Naidenko, S. and Antonevich, A. L. (2009). Sibling aggression in Eurasian lynx (*Lynx lynx*) (Agresión entre hermanos de camada en el lince euroasiático (*Lynx lynx*)). In Iberian Lynx *Ex Situ* Conservation: An Interdisciplinary Approach (Conservación *Ex Situ* del Lince Ibérico: Un Enfoque Multidisciplinar): 147-155. Vargas, A., Breitenmoser-Würsten, C., and Breitenmoser, U.(Eds.). Madrid: Fundación Biodiversidad in collaboration with: IUCN Cat Specialist Group.

Abstract: Sibling aggression has been studied mainly in birds, but it has also been described for a few mammalian species. In Eurasian lynx these fights occur at a specific age, mainly at the 7th week of postnatal development (63% of fights). This is not an obligate phenomenon and in a half of all litters these fights were not observed at all. Usually, fights start spontaneously, last from few minutes to a few hours and are not repeated during ontogeny in the same litter. These fights coincide with a critical period in lynx ontogeny: cubs switch to solid food, change their growth rate, intensify social relations and establish a hierarchy among littermates. Fight winners increase their growth rate during this critical period, which may provide them a better chance to survive in the wild. They also initiate more social contacts in the litter. Although there were no clear relations between probability of fights and cub's hormonal status, the stimulation of adrenal glands with ACTH injection seemed to increase the occurrence of fights.

Notes: Incl. Spanish abstract

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Sibling aggression in Eurasian lynx *(Lynx lynx)*

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Photo: Sergey Naidenko

Resumen

La agresión entre hermanos ha sido estudiada principalmente en aves, pero sólo ha sido descrita en algunas especies de mamíferos. En el lince euroasiático, las peleas entre hermanos de camada son relativamente comunes y se producen a una edad determinada, principalmente en la 7ª semana de desarrollo postnatal (63%). Este fenómeno no se produce siempre, y se ha observado en aproximadamente la mitad de las camadas que han sido objeto de este estudio. Las peleas suelen iniciarse de forma espontánea, con una duración que varía desde pocos minutos hasta varias horas, y –en el caso de lince euroasiático– no se repiten durante la ontogénesis de una misma camada. Las peleas coinciden con un período crítico en el desarrollo del lince, en el que los cachorros pasan de alimentarse de leche materna a comer comida sólida. Durante este período, también se produce un cambio en la tasa de crecimiento de los cachorros; sus relaciones sociales con sus compañeros de camada se intensifican, y se establece una jerarquía entre ellos. Los ganadores de las peleas entre hermanos aumentan su tasa de crecimiento durante esta fase crítica, lo cual podría proporcionarles mayores posibilidades de supervivencia en el medio silvestre. Además, los cachorros ganadores también inician más contactos sociales en la camada. Aunque no se ha observado una relación clara entre la probabilidad de peleas y el estado hormonal de los cachorros, la estimulación de las glándulas suprarrenales mediante la inyección ACTH parece aumentar la probabilidad de las peleas. Son necesarias más investigaciones para comprender el mecanismo que desencadena el comportamiento agresivo en el lince.

Palabras clave

Agresión entre hermanos de camada, lince euroasiático, masa corporal, relaciones sociales, glándulas suprarrenales

ABSTRACT

Sibling aggression has been studied mainly in birds, but it has also been described for a few mammalian species. In Eurasian lynx these fights occur at a specific age, mainly at the 7th week of postnatal development (63% of fights). This is not an obligate phenomenon and in a half of all litters these fights were not observed at all. Usually, fights start spontaneously, last from few minutes to a few hours and are not repeated during ontogeny in the same litter. These fights coincide with a critical period in lynx ontogeny: cubs switch to solid food, change their growth rate, intensify social relations and establish a hierarchy among littermates. Fight winners increase their growth rate during this critical period, which may provide them a better chance to survive in the wild. They also initiate more social contacts in the litter. Although there were no clear relations between probability of fights and cub's hormonal status, the stimulation of adrenal glands with ACTH injection seemed to increase the occurrence of fights.

KEYWORDS

Sibling aggression, Eurasian lynx, body mass, social relations, adrenal glands

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IBERIAN LYNX *EX SITU* CONSERVATION: AN INTERDISCIPLINARY APPROACH
ASTRID VARGAS, CHRISTINE BREITENMOSER & URS BREITENMOSER
FUNDACIÓN BIODIVERSIDAD / IUCN CAT SPECIALIST GROUP

Sibling aggression in Eurasian lynx *(Lynx lynx)*

SERGEY NAIDENKO AND ANASTASIA L. ANTONEVICH

INTRODUCTION

Sibling aggression has been described in a variety of avian species (e.g. American white pelican *Pelecanus erythrorhynchus*, eurasian kestrel *Falco tinnunculus*, laughing kookaburra *Dacelo novaeguineae*) (Mock and Parker, 1997; Nathan et al., 2001; Massemin et al., 2003). This phenomenon (resulting sometime in the death of nestlings) should bring some advantages for the winners. The degree of such advantages may change depending on food supply, and is thought to be a way of brood size modification according to available resources (Mock and Parker, 1997; Drummond, 2001).

In mammals, competitive behaviour among siblings has been described in few species. Serious aggression has been described among litter-mates in some canids (Bekoff, 1974; Wandrey, 1975; Ovsyannikov, 1993). In two mammalian species sibling aggression sometimes results in the death of one littermate ("siblicide"). These are the domestic pig *(Sus scrofa)* (Fraser, 1990) and the spotted hyaena *(Crocuta crocuta)* (Frank et al., 1991). In both cases, siblings compete for the mother's milk as the only food source for the young animals. The losers are likely to starve to death (Fraser, 1990; Smale et al., 1995; 1999; Golla et al., 1999). The probability of this phenomenon in hyenas depends on the availability of food for adult animals (Wachter et al., 2002).

Eurasian lynx *(Lynx lynx)* became the third mammalian species where the fatal sibling aggression was described (Sokolov et al., 1994). It was noted in captivity, in five litters out of 10 with two to three cubs, and in one case it resulted in the death of one cub. In the wild this phenomenon was never observed, although high postnatal mortality was described in some studies (Jedrzejewski et al., 1996) and some indirect findings may indicate sibling aggression (U. Breitenmoser, pers. comm.). The monitoring of an Iberian lynx *(L. pardinus)* population in nature provides some indirect data that sibling aggression may occur in the wild as well (Palomares et al., 2005). Sibling aggression has also been described for Iberian lynx in captivity (Vargas et al., 2005; Antonevich et al., this volume).

Eurasian lynxes have reproduced successfully in many zoos. The average litter size is around two cubs (for review see Naidenko and Erofeeva, 2004). Usually, about 75% of the litters have more than one cub. Physical development of cubs has been described by different authors (e.g., Stehlik, 1980; Naidenko, 2006), but the ontogeny of social behaviour is poorly studied. The long-term research of a captive lynx population

in Tchernogolovka, Russia, allowed us to collect data on lynx behavioural development during their postnatal ontogeny. The aim of this study was to sum up the data on lynx sibling aggression and to look at the effect of this phenomenon in the development of cubs.

MATERIAL AND METHODS

This study was conducted at the experimental station Tchernogolovka of the A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (56º00' N, 38º22' E) from 1989 to 2006. Average annual temperature varied from +3.5 °C to +4.3 °C; average temperature in July was +19 °C and in January -11 °C. The station keeps the Northern lynx *(L. l. lynx)* subspecies (Versteege, this book) Adult lynx lived separately in three types of outdoor enclosures: treeless small enclosures of 8 m² (n=26) and 74 m² (n=6); and a large enclosure of 7500 m², which is a fenced part of natural mixed forest *(Pinus silvestris, Betula pendula, Picea abies)* with the dense brush *(Sorbus oucuparia, Rubus idaeus)*. More details of lynx husbandry conditions have been described earlier (Sokolov et al., 1994; Naidenko, 2001).

Females with cubs until the age of three months (n=28) lived mainly in medium sized enclosures (74 m²). We were not able to conduct statistical analyses effect of the husbandry conditions on the occurrence of sibling aggression because too few litters were kept in small cages (n=3) and in the large enclosure (n=2), but both "aggressive" and "non-aggressive" litters were found in all types of enclosures.

Lynx reproduced every year at the station. Males and females were placed together during mating season in March (Naidenko and Erofeeva, 2004). All litters were born between May 12 and June 19. Litter size varied from 1 to 4. There were 31 litters with two to four kittens at the age of 45 days (peak of fights, see below) (Table 1). These litters belonged to 12 different females and were sired by six different males. Cubs born at the station stayed with their mothers until they were 10 months old, when they would disperse in nature (Schmidt, 1998; Zimmermann et al., 2005).

Females with cubs were fed daily a beef or chicken diet. In addition, they also received live and dead rats and rabbits, eggs, fish, curd and vitamins. The size of the daily amount of food varied from year to year, but was always more than 1 kg per day (Sokolov et al., 1994; Naidenko, 2001). Usually all cubs were weighed once per week (starting at 3-5 days of age), although this frequency was not constant for different litters (Naidenko, 2006). The weight of cubs was measured to the nearest 5 g. To estimate cub's daily growth rate (in g) we used the results of two successive weightings divided by the number of days between weighing them. To estimate increase in weight we calculated the ratio of the daily growth rate (in g) to the number of the last weighing and expressed it in percent (Naidenko, 2006). We estimated average cub's body mass at the time of fighting (for litters where fights were not observed, body mass was estimated for cubs at 45 days of age), representing as well the standard error and standard deviation.

Regular observations were conducted on cub's ontogeny using the data continuous recording method (Martin and Bateson, 1993). The frequency of observation was usually one six-hour period per every three days (Naidenko, 1997) and one to two 24-hour observations per month for each litter. The observations were conducted from a special shelter. Lynx fights were observed only three times during these regular observations; fights were mainly noted by accidents. In 2003-2004 we conducted detailed observations of kitten's behavior in four litters from three females (three triplets and one twin) comprising four males and seven females. For each social interaction we noted the initiator and the object. For further analysis cubs were categorized according to the results of fights: winners, losers and neutral cubs (in triplets).

Litter size	2	3	4	Total
Number of litters	12	17	2	31
Number of litters where the fights or their consequences were observed	5	11	0	16
Sex ratio (m/f)	11/13	26/24*	3/5	40/42

* - SEX OF ONE KITTEN WAS NOT DETECTED BEFORE IT DISAPPEARED.

* - EL SEXO DE UNO DE LOS CACHORROS NO FUE DETECTADO ANTES DE DESAPARECER.

TABLE 1. LITTER SIZE AND OTHER PARAMETERS RELATED TO SIBLING FIGHTING BEHAVIOUR IN EURASIAN LYNX LITTERS.

TABLA 1. TAMAÑO DE CAMADA Y OTROS PARÁMETROS REALCIONADOS CON EL COMPORTAMIENTO AGONÍSTICO EN EL LINCE EUROASIÁTICO.

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We divided the data into two-week intervals to establish the influence of sibling aggression on cub's behavior, taking the age at which fights occurred in each litter as the reference point. The frequency of each form of behavior was recalculated per one-hour unit of activity using the formula:

$$Nh=N*60/A$$

where Nh=number of behavioral acts per one hour of activity, N=number of behavioral acts per six hours of observation, A=activity time (in min) for six hours. To define the differences and individual partner preferences for social interactions we compared observed frequencies with frequencies expected by chance. Expected frequencies were calculated for each litter (total number of social contacts per litter divided by the number of cubs), and the degree of difference between the observed and expected frequencies estimated using the Chi-square test (Lehner, 1996). An analysis of variance was used to test factors possibly affecting kitten's play behavior. All data analyses were conducted with the software Statsoft Statistica 6.0.

Blood sampling was conducted for all kittens at the 7th week of their life at the same time (8.00-11.00 h) to exclude the effect of the diurnal cycles of hormone excretion. Enzyme Immuno Assay (EIA) was conducted to estimate the concentration of testosterone, dehydroepiandrosterone, cortisol (commercial kits of "Immunoteck", Russia) and androstenedione ("DRG", USA) (Naidenko and Erofeeva, 2005; Naidenko, 2005). The level of the hormones of the adrenal glands was also measured one hour after ACTH-injection ("Synacten Depot", Novartis, Switzerland, 2,5 IU/kg of body mass) (Naidenko et al., 2007).

RESULTS
DESCRIPTION OF FIGHTS

We observed fights in 16 out of 31 litters (52%) with two to four kittens. Fights were observed in five out of 12 (42%) litters with two kittens and in 11 out of 17 (65%, difference test (%), P=0.24) litters with three kittens. In two litters with four kittens we observed no fights. They occurred in different litters at the age of 36-64 days (6th -10th postnatal weeks), with a highest frequency during their 7th week of life (n=10, 63%). Fights started with the spontaneous attack of one of the sibs on another one. No aggressive interactions between sibs were ever observed before the attack. Both males and females were aggressors and they attacked kittens of the same or another sex. When the aggressor was identified, females were aggressors in eleven cases (total

number of females in these litters was 24), males –in four cases (n=18; difference test (%) P=0.11). The aggressor tried to bite the victim on the back of the head or throat (Figure 1). The attacked sib rolled up to the back and tried to defend itself. The female tried to stop fights using her forelegs and mouth. When the mother separated her cubs, the aggressor tried to continue the attack. The motivation level was sometimes so high that the aggressor lost its fear of humans. The attempts to continue the fight lasted for some hours. Lynx mothers sometimes stayed near the injured/attacked kitten and tried to prevent the aggressor to come nearby. Probability of fights was approximately the same for primeparous (50%; n=10) and multiparous (52.3%; n=21) females as well as the probability of the lethal result (10% and 14%, respectively). The attacked kitten continued to show defensive behaviour for a few more hours. In four cases, fights resulted in the death of kittens. Altogether, fights resulted in the death of less than 10% (4 over 43) of cubs in aggressive litters.

Photo: Sergey Naidenko

FIGURE 1. ATTACKED CUB PRESENTING A SEVERE THROAT BITE.

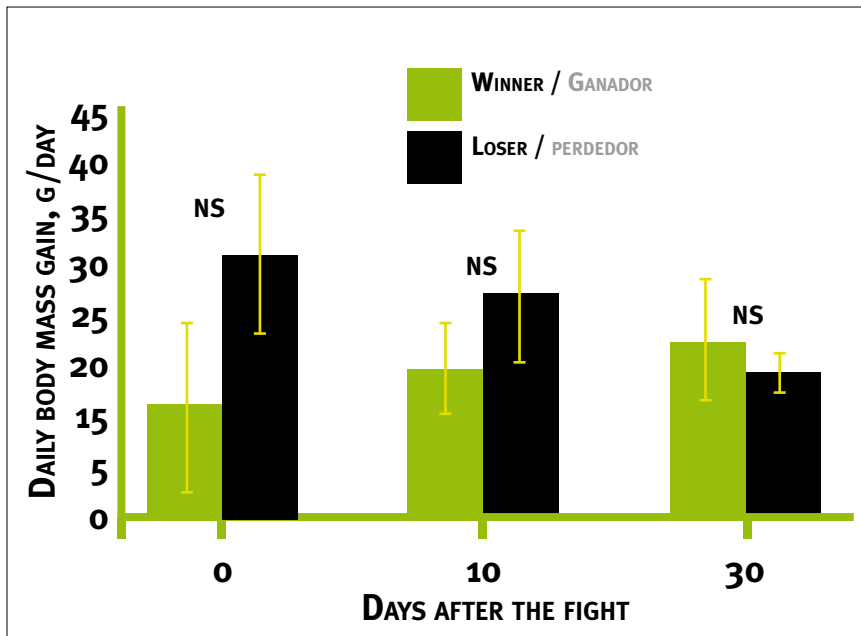FIGURA 1. CACHORRO ATACADO QUE PRESENTA UN SEVERO MORDISCO EN LA GARGANTA.

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Fight effect on kitten's physical development

Body mass of kittens was analysed very precisely for seven litters, where kittens survived after the fights and winners and losers were clearly detected. We did not find significant differences in body mass of kittens (winners and losers) and their growth rate after the fights (Figure 2). We tried to estimate the changes in growth rate of kittens at 10 and 30 days after the fight, in comparison to their growth rate at the day of fight. The results are significantly different 30 days after the fights, where the changes in the growth rate of winners are much higher than that of losers (Figure 3). These parameters varied a lot for different litters (-28 to 56 g/day for winners and -52 to 39 g/day for losers), but for all litters the winner got some advantage in changes of growth rate in comparison to the victim.

Kittens killing a sib should expect even more advantages after the death of a competitor. Their daily growth rate was significantly higher than in all other aggressors in the first ten days after the fight (47 ± 8, n=3, and 20 ± 16, n=7; U=1; Z=2.17; P< 0.05). So, the daily body mass gain of killers was almost 2.5 times greater than the weight gain of other aggressors. However, these differences disappeared in the following three weeks.

Fight effect on kitten's social behaviour

Fighting among cubs was observed during the developmental period for social play. The first elements of playing were observed at the age of one month, and by the end of the second month the frequency reached its maximum for the whole developmental period. However, frequency of play decreased significantly for some time after fights. For the first days after the fights the frequency of social play was significantly lower in comparison to other observations (ANOVA-test F=4.18; df=1; P<0.05).

The frequency of play also varied among littermates. Before fights, observed and expected play frequencies differed significantly (it was higher and lower, respectively, than the expected value) in two of the 11 cubs (18%) from four litters. In contrast, during the first two weeks after the fights, differences between expected and observed frequencies were registered for six cubs (55%; difference test (%) P<0.05). The most marked changes were seen on winners (in three of four cubs), which initiated play interactions in two cases significantly more often and in one case less often than expected. After another two weeks, differences between observed and expected frequencies of play were still seen in five cubs (45%; difference test (%) P=0.08). Thus, the occurrence of fights resulted in an increase in the asymmetry of play behavior. Play frequency for losers in the triplet litters never exceeded expected levels. In two cases there was no significant difference, and in one case the frequency was significantly lower. The frequency of loser's play was significantly higher only once: in twin litters during the third to fourth week after the fight.
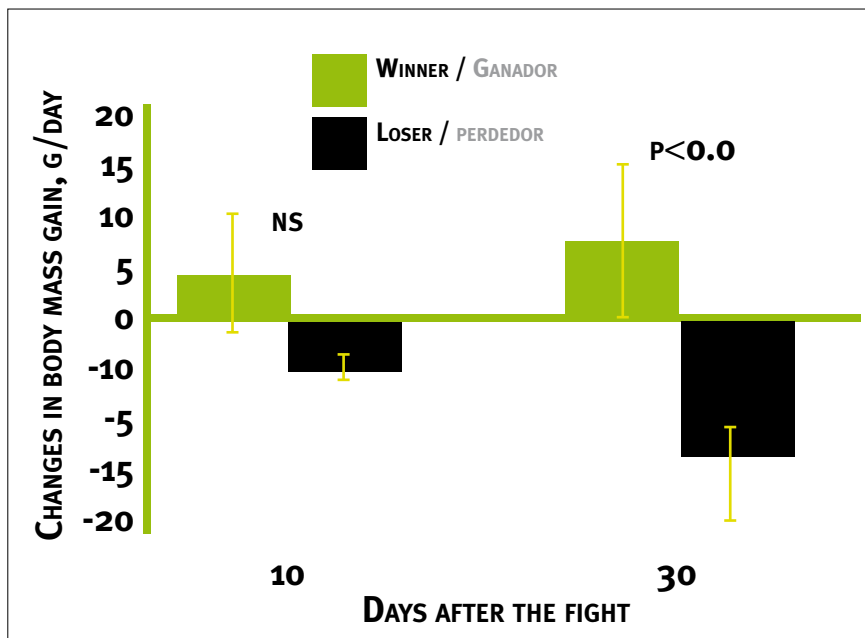
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Figure 3. Changes in daily body mass gain in Eurasian lynx cubs after 10 and 30 days, respectively, from the fights.

Figura 3. Cambios en el aumento diario de masa corporal en cachorros de lince euraoasiático tras 10 y 30 días después de las peleas.

Hormonal status of the kittens

Hormonal status of winner and loser cubs during the fights, as well as that of neutral cubs, was compared. We did not find any significant difference in hormone concentration in the blood of winners and losers. The level of testosterone was similar for kittens that initiated fights and for the victims (Wilcoxon pair-matched test: T=5; Z=0.67; n=6; ns). Average levels of cortisol were slightly higher (158±33 ng/ml) in aggressive cubs compared to neutral kittens (147±41 ng/ml; ns) and victims (113±10 ng/ml; T=3; Z=1.21; n=5; ns). Also, cortisol levels did not differ in cubs from litters where no fights occurred. There were no significant differences in androstenedione during this period (T=7; Z=0.73; n=6; ns) for aggressors and losers.

A single injection of ACTH increased sharply the level of cortisol in the cub's blood plasma (Z=2.39; n=10, P<0.01). Sixty minutes after injection, the cortisol level increased 1.4-8.1 fold for different animals and more than three times on average (98±13 and 313±54 ng/ml, respectively). The level of androstenedione increased significantly as well (0.049±0.010 and 0.081±0.013 ng/ml; Z=2.60; n=10, P<0.01). The level of dehydroepiandrosterone and testosterone did not increase significantly. Two kittens attacked the sibs during the first hour after the ACTH injection. The probability of these fights was 18%, which was much higher than potentially expected values (0.02%). It seems that the adrenal glands play a crucial role in kitten's sibling aggression.

Discussion

Serious sibling aggression in lynx has been observed during the period of cub ontogenesis. Only 36-64 day-old cubs fought with each other. Usually, interactions of litter-mates in July (about 35-65 days of age) are mainly (more than 90%) playful contacts (Naidenko, 2001). Few aggressive interactions, which tend to happen around food, are much more ritualized than specific sibling fights (Sokolov et al., 1994). In contrast to spotted hyaenas, lynx fights usually happen only once. They may last for a few hours but when they stop the aggression is usually over.

Sibling aggression in lynx does not depend on the sex of either the aggressor or the attacked cubs. The behaviour of adult females was consistent in case of sibling fights: they always tried to stop the aggressive interactions. Although some cubs may get some advantage if the sibling dies, the mother will get a clear disadvantage with the decrease of it's reproductive success.

These fights rarely result in the death of one of the cubs; about 10% of them die. It does not look like the death of the competitor is a main result of sibling aggression in lynx. This phenomenon was never observed in the wild, but in captivity it was noted under different husbandry conditions (our station, St Petersburg and

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Wuppertal zoos, Oslo University and El Acebuche Iberian lynx Breeding Centre (Vargas et al., 2005; Vargas et al., this book, Antonevich et al., this book). So, the effect of captivity on lynx sibling aggression could not be ruled out but needs more detailed research.

It has been suggested that fights result in the formation of a hierarchical structure in lynx litters (Sokolov et al., 1994). It may provide some advantages to the winner of the fight, especially if food is limited. The period of sibling aggression coincided with the development of social play (Naidenko, 1997). However, fights were followed by a decrease in frequency of play behavior, after which it increased again. In addition, we found an increase in the asymmetry of play interactions after the fights. During the first hours after a fight the injured kittens (losers) often showed defensive behavior towards the aggressors, the neutral sibs and their mother. This reaction disappeared a few hours later but was followed by asymmetry in the kitten's further play interactions (i.e., winners usually initiate playful contacts more often than we expected). For the first month after fights, a relatively high level of asymmetry in play interactions was seen. Such way, asymmetry in play behavior during this period allowed us to consider the possibility that hierarchical relationships were established in lynx litters during this period, even though the number of aggressive encounters was low.

The second month of cub's development in Eurasian lynx is very important. During this period, they start to take solid food at approximately 42-45 days of age (sometimes slightly earlier or later). The period after fights (after 60 days of age) –coinciding with when cubs start to take solid food– was characterised by an increase in the cub's growth rate (Naidenko, 2006). At 60 days, meat seems to become more important than milk (Naidenko, 1997). In the wild, we don't have any obvious evidence that females bring meat to the den.

In captivity, food was provided ad libitum for females with cubs (Sokolov et al., 1994; Naidenko, 2001). That might decrease the intra-litter competition and the differences in kitten's body mass dynamic. Regardless of this fact, fights seemed to always bring advantages to the winners. At least, changes in body mass gains were positive for the winners and negative for the losers. "Killers" had even a higher growth rate than non-killer winners. Probably, in case of food shortage, dominant cubs will get more chances to survive in nature.

The mechanisms of sibling aggression in lynx are not yet clear. For this species, the phenomenon does not correspond to high level of blood-circulating androgens, as it was assumed before (Naidenko and Erofeeva, 2005). Measurements of cortisol did not allow us to see clear differences between aggressors and other kittens. However, stimulation of cub's adrenal glands by an ACTH-injection increased both probability of fights and level of adrenal hormones (cortisol and androstenedione). Results indicate that sibling aggression in lynx might be related to the function of adrenal gland. Further research is needed to understand the trigger mechanism of aggressive behaviour in lynx.

ACKNOWLEDGEMENTS

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