Bunevich A. N. and Miłkowski L. 1996. Population dynamics (1869–1994), demography, and home ranges of the lynx in Białowieża Primeval Forest (Poland and Belarus). Ecography 19: 122–138.

Kaczensky P. 1991. Untersuchungen zur raumnutzung weiblicher luchse (*Lynx lynx*), sowie zur abwanderung und Mortalität ihrer jungen in schweizer Jura. MSc thesis, University of Münich, Münich: 1–80.

Kucherenko S. P. 1996. [Amur lynx]. Okhota i okhotniche khozyaistvo 9: 28–31. [In Russian]

Kunc C. L. 1970. Breeding and rearing the nothern lynx at Ostrava Zoo. International Zoo Yearbook 10: 83–84.

Kvam T. 1991. Reproduction in the european lynx, *Lynx lynx*. Zeitschrift für Säugetierkunde 56: 146–158.

Lariviere S. and Walton L. R. 1997. *Lynx rufus*. Mammalian species 563: 1–8.

Lindemann W. 1955. Uber die Jugendentwicklung beim Luchs (*Lynx l. lynx,* Kerr) und bei der Wildkatze (*Felis s. silvestris*, Schreber). Behaviour 8: 1–44.

Malafeev Yu. M., Kryazhimskii F. V. and Dobrinskii L. N. 1986. [Analysis of lynx population of Middle Ural]. UNTs AN SSSR, Sverdlovsk: 1–120. [In Russian]

Matjushkin E. N. 1978. Der Luchs. Neue Brehm-Bucherei. A. Ziemsen Verlag, Wittenberg Lutherstadt 517: 1–160.

Mendl M. 1988. The effects of litter size variation on mother offspring relationships and behavioural and physical development in several mammalian species (principally rodents). Journal of Zoology, London. 215: 15–34.

Naidenko S. V. 1997. [Lynx (*Lynx lynx L.*, Felidae, Carnivora) social behaviour and some features of its development in ontogenesis]. PhD thesis, IPEE, Moscow: 1–251. [In Russian]

Naidenko S. V. 2000. Eurasian lynx (*Lynx lynx*) reproduction, kitten growth and siblicide. Advances in Ethology, Supplements to Ethology 35: 99.

Naidenko S. V. 2001. An aggression in lynx adults-kittens relations: can it be a reason of litters dissolution? Ethology Ecology and Evolution 13: 283–295.

Naidenko S. V. and Erofeeva M. N. 2004. Eurasian lynx reproduction and traits of females reproductive strategies. Zoologicheskii Zhurnal 83(2): 261–269. [In Russian with English summary]

Naidenko S. V., Antonevich A., Erofeeva M., Stoebel K. and Jewgenow K. 2004. Sibling aggression in lynx: traits and consequences. Advances in Ethology. Supplement to Ethology 38: 68.

Nelson N. S., Berman E. and Stara J. F. 1969. Litter size and sexual distribution in an outdoor feline colony. Carnivore Genetic Newsletter 8: 181–191.

Nikitenko M. F. and Kozlo P. G. 1965. [Ecological and morphological description of lynx living in Bialovieza primeval forest]. [In: Ekologiya pozvonochnikh zhivotnikh Belorussii. P. F. Rokitskii and I. N. Serzhanin, eds]. Minsk: 58–63. [In Russian]

Nowell K. and Jackson P. 1996. Wild cats: Status survey and conservation action plan. IUCN, Gland, Switzerland: 1–382.

Oftedal O. T. 1984. Body size and reproductive strategy as correlates of milk energy yield in lactating mammals. Acta Zoologica Fennica: 171: 183–186.

Rukovskii N. N. 1977. [Traits of winter behaviour of lynx (*Lynx lynx* L.) litter]. In: Povedenie mlekopitayushchikh. Voprosi teriologii]. Nauka: 179–186. [In Russian]

Rymareva E. 1933. [To lynx biology]. Byullyeten zooparkov i zoosadov 8/9: 22–26. [In Russian]

Saunders J. K. 1964. Physical characteristics of the Newfoundland lynx. Journal of Mammalogy 45: 36–47.

Shilo R. A. and Leonova O. V. 1986. [Reproduction of members of feline family in Novosibirsk Zoo]. [In: Pervoe vsesoyuznoe soveshchanie po problemam zookulturi. V. E. Sokolov, ed]. RU Centra Rosagropromnopt, Moscow 2: 263–264. [In Russian]

Sokolov V. E., Naidenko S. V. and Serbenyuk M. A. 1994. Specific fights of young lynxes (*Felis lynx*, Carnivora, Felidae). Zoologicheskii Zhurnal 73: 132–138. [In Russian with English summary]

Sokolov V. E., Naidenko S. V. and Serbenyuk M. A. 1995. Marking behaviour of the European lynx (*Felis lynx*, Felidae, Carnivora). Izvestiya of RAS, Serya biologicheskaya N 3: 304–315. [In Russian with English summary]

Stehlik J. 1980. Zur ethologie, insbesonders zur fortpflanzung von luchsen in gefangenschaft. [In: Der Luchs in Europa. A. Festetics, ed]. KildaVerlag: 196–215.

Stehlik J. 1984. [Lynx (*Lynx lynx* Linnaeus, 1758) reproduction in captivity]. Folia Venatoria 14: 163–179. [In Czech]

Stehlik J. 2000. Reproductive biology of the European lynx, *Lynx lynx* (Linnaeus, 1758) at Ostrava Zoo. Der Zoologische Garten N. F. 70: 351–360.

Stoyanova V. K. and Svarinskaya V. G. 1964. [Observations of lynxes in Riga Zoo]. [In: I i II konferentsii zooparkov, Riga, 1961–1962]. Riga: 21–25. [In Russian]

Sulc P., Brantlova S. and Brodsky O. 1979. Hand breeding of European lynx, *Lynx l. lynx* (Linnaeus, 1758) at Prague Zoo. Gazella 2: 43–49.

Tumanov I. L. 2000. Traits of lynx (*Lynx lynx*) reproduction and postnatal ontogenesis. Zoologicheskii Zhurnal 79: 763–766. [In Russian with English summary]

Valyus M. I. and Raudelene V. A. 1988. [Reproduction of Holarctic mammals in Kaunas Zoo]. [In: Teriologicheskie issledovaniya v Litve. Y. A. Prusaite, ed]. Institut Zoologii i Parazitologii AN LitSSR, Vilnyus: 39–40. [In Russian]

Yudina E. V. and Yudin V. G. 1990. [Reproduction of far-east lynx in captivity]. [In: V S"ezd Teriologicheskogo obshchestva Akademii nauk SSSR. 29 yanvarya – 2 fevralya 1990. Moscow. V. E. Sokolov, ed]. Moscow 2: 127–128. [In Russian]

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