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Effect of inbreeding on kittens' body mass in Eurasian lynx (*Lynx lynx*)

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Abstract

The development of industry and agriculture and the continuous growth of human population on Earth have dramatically increased anthropogenic pressure on natural ecosystems and wildlife. As a result, fragmentation of the natural habitats and the decrease in genetic diversity in these populations increase the probability of reproduction with genetically closely related individuals (inbreeding). However, the effect of inbreeding in felids has been studied insufficiently and data are scarce. We decided to study the effect of inbreeding on kittens' body mass in captivity in the Eurasian lynx (*Lynx lynx*) colony which we keep near Moscow to study behavior and reproductive physiology of this species. This study analyzed the data on lynx kittens' body mass in inbred and non-inbred litters. Newborn kittens' body mass correlated negatively with the parents' inbreeding coefficient. Inbred parents had smaller kittens at birth in comparison with non-inbred ones. These differences disappeared when kittens reached 2 months of age. It is probable that this correlates with the maternal effect (higher investment in smaller kittens) and changes in the diet of kittens.

Keywords Eurasian lynx · Body mass · Ontogenesis · Inbreeding

Introduction

The development of industry and agriculture and the continuous growth of human population on Earth have dramatically increased anthropogenic pressure on natural ecosystems and wildlife. One of the most well-known problems is the fragmentation of natural habitats. Decrease in total area of the habitats, increase in local human population, and the development of infrastructure (roads, high-voltage electric lines, agricultural fields, etc.) destroy valuable habitats of wildlife species. One of the consequences for mammals is the reduction in local

populations' size (Wiegand et al. 2005) and, subsequently, constraints of dispersion (Brooker et al. 1999) and decrease/changes in genetic diversity in these populations (Berg et al. 2008). It results in increased probability of mating and reproduction with genetically closely related individuals (inbreeding) (Andersen et al. 2004; Stow and Sunnucks 2004; Banks et al. 2005). The inbreeding may have an important effect on survival and quality (fitness, fertility, etc.) of offspring (Darwin 1872), and thus on local population survival. The effect of inbreeding on reproduction has been described for many species of animals (Asa et al. 2007; Ala-Honkola et al. 2015; Vitikainen et al. 2015; Chen et al. 2017). Inbred parents have a lower number of offspring (Ala-Honkola et al. 2015; Vitikainen et al. 2015), lower quality (fitness, fertility, etc.) (Ralls et al. 1988; Laikre and Ryman 1991; Asa et al. 2007; Walling et al. 2011), and lower survival (Ralls et al. 1988; Laikre and Ryman 1991; Walling et al. 2011; Vitikainen et al. 2015) than non-inbred parents. The offspring of the inbred parents also have lower reproductive success (Laikre and Ryman 1991; Asa et al. 2007; Huisman et al. 2016). Inbreeding may affect immunity of the offspring and their fertility (e.g., result in teratospermia in cats) (Wildt et al. 1987; Neubauer et al. 2004). Together, these consequences were assigned the name “inbreeding depression” (Hedrick and Garcia-Dorado 2016).

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The prevention of inbreeding is the key factor in evolution of mating strategies. Animals often try to lower the chance of inbreeding (mammalian offspring usually disperse from natal home ranges (McLellan and Hovey 2001; Karlin and Chadwick 2012), and individuals prefer to mate non-related partners or/and partners differing in MHC (major histocompatibility complex) genes (Huchard et al. 2010; Winternitz et al. 2017). Inbreeding depression is a grievously important factor for endangered species of mammals. However, estimating the effect of inbreeding in the wild is very difficult. The main reason is the difficulty of estimating the relatedness of the individuals in the wild. Normally, calculating the inbreeding coefficient is very difficult because it requires knowledge of the pedigree of the individual animal. It is possible during long-term studies, but these cases are unique (Laws et al. 2010; Huisman et al. 2016). Even the modern molecular-genetic methods sometimes lead to mistakes and may not provide comprehensive information (Berenos et al. 2016).

Similarly, inbreeding in the wild felids and the consequences of this phenomenon for cat species is not yet clear. Researchers and conservationists discuss actively the effect of the loss and fragmentation of habitats on felids genetics. A subpopulation of Amur tigers (*Panthera tigris altaica*) at Russian Far East, isolated for 50 years, is significantly different from the tigers' subpopulation in the main range (Henry et al. 2009; Sorokin et al. 2016). Far-Eastern leopards (*Panthera pardus orientalis*) show an extremely low level of genetic diversity that has been suspected to correlate with potential inbreeding depression (Uphyrkina et al. 2002). Inbred (with low genetic diversity) Gir Forest lions (*Panthera leo*) have extremely low sperm quality and give birth to only one kitten per litter (Wildt et al. 1987). A population of lions from Ngorongoro with very low genetic variation, when compared to the nearest neighbors, also has lower sperm quality (Wildt et al. 1987). The teratospermia effect was considered to correlate with the low genetic diversity and with inbreeding in captivity (Neubauer et al. 2004; Pukazhenti et al. 2006). Teratospermic males have lower reproductive success than normospermic males (Naidenko et al. 2007; Erofeeva et al. 2018). The data on immune depression in inbred felids is scarce (Trinkel et al. 2011), but it was widely described for many different mammals and birds (Reid et al. 2007; Ilmonen et al. 2008). Thus, low genetic diversity of felids' population (and presumably the high level of inbreeding) may dramatically affect cats' reproductive success and sperm quality; however, proving it in the wild is very difficult. The felids are widely and unpredictably distributed in their habitats and live secretly.

Eurasian lynxes live solitarily (Heptner and Sludskii 1972; Nowell and Jackson 1996). They have large home ranges, varying from 100 to 1400 km² for males and from 70 to 800 km² for females (Zheltukhin 1984; Breitenmoser et al. 1993; Jedrzejewski et al. 1996; Linnell et al. 2001); therefore, studying the consequences of inbreeding in the wild is difficult. Usually, a male's home range overlaps fully/partly with

two to three home ranges of different females (Breitenmoser et al. 1993; Jedrzejewski et al. 1996). However, home ranges of the individuals of the same sex may overlap significantly as well (Jedrzejewski et al. 1996). The overlapping extent depends on population density. In Switzerland, where the density of lynx population is about 1 individual per 100 km², the males' home ranges overlap for less than 10% (Breitenmoser et al. 1993), but in Bialowieza Forest with the higher lynx population density (about 5 animals/100 km²) the overlapping percentage is much higher (about 50%) (Jedrzejewski et al. 1996). The dispersion of young animals from their maternal home ranges differs for males and females. Young males disperse further than young females. For example, in Scandinavia young males disperse in average for 148 km and females for 47 km (limits were 32–428 and 3–215 km respectively) (Samelius et al. 2012). In Bialowieza Primeval Forest, subadult males disperse for 60 km (limits 11–129 km, $n = 4$), subadult females for 7 km (limits 5–9 km, $n = 2$). Some of the subadult females may stay at mothers' home range or establish their home ranges, which overlap fully or partially with the maternal home range (Breitenmoser et al., 1993; Samelius et al. 2012). Respectively, although 100% of subadult Eurasian lynx males disperse from the maternal home ranges, only 65% of subadult females do the same (Samelius et al. 2012). This pattern of dispersion increases the chance that adult resident males may come into contact with their adult daughters during the mating season, which increases the chance of inbreeding. Usually, the young females give birth when they reach the age of 2 years (Naidenko 2005; Nilsen et al. 2012); in some cases, they can have their first litter 1 year earlier (Stehlik 2000). The Eurasian lynx has become the object of research on hormonal regulation (Jewgenow et al. 2006a; Dehnhard et al. 2010; Pribbenow et al. 2014) and reproductive biology (Jewgenow et al. 2006b; Goritz et al. 2009; Painer et al. 2014), ontogenesis (Sokolov et al. 1994; Naidenko 1998; Antonevich and Naidenko 2008; Alekseeva et al. 2014), and behavioral strategies (Sokolov et al. 1994, 1995, 1996; Naidenko and Erofeeva 2004; Erofeeva and Naidenko 2012). Many of these studies were conducted at the long-existing breeding colony of Eurasian lynxes at the Tchernogolovka station (Russia).

We decided to study the effect of inbreeding on kittens' body mass in captivity in the Eurasian lynx colony, which we keep near Moscow to study the behavior and reproductive physiology of this species. The aim of this study was to estimate body mass of kittens from the parents with a different inbreeding coefficient.

Materials and methods

This study was conducted at the Joint Usage Center "Live collection of wild species of mammals" at A.N. Severtsov

Institute of Ecology and Evolution (the biological station Tchernogolovka), Russia. This station is situated in 50 km to north-east from Moscow (56° 00' N, 38° 22' E). The Institute keeps the breeding colony of Eurasian lynxes (*Lynx lynx*) for behavioral and physiological research (Naidenko and Erofeeva 2004; Naidenko 2006; Jewgenow et al. 2006b). Animals-founders were captured in the wild at the end of 1980 (Naidenko 2005).

The husbandry conditions were described in detail earlier (Sokolov et al. 1994; Naidenko 2005). This research is based on the data on lynx reproduction in 1996–2016. During the whole period of the study, all animals were kept in the same enclosures and had the same diet. Animals were kept in the complex of six enclosures. Each octagon enclosure (74 m²) was connected to the 8-m² cage. Each cage and each enclosure had a wooden shelter for the animal (1.8*1.0*0.8 (l*w*h) m), covered by a stainless metal sheet and situated about 30–50 cm above the ground. Neighboring enclosures were connected to each other through aluminum shutters, which allowed moving animals without immobilization. The animals were kept individually excluding the mating season, and the females were kept with their litters for up to 10 months (the natural dispersion period (Schmidt 1998)). Animals had access to water ad libitum. The daily ration of adult lynx consisted of 1 kg of chicken meat with the addition of vitamins. Females with litters received an increased daily ration (1.5–2 times) accordingly to the number and age of the kittens. Animals received food 6 days per week; they stayed hungry for 1 day to simulate natural conditions. The food ration did not change over the whole study period.

Eurasian lynxes, oppositely to other cats, especially living in tropical zones, reproduce seasonally with high consistency (once per year (Naidenko and Erofeeva 2004)). Ordinarily, mating occurs in March and females give birth in the last 10-day period of May or the first 10-day period of June (Naidenko 2005). Respectively, the weighing of all kittens was conducted during the same season of any given year. The litter size in lynxes at Tchernogolovka biological station varied from 1 to 4 kittens.

All studied kittens were born at the experimental station Tchernogolovka in 1996–2016. Lynx kittens were weighed on the third or fourth day after birth, on the seventh day and every week after it. In our work, we used three age periods to analyze the weight of kittens: 3–4 days of age (age at birth), 30 days (lactation period), and 60 days (age when kittens already eat solid food and are not so dependent on the mother's milk). Before the weighing, the mother was separated in a neighboring enclosure/cage. The kittens were weighed in a special cage with the hand-scale (RST, Lund, Sweden) with the precision of 10 g. The whole litter was weighed in 5–10 min after the mother was separated, and the litter was returned to her immediately after the experimental procedure was complete. Females always accepted the kittens after the

experimental procedures. The risk that the female will abandon the litter was the maximum in the first days after birth, and it was the reason for not disturbing the litter on the first 2 days after the parturition. Eurasian lynx females are strong 20-kg predators that defend kittens very aggressively. It often made regular weighing of kittens at the exact scheduled day impossible (not wanting to stress mothers, we did not use immobilization). Lynx females were attracted into the neighboring enclosure/cage with bait, but it resulted in some variation (\pm 2 days) in weighing dates (instead of 30th, the kittens might be weighed on the 28th–32nd days after birth; instead of 60th, the kittens might be weighed on the 58th–62nd days after birth). However, the first weighing of kittens was conducted exactly when they were 3–4 days old. If we were unable to separate the mother in these days and the kittens were weighed at a different age (for example, at 5–6 days instead of 3–4, etc.), the data were not included in this analysis. The weighing after the birth was most complicated (females did not want to abandon the newborns), so it resulted in a decreased sample size at this age. Moreover, some of the cubs were transferred to different zoos (at the age of 1.5 months) or died due to intraspecific fights (Sokolov et al. 1994) or infections (Naidenko 2005). Therefore, sample size at the age of 2 months was limited. As a result, the number of litters we analyzed in each data set was different. Altogether, we used body mass data for 22 litters (58 kittens) at the age 3–4 days, 42 litters (106 kittens) at the age 28–32 days, and 33 litters (82 kittens) at the age 58–62 days.

While the inbreeding coefficient of the parents affects litter size in some mammals (Lacy and Horner 1997; Liberg et al. 2005), we did not find any correlation between the parents' inbreeding coefficient and the litter size in Eurasian lynx (Pearson product-moment correlation coefficient: $r = 0.2$; $t = 0.8$; ns). However, litter size can affect offspring body mass, for example in domestic cats, where kittens from smaller litters are heavier than in large litters (Deag et al. 1987). Earlier study (Naidenko 2006; Antonevich et al. 2020) showed that there were no differences in body mass of kittens from litters with 2 and 3 offspring. Based on this and on the fact that in the initial data set there were only 3 litters with 1 and 4 kittens, we neglected these data and used only the data obtained by weighing litters with 2–3 kittens.

All six lynx-founders belonged to the same subspecies (*L. lynx lynx*); the four of them were captured in different parts of the range and were considered to be unrelated to each other, and two other animals came from different zoos and were not related to each other either. The lynx colony at Tchernogolovka station has been reproducing since 1989, and the pedigree of all animals is known. Thirteen females and nine males were the parents of the kittens in this study. The inbreeding coefficient (IC, (or coefficient of relatedness)) was calculated for each pair of parents (Malecot 1969; Lange 1997; Oliehoek et al. 2006). We estimated this inbreeding

coefficient as the percentage of common genes of two animals (mother-offspring and siblings have 0.5; half-siblings and grandparents-grandchildren 0.25, etc.). We considered the litters/kittens that were mothered by the parents with $IC = 0$ as non-inbred, and we considered all others as inbred litters. The IC for the parents of inbred litters varied from 0.19 to 0.46.

When breeding in captivity, the age of the mothers is known from the pedigree. Weighing of adult animals is regularly carried out during procedures using immobilization (for example for health investigation). We did not find a direct correlation between kittens' body mass and the age of females (Pearson product-moment correlation coefficient: $r = 0.02$; $t = 0.1$; ns) and the body mass of females (Pearson product-moment correlation coefficient: $r = -0.2$; $t = -0.8$; ns). So, in the analysis of the body mass of the kittens, we neglected the data on the age and weight of the mothers.

Since the coefficient of parental inbreeding is the same for each kitten in the same litter, to exclude autocorrelation of the data we calculated the average body mass of a kittens for each litter firstly and then used these data for statistical analysis. Based on earlier studies which showed the absence of sexual differences in body mass of lynx kittens up to 4 months of age (Naidenko 2006; Antonevich et al. 2020) and on the fact that we calculated the mean kitten's body mass for each litter we did not include factor "sex" in our model. Thus, to study the influence of the inbreeding coefficient of parents on the mass of offspring, we used the average mass of kittens in the litter, litter id, three age periods (the first few days of their life; 30 days of age; 60 days), and the inbreeding coefficient of parents (IC).

We performed linear mixed-effect models (LMM) to analyze effects of inbreeding coefficient (IC) and age period using the library lme4 in R package (Bates et al. 2015). We evaluated sets of candidate models with all combinations of predictors using model selection based on Akaike's information criterion ($AICc$) in the library MuMIn (Burnham and Anderson 2002; Barton 2018). The $AICc$ weights were calculated, and estimates with their errors were averaged for models with $\Delta AICc < 7$ (Burnham et al. 2011). We initially fitted full models with all main effects and interactions. Interactions were insignificant ($p > 0.1$); thus, we did not include them in the set of candidate models. The litter identity was fitted in all models as a random factor. The repeated measure design could not be used because the datasets contained missed cells. Post hoc comparisons were performed with Tukey HSD test using emmeans package in R (Lenth et al. 2019). Statistical analyses were performed using R 3.5.2 (Team RDC 2019).

We used Microsoft Excel and Statistica 6.0 to conduct statistical analysis in every age period. The correlation between average kittens' body mass in litters and relatedness (IC) of their parents was estimated by correlation analysis (Pearson product-moment correlation coefficient r).

Results

In our study, the litter size in lynxes was similar in inbred and non-inbred litters: respectively 2.48 ± 0.11 ($n = 14$) and 2.44 ± 0.18 ($n = 8$). The best-fitted model with the lowest $AICc$ for mean kitten body weight included inbreeding coefficient (IC), age period, and litter size as significant predictors. The higher was the IC between parents, and the lower was the average weight in their offspring (LMM, $B = -0.07$, $SE = 0.03$, $p = 0.039$; Table 1); kittens from litters with two kittens were heavier than the ones from the litters with three kittens ($B = -0.22$, $SE = 0.07$, $p = 0.001$). The kittens gained body weight considerably between two consecutive periods: on the average, the mean weight in litters increased 2.8 times between the first and the second weighing (Tukey post hoc test, $t = 17.5$, $p < 0.0001$) and 1.7 times between the second and the third ones ($t = 36.8$, $p < 0.0001$). Random term (litter identity) was significant ($\chi^2 = 5.7$, $p = 0.02$; Table 1).

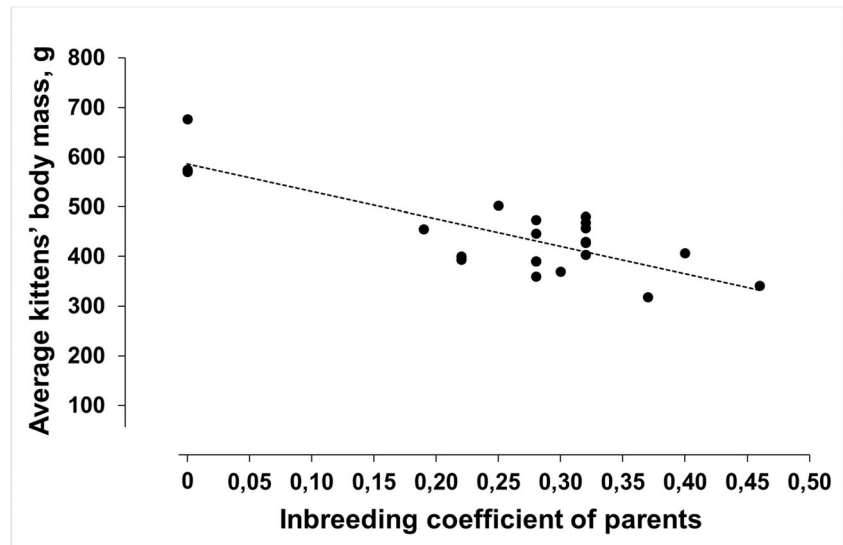
Correlation analysis of the body mass of kittens born from parents with different inbreeding coefficients showed a significant negative correlation between these two parameters. Kittens' body mass in litters in the first few days of their life correlated negatively with the inbreeding coefficient of their parents ($r = -0.8$; $t = 6.02$; $p < 0.001$). Average kittens' body mass in litters at the third–fourth days after birth varied from 329.4 ± 11.1 g (kittens of the parents with a high inbreeding coefficient (more than 0.35)) to 607.2 ± 34.8 g (kittens of unrelated parents) (Fig. 1).

The correlation of parents' inbreeding coefficient and kittens' body mass in litters at 30 days of age was still negative and significant although it was weaker ($r = -0.41$; $t = 2.83$; $p < 0.01$). Kittens' average body mass varied from 1192.6 ± 72.7 g (kittens of parents with high (> 0.35) inbreeding coefficient) to 1430.0 ± 82.3 g (kittens of non-inbred parents) (Fig. 2). The correlation becomes insignificant by the age of 2 months (60 days) ($r = -0.11$; $t = 0.63$; ns). The average body

Table 1 Effects of inbreeding coefficient (IC), litter size, and age period on the average juvenile body weight in European lynx litters. B and SE correspond to model-averaged parameter estimates and standard errors in linear mixed-effect models, χ^2 corresponds to likelihood ratio tests. Litter identity was fitted as a random term in all LMMs. All effects were significant ($p < 0.05$)

Predictors	Statistics
Intercept	$B = -1.26 \pm 0.06$, $\chi^2 = 9.4$, $p < 0.0001$
Inbreeding coefficient (IC)	$B = -0.07 \pm 0.03$, $p = 0.039$
Age periods	$\chi^2 = 229.1$, $p < 0.0001$
Period 2	$B = 1.17 \pm 0.06$, $p < 0.0001$
Period 3	$B = 2.43 \pm 0.06$, $p < 0.0001$
Litter size	$B = -0.22 \pm 0.06$, $\chi^2 = 10.4$, $p = 0.001$
Litter identity	$\chi^2 = 5.7$, $p = 0.02$

Fig. 1 Correlation of average kittens' body mass in the first days after the birth in litters with the inbreeding coefficient of parents



mass of kittens from the highly inbred parents was 1945.9 ± 97.8 g and from non-inbred parents 2168.36 ± 79.91 g (Fig. 3).

Discussion

Mating with genetically related partners may result in negative consequences for offspring in many species. High mortality of offspring born of inbred animals was described in comparison to non-inbred individuals (Ralls and Ballou 1982a, b; Ralls et al. 1988; Vitikainen et al. 2015). For some species, these differences may be very significant. For example, the survival of red deer calves (*Cervus elaphus*) born of inbred parents was 77% lower than in offspring of non-inbred parents (Walling et al. 2011). The consequences of inbreeding and low genetic diversity were discussed for some felids as well. The inbred

Gir Asiatic lions (the descendants of 10 (possibly) surviving lions in 1910) give birth only to one kitten and have lower sperm quality than Serengeti and Ngorongoro lions (Wildt et al. 1987). The Amur tiger shows low genetic diversity and genetic differences in two spatial groups which are separated from each other (Henry et al. 2009; Sorokin et al. 2016). The Far-Eastern leopard has extremely low genetic diversity (Uphyrkina et al. 2002) that was assumed to correlate with the inbreeding; however, the negative consequences were only an unconfirmed hypothesis (Uphyrkina et al. 2002). Thus, in wild felids the inbreeding effect has been discussed very often but has been described in few studies (Ralls et al. 1988; Trinkel et al. 2011).

We found that inbreeding indeed has a negative effect on offspring quality in Eurasian lynxes. However, this effect was not as obvious as, for example, in red deer (*Cervus elaphus*) (Walling et al. 2011). Inbred parents gave birth to smaller

Fig. 2 Correlation of average kittens' body mass at 30 days with the inbreeding coefficient of parents

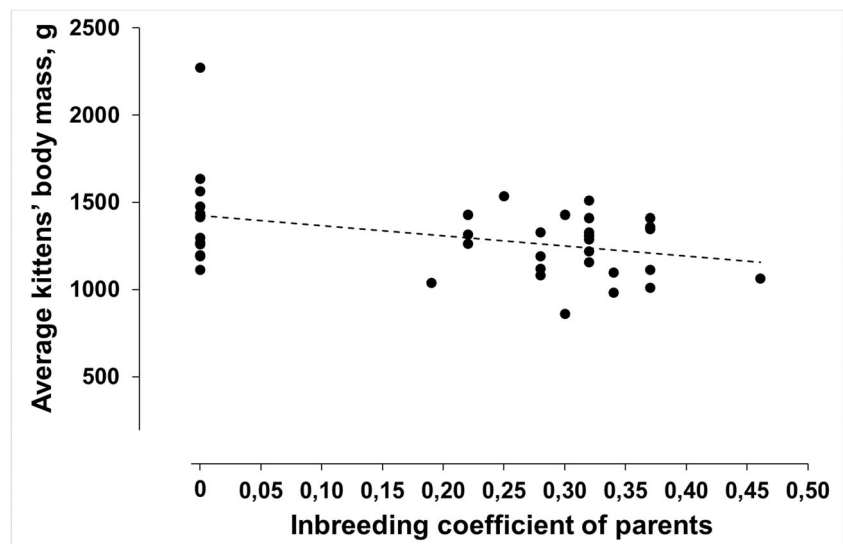
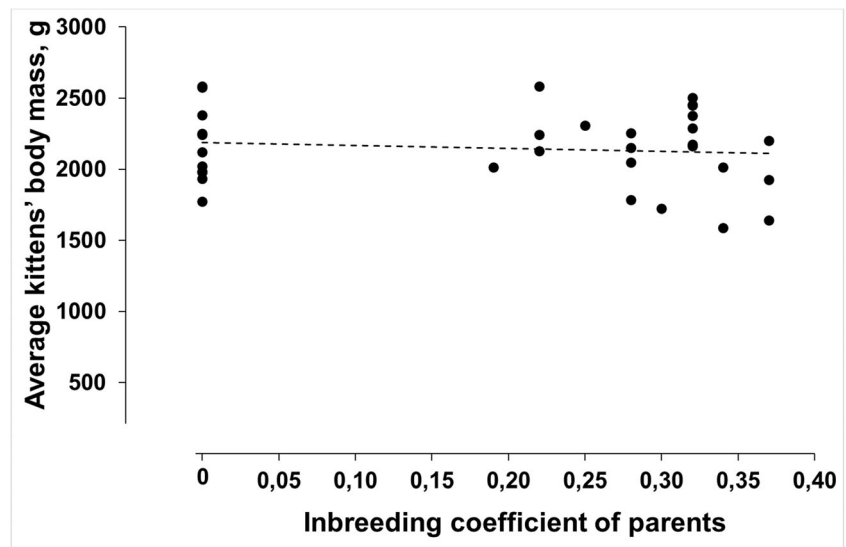


Fig. 3 Correlation of the average kittens' body mass at the age of 60 days with the inbreeding coefficient



kittens. Lynx kittens born of non-inbred parents had almost twice the body mass of the offspring of highly inbred parents. We did not find the data on effect of inbreeding on felids body mass in the wild; however, there are some data on zoo animals. In Sumatra tigers (*Panthera tigris sumatrae*), the decrease in kittens' survival and body mass was described for the offspring of inbred parents (Ralls et al. 1988). In cheetahs (*Acinonyx jubatus*), inbred breeding resulted in non-significant decrease in kittens' body mass (Beekman et al. 1999). In Canids, breeding in captivity resulted in the same inbreeding effect (Laikre and Ryman 1991; Asa et al. 2007). However, in gray wolves (*Canis lupus*) inbreeding led not only to a body mass decrease but also to lower survival rate of the offspring (Laikre and Ryman 1991). Inbred parents may also have blind kittens (Laikre and Ryman 1991; Asa et al. 2007).

Inbred parents may also have a lower number of offspring (Ala-Honkola et al. 2015; Vitikainen et al. 2015). The effect of litter size on offspring body mass was often described for different mammalian species (Deag et al. 1987; Sikes 1998): usually, offspring from the litters with smaller litter size are heavier than the ones from larger litters. In this study, lynxes' litter size affected offspring body mass, although earlier in the same population (but on another data set) we did not see this effect, at least when the litter size of two and three (Naidenko 2006; Antonevich et al. 2020). The animals from the litters with two kittens were heavier than in litters with three kittens. However, in Eurasian lynx inbreeding did not affect the litter size: it was similar both for inbred and non-inbred litters. However, inbreeding affected significantly the body mass of newborn kittens. Moreover, in lynxes the negative effect of inbreeding on kittens' body mass disappeared by the age of 2 months. This effect was the most obvious right after birth, became weaker when kittens were 30 days old, and became non-significant for kittens of 60 days old. These changes may be explained by the maternal effect. Maternal effect was

described for many species in the wild and in captivity (Margulis 1998; Beekman et al. 1999; Naidenko 2006; Reznick et al. 1996; Beckerman et al. 2006). The differences in mothers' productivity may affect the kittens' growth rate. Mothers may change their investment depending on environmental conditions and the sex of the offspring (Parker and Begon 1986; Beckerman et al. 2006; Carranza et al. 2009; Schrader and Travis 2012; Murphy et al. 2014). Lynx kittens during the first 2 months of their life feed mainly on maternal milk. However, we did not find any significant differences in kittens' body mass in litters relating to the sex of the animals. The earlier studies also showed that sex differences in body mass in lynx kittens were not detected (Naidenko 2006; Antonevich et al. 2020).

Usually, offspring body mass in mammals increases linearly with age. It was also described for different felids (Deag et al. 1987; Beekman et al. 1999; Naidenko 2006; Yerga et al. 2014), as well as for other mammalian species (Gosling et al. 1984; Allaine et al. 1998; Shen and Lee 2000; Arnould and Hindell 2002; Pilorz et al. 2005; Andersen et al. 2011). The famous phenomenon—lynxes' early sibling aggression (Sokolov et al. 1994)—correlates negatively with lynx kittens' body mass at birth (Antonevich et al. 2012) and kittens' growth rate before fights (Naidenko and Antonevich 2009; Antonevich et al. 2012). Lynx kittens that were smaller at birth had higher growth rate over the next months in comparison to the kittens that were bigger at birth (Antonevich et al. 2012). Our study showed similar results. By the age of 2 months, the differences in body mass of kittens that were born to inbred and non-inbred parents disappeared. It may be explained by the maternal effect (higher investment in smaller kittens), but another explanation is that by the age of 45 days lynx kittens start to take solid food and depend less on mothers' milk although the lactation lasts up to three and half months (Naidenko 2005). When lynx kittens start to take solid food,

their growth rate increases significantly (Naidenko 2006). It is possible that the smaller kittens start to take meat earlier (possibly due to food restriction) than larger ones.

Negative effects of inbreeding on reproductive success and offspring quality were not found to be universal in studies on different groups of animals. The study on Passeriformes did not discover any effects of inbreeding on quantity and quality of the offspring in these birds (Sardell et al. 2014). In wolf spiders (*Pardosa astrigera*), inbred parents gave a lower number of offspring that has a better survival rate than offspring born from non-inbred parents (Chen et al. 2017). The study on cheetah did not show significant differences in kittens' body mass between inbred and non-inbred parents (Beekman et al. 1999). Inbreeding in domestic tomcats leads to teratospermia; however, sometimes inbred males have sperm parameters similar to those of normal tomcats (Neubauer et al. 2004; Glukhov and Naidenko 2013) because they have compensatory mechanisms to prevent the negative effect of teratospermia (Pukazhenti et al. 2006). The negative effect of inbreeding in lynx kittens disappears by the age of 2 months. However, we may assume that inbred mating may still affect the sperm quality in lynxes (like in many other cat species (Wildt et al. 1987; Pukazhenti et al. 2006)), which may cause teratospermia (Erofeeva et al. 2014) and affect their reproductive success in the future (Naidenko et al. 2007; Erofeeva et al. 2018).

This study was conducted in captivity where the effect of environmental factors was minimized. It was presumed that animals demonstrate higher effects of inbreeding in the wild than in captivity (Crnokrak and Roff 1999). The effect of inbreeding is higher under unfavorable environmental conditions (Armbruster and Reed 2005; Fox and Reed 2011; Reed et al. 2012) and may lead to population extinction (Liao and Reed 2009). However, although experimental studies show a more pronounced effect of inbreeding, in the wild this effect is comparatively low (Pemberton et al. 2017). This situation may be explained through different reasons. First of all, the “wilderness” studies are unable to account for or to include all factors affecting the analyzed population. Secondly, the level of observed inbreeding in natural populations is generally low compared with that used in experimental studies. Also, in experimental studies the husbandry/experimental conditions may result in stress of animals because of novelty effect (Pemberton et al. 2017). These contradictory results did not provide us with a universal answer about the effect of inbreeding. In our case, the negative effect of inbreeding on kittens' body mass in litters disappeared by 2 months of age, probably because females with kittens had almost unlimited access to food. In the wild, food restriction could be the reason of lower survival of smaller kittens (Bowen et al. 2015) which increased the perceived effect of inbreeding.

Eurasian lynxes, as well as many other felids and carnivores, mate with more than one partner (Say et al. 1999;

Lariviere and Ferguson 2003). These mating habits result in an increase of the litter size (Erofeeva, Naidenko, 2011; Erofeeva et al. 2018), also leading to multiple paternity in litters (Yamane 1998; Say et al. 1999; Naidenko et al. 2007; Erofeeva, Naidenko, 2011; Erofeeva et al. 2018). In the wild, even in isolated populations (even when the daughters stay at the mothers' home range), the probability of the appearance of inbred litters in Eurasian lynxes is very small (Schmidt et al. 2016). The multiple matings (with different partners) may decrease the probability of inbred offspring. However, if the population is isolated receiving no gene supply, and also consists of the descends from a limited number of founders (for example, in reintroduced populations), the probability of inbred depression definitely increases (Sindicic et al. 2013; Müller et al. 2014).

In summary, we showed that in Eurasian lynxes inbred mating results in a decrease of newborns' body mass in comparison to the non-inbred kittens. Although these differences disappear by the age of 2 months, this may be an effect of high food availability in the captivity. However, how this mechanism affects animals in the wild populations with the restricted food resources remains unclear.

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