



Meeting with a male can lead to stress: Female reaction to a pairing with a partner in Felidae

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ABSTRACT

The aim of this study was to test the hypothesis that the level of sexual dimorphism modulates the effects of male-female social interaction on the female physiological condition in felids. We predicted that: 1 – contacts of females with males in species with low level of sexual dimorphism in body size will not lead to significant changes in the activity of the hypothalamus-pituitary-adrenal axis (female stress); 2 - contacts of females with males in species with a high level of sexual dimorphism can result in significant increase in the cortisol level in females. Our study did not support these hypotheses. Despite the fact that sexual dimorphism influenced partner relationships, changes of the activity of HPA in response to social interaction with a partner appeared to be determined by the biology of the species rather than by the degree of sexual dimorphism. In species with unexpressed sexual dimorphism in body size, females determined the character of relationships in the pair. In species with pronounced sexual dimorphism biased towards males, the pattern of relationships was determined by males. However, meeting a partner led to increased cortisol levels in females not in pairs with pronounced sexual dimorphism, but in pairs with a high frequency of partner interactions. This frequency was determined by the species life history and was probably related to the seasonality of reproduction and the degree of monopolization of the home range.

1. Introduction

Sexual dimorphism is related to many aspects of animal life: ecology, behavior, population dynamics, and the evolution of animal life strategies (Boonstra et al., 1993; Allaine et al., 1998; King and Allaine, 2002; Isaac, 2005; Pörschmann et al., 2010). In most mammals, sexual dimorphism is quite pronounced, including body size: as a rule, males are larger than females (Trivers, 1972; Anderson, 1994; Lindenfors et al., 2007). It is not surprising that in sexual selection studies, the interest of researchers is mainly focused on reproductive success and forms of competition in males (Yamane, 1998; Pörschmann et al., 2010; Lidgard et al., 2008; de la Peña et al., 2021). It is believed that the more

pronounced sexual dimorphism in body size is, biased in mammals toward males, the greater the variance in reproductive success of males in a particular species (Yamane, 1998; Pörschmann et al., 2010). At the same time, high levels of competition for mating can lead to stress in males (de la Peña et al., 2021). The ability to exhibit an adaptive response to stress-inducing factors by maintaining low cortisol concentrations during reproduction may increase their reproductive success (Lidgard et al., 2008). However, such studies usually do not take into account the behavior and stress levels of females, which are often recipients of intensive and persistent attention from males. Thus, it is reasonable to expect significant physiological response to such interactions.

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Often, competition between males for a female can take the form of sexual coercion, which is widespread in species with pronounced sexual dimorphism in body size biased towards males (Clutton-Brock and Parker, 1995; Cassini, 2020). Males coerce females because they are able to do it – they are physically stronger and larger than females, and such tactic increases their reproductive success (Clutton-Brock and Parker, 1995). If the female cannot avoid “the courtship” of the male, she becomes coercive towards the male in order to avoid injury from too intense courtship (Clutton-Brock and Parker, 1995; Birkhead, 2000). Such interactions can reduce the possibility of precopulatory mate choice and be stressful for the female.

Among Felidae species, the level of sexual dimorphism in size / body mass varies greatly. It varies from 2 (when the male is twice as large as the female, as in the golden cat (*Profelis aurata*)) to close to 1 (when male and female are almost the same size, as in Eurasian lynx (*Lynx lynx*), cheetah (*Acinonyx jubatus*) and Canadian lynx (*Lynx canadensis*)) (Geptner and Sludskii, 1972; Nowell and Jackson, 1996). Males are very active in search of reproductively active females, making long excursions far beyond their home range (Breitenmoser et al., 1993; Naidenko and Hupe, 2002). A female may be followed by several males during the mating period (Dards, 1983; Izawa et al., 1982; Zheltukhin, 2003). Female domestic cats in high-density conditions can have up to nine sexual partners (Izawa et al., 1982). Such high competition can lead to increasing sexual activity of the male. Even the presence of another male per se was shown to increase the reproductive effort of the male (delBarco-Trillo and Ferkin, 2004; Erofeeva and Naidenko, 2012). Therefore, during the mating season, some felid males also demonstrate pursuit of females and sexual coercion. For example, this behavior has been described in a domestic cat (*Felis silvestris var. catus*) and Amur leopard cat (*Prionailurus bengalensis euptilurus*) (Erofeeva and Naidenko, 2020). In some species, such tactic may result in the death of the female (for example, the clouded leopard (*Neofelis nebulosa*) (Brown et al., 1995). In such a situation, it is quite expected that for females the encounter with a larger conspecific can be stressful and lead to an increase in HPA (the hypothalamus-pituitary-adrenal) axis activity (Pavlova, 2010). High levels of stress (glucocorticoids) in females during the breeding season may affect their reproductive success negatively. Females with high cortisol level may produce fewer offspring (Aleksieva et al., 2020).

In our earlier study, it was shown that sexual dimorphism can affect partner relationships in felines during the mating season (Erofeeva and Naidenko, 2020). In the Eurasian lynx *Lynx lynx*, the character of interactions with a partner during mating is largely determined by females. It is a species with a low level of sexual dimorphism (the ratio of the body mass of males to females being on average 1–1 (Naidenko, 2005)). Eurasian lynx females initiate friendly contacts with males more often when meeting a potential mate and show a high frequency of sexual behavior toward him (Erofeeva and Naidenko, 2020). In the bobcat *Lynx rufus* and Amur leopard cat *Prionailurus bengalensis euptilurus*, males determined the relationship during the mating season. The males were very persistent in their attempts to mate with the female. These species are similar to the Eurasian lynx in social and spatial organization (solitary predators with large individual home ranges), but they are characterized by more pronounced sexual dimorphism (bobcat - the ratio of the body mass of males to females in on average 1.3 (our data; Jones and Coman, 1982); Amur leopard cat - the ratio of the body mass of males to females in on average 1.5 (our data; Geptner and Sludskii, 1972)). The domestic cat differs greatly from other species in its high variability of social and spatial organization. In different conditions, this predator can live solitary as well as in large and complex social groups (Pontier and Natoli, 1996; Naidenko and Hupe, 2002; Say et al., 1999, 2002), and the breeding system can vary from monogamy to promiscuity (Say et al., 1999). However, the domestic cat is also characterized by a pronounced sexual dimorphism shifted towards males (the ratio of the body mass of males to females being on average 1.3 (our data)). The character of relations in domestic cats during the mating

season is also determined by males (Erofeeva and Naidenko, 2020). Therefore we can ask, to what extent may the male-female relationships cause stress-related consequences in these species?

The aim of this study was to test the hypothesis that the level of sexual dimorphism modulates the effects of male-female social interaction on the female behavior and physiological condition in felids. We predicted that: 1 – the intensity of male social activity will modulate the nature and level of the female social behavior; 2 – in species with low level of sexual dimorphism in body size contacts of females with males will not lead to significant changes in the activity of the hypothalamus-pituitary-adrenal axis (female stress) and females will demonstrate higher frequency of affiliative contacts toward the partner than in high-dimorphic species; 3 - in species with a high level of dimorphism contacts of females with males will result in increase in the cortisol level in females and males will demonstrate a high frequency of contacts toward females; 4 - during the non-reproductive period, the encounter of females with males will not lead to HPA activation in any of the studied species.

2. Materials and methods

2.1. Subjects of research

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 in 2015–2018. The Center has a unique collection of felines on which various aspects of reproductive biology have been studied for more than 20 years. All animals are kept at the biological station “Chernogolovka”, Moscow region, Russia. Four species were used in this study: the Eurasian lynx, the bobcat, the Amur leopard cat and domestic cat. All animals were of reproductive age (numbers of animals and pairs are given in Table 1).

2.2. Housing conditions

Eurasian lynxes were kept in a complex of octagonal outdoor enclosures without trees of 74 m² each. Every enclosure was equipped with a wire cage (8 m²) that was connected to the enclosure through gate valves. Bobcats were kept in a complex of cages with an area of 6 m² each. Each enclosure/cage contained a wooden box (1.2 × 0.8 × 0.8 m) on an iron frame about 40 cm high serving as an artificial shelter, logs and stumps (Naidenko, 2005; Erofeeva et al., 2020). Amur leopard cats were kept in a complex of enclosures with areas of 16 m² or 8 m² each. Each of the enclosures/cages had an artificial shelter (a wooden box with an iron roof) (0.8 × 0.5 × 0.5 m), logs, stumps, and wooden shelves 1.3 m above the ground surface (Pavlova and Naidenko, 2008). Domestic cats were kept in a complex consisting of 2 m² cages. Each of the enclosures/cages had an artificial shelter (a wooden box with an iron roof) (0.8 × 0.5 × 0.5 m), logs, stumps (Aleksieva et al., 2020). The presence of shelters in the enclosures allowed the animals to avoid

Table 1
Number of animals, pairings and samples used in the work.

Species	Eurasian lynx	Bobcat	Amur leopard cat	Domestic cat
SD*	1	1,3	1,5	1,3
Mating season	March	February-March	March-April	year-round
Live stile	solitary	solitary	solitary	solitary-social
N animals (female / male)	4/3	3/3	6/2	12/7
N pairing (mating season / non-reproductive s.)	12/10	12/12	12/18	19/33
N of feces samples	260	250	268	278

* - Sexual dimorphism – the ratio of males/females body mass

contact with their partner if necessary. Within each complex, all enclosures/cages were connected to each other using a system of gates or corridors, which made it possible to move animals within the complex and to pair them without direct physical contact with the researcher. Throughout the year, all animals were kept separately, with the exception of females with their offspring.

The cats were fed with chicken meat supplemented with vitamins. The animals were fed 6 times a week at the rate of 1 kg of meat for lynxes, 0.5 kg for Amur leopard cats, and 0.25–0.35 kg for domestic cats. All animals had constant access to water.

2.3. Experimental design

To study the reaction of females to a meeting with a partner, two sets of tests were carried out. In every test a female was paired with a single conspecific male.

- 1) Tests during the mating period. The tests were performed in March for Eurasian lynxes, bobcats and Amur wildcats and in domestic cats in March–April (the mating season of these species). During these tests males mated or tried to mate with females.
- 2) Tests during the non-reproductive period (October–November for all species). During these tests the paired cats did not try to mate. For the domestic cat, females were examined visually before the trials and paired with males only if no signs of estrus were found (the domestic cat is reproductively active regardless of the season).

For three days before each pairing, feces were collected from females to determine basal glucocorticoid levels. Right before the test the sliding doors between the female and male compartments were opened and the male moved to the female enclosure/cage. All pairings always took place on the female territory. All tests were recorded on a digital video recorder at normal speed. The camera was placed in such a way that the entire female enclosure was in the camera's sight and the camera filmed from the moment the animals were paired until they were separated. 4 h after the pairing had started, the male was removed from the female. Excrements were then collected from the female enclosure for three days after the test to determine changes in HPA (hypothalamus-pituitary-adrenals) axis in response to pairing with a partner. The presence of feces in enclosures was checked twice a day (morning and evening) throughout the experiment (3 days before and 3 days after the pairing).

Some females participated in two trials during the same mating season or during the same non-reproductive season (in 20 of 128 pairs, females were alternately paired with two different males during the same period). If the female was tested twice during the mating season, the second trial was performed on the 3rd day after the first trial, and the male partners were always different. If the female participated in two trials during the non-reproductive period, the second trial was performed within 3–7 days after the first one. The same animals were used during the mating and non-reproductive periods.

2.4. Processing of excrement samples

The collected fecal samples were frozen at $T = -18\text{ }^{\circ}\text{C}$ until subsequent extraction and analysis of cortisol levels. Extraction of samples was carried out according to the previously described method (Jewgenow et al., 2006; Pavlova and Naidenko, 2008). On a "Scout Pro SPS202F" electronic balance (Ohaus Corporation, USA), 0.1 g of excrement was weighed with the precision to 0.01 g in an Eppendorf tube, and 0.9 ml of 90% methanol was added. The tubes were stirred for 30 min using an "Ekros" stirrer (Ecohim, Russia). After that, the tubes were centrifuged (centrifuge – Eppendorf AG (Eppendorf, Germany)) for 10 min at a speed of 4000 rpm. 200 μl of the supernatant were taken into a separate tube with a pipette, adding 200 μl of distilled water. The resulting extracts were stored at $-18\text{ }^{\circ}\text{C}$ until measurements were taken. This method appears to provide a more complete extraction of hormones

from Felidae feces than other commonly used approaches (Naidenko et al., 2019).

2.5. Measuring of hormone concentrations

The concentration of hormones in the excrement of animals was determined by heterogeneous enzyme immunoassay (EIA) using a Multiscan EX plate reader (ThermoElectron Corporation), measuring the optical density in the wells of the plate at wavelengths of 450 and 620 nm and comparing it to standard values. The measurements were carried out in duplicate, determining the coefficient of variation. With a coefficient of variation (CV) of more than 5%, the measurements were repeated, with a CV of less than 5%, their average value was taken for further analysis. To determine the level of cortisol metabolites (hereinafter, cortisol) in a domestic cat and an Amur leopard cat, we used the ImmunoFA_Cortisol kits (Immunotech, Moscow, Russia). The cross-reactivity of the used antibodies to cortisol was 6% for prednisolone, for all other tested steroids it was less than 1%. These kits were previously validated for the domestic cat and the Amur leopard cat (respectively, Pavlova et al., 2014 and Pavlova and Naidenko, 2008). Cortisol-IFA kits (Khema, Moscow, Russia) were used to determine the level of cortisol in the bobcat and the Eurasian lynxes. These sets were validated during the ACTH test according to the classical scheme (Pavlova and Naidenko, 2008; Naidenko et al., 2011). The cross-reactivity of the used antibodies to cortisol was 5.6% for prednisolone, for all other tested steroids it was less than 1% (for more details, the method for measuring cortisol is described in Pavlova and Naidenko, 2008, 2012).

2.6. Analysis of changes in cortisol metabolite levels

The basal level was determined by the average level of cortisol metabolites from all samples collected within 3 days before pairing. The peak of cortisol was taken as the maximum level of cortisol metabolites in the feces of females after pairing with a male. As a rule, the rise in cortisol levels was observed 24–48 h after pairing. We took the difference between basal cortisol levels in female feces and the cortisol peak in response to pairing with a male to be the reaction of females to meeting a mate. We did not perform an interspecies comparison of absolute cortisol values because the measurement technique was different for different species (the use of different kits and possible interspecies differences in hormone metabolite excretion make it impossible to compare absolute values). Accordingly, we used only the difference between the peak and basal cortisol levels of females for interspecific comparisons of female reactions to mate meetings. This technique of noninvasive monitoring of glucocorticoids has proven effective on all the species we studied (Pavlova and Naidenko, 2008, 2012; Naidenko et al., 2011).

2.7. Behavioral monitoring

To determine the effect of interactions between animals on cortisol levels, we analyzed video recordings of the animals' behavior during the pairing. Animal behavior was recorded using the method of continuous data recording (Martin and Bateson, 2007; Alekseeva et al., 2014). Primary attention was paid to the total number of interactions between the female and the male, evaluating the frequency and ratio of aggressive and affiliative interactions, identifying and mating behavior. In all animal interactions, the initiator of interactions was distinguished.

When processing the data, we used only those pairs of animals for which the full set of data was collected - the basal level of cortisol, behavior during the pairing with a partner and the level of cortisol after the pairing (Table 1).

2.8. Data analysis

To describe the relationships between the behavior and physiology

of the cats we used three categories of variables (all forms of social behavior of the studied species were described in detail earlier (Erofeeva and Naidenko, 2020)). All variables were calculated for every test in the sample.

- 1) Female behavior. We classified the most frequent female social behavior that was initiated by the female towards the partner during the behavioral tests in four categories. Therefore, we calculated the frequency of each category of contacts (per hour of activity):
 - a. frequency of affiliative behavior (affiliative vocalization, social play (chase, fight, invitation to play), allogrooming, and butting (male and female butted each other's heads (behavior is characteristic of the Eurasian lynx)));
 - b. frequency of aggressive behavior (roar and hiss, swing, lunge, paw strike, fight);
 - c. frequency of "identifying" behavior towards the partner (social sniffing, flehmen behavior (process chemical cues with the vomeronasal organ, cats engage in a behavior called flehmen in which they slightly open their mouth into a grimace, allowing the ducts to open and heavy molecules to pass into the vomeronasal receptors));
 - d. frequency of mating behavior (copulation and "courtship"). In females, we considered all behaviors aimed at attracting a partner and leading to further mating as courtship elements (following the male and exposing the anal-genital area for the male, adopting the lordosis pose, "rubbing against the partner," and moving "shoulder to shoulder" (the female and the male are pressed to each other and move along the enclosure, this behavior being accompanied by affiliative vocalization)). Unlike females, in males the elements of "courtship" were more likely aimed not at attracting a partner (such as affiliative rubbing against the partner in the Eurasian lynx female), but at forcing mating (in more detail the method of observing the behavior of animals is described in Erofeeva et al., 2018; Erofeeva and Naidenko, 2020).
- 2) Male social activity. We characterized the male behavior using the total frequency of all social contacts initiated by the male towards the females. We used the total frequency of social contacts (affiliative, aggressive, identifying and sexual behavior) because all forms of social contacts did not correlate with each other, but the total frequency of contacts correlated with all forms of contacts.
- 3) The change of the female cortisol level. Since we aimed to compare different species, it was not informative to use absolute values of the cortisol level due to high between-species variation of the basal level measurements. Thus, we used the ratio of the maximum value registered after the test to the basal level of the cortisol fecal metabolites (average level calculated between samples collected within the three days before the tests). We log-transformed the ratio to fit the data to the normal distribution.

To reduce the number of the female behavior variables in further analysis and to reveal the structure of the data, we conducted a preliminary principal component analysis for the frequencies of

different types of the female's social contacts initiated towards the male partners (see Results, Table 2). We extracted two components - "friendly behavior" and "aggressive behavior".

Afterwards we constructed three main models:

- 1) We studied the effects of the male social behavior on the female's social activity using linear mixed effects models (LMM nlme package, Pinheiro et al., 2021). First, we used the "friendly behavior" as the dependent variable and the frequency of male contacts, study species (*F. catus*, *L. lynx*, *L. rufus*, *P. bengaliensis*), season (mating/non-reproductive) and their interaction as predictors in the model. Second, the model with the same predictors was constructed for the "aggressive behavior" as a response.
- 2) Next, using the LMM, we analyzed the effects of the female social behavior towards the mates on changes in female cortisol levels. The logarithm of the change in cortisol levels was included in the model as a response; "friendly behavior" and "aggressive behavior", species, the season and their interaction were fitted as fixed effects in the model.
- 3) Since the species-season interaction was significant in the first two models we fitted additional models with the two female behaviors and species as predictors and the female cortisol change as a response for mating season and non-reproductive season separately.

We used the ratio of the peak and the basal levels for every individual as a new variable (cortisol ratio). For further analysis, the difference between the peak and basal female cortisol levels (cortisol ratio) was logarithmed to access normality. We used linear mixed-effects models to analyze the effects of season and species and their interactions on the hormonal response of females to mate meeting using the R package nlme4 (Pinheiro et al., 2021; Bates et al., 2015). Female identity (ID) was included in all models as a random factor. Post-hoc comparisons were performed using the Tukey HSD in the library emmeans in R (Lenth et al., 2019).

Since most individuals were tested more than once, female identity (ID) was included in all models as a random factor. For all main models we constructed the set of candidate models with all combinations of predictors and factor interactions and compared them using model selection procedure based on the Akaike Information Criterion (AICc) in the MuMIn library (Burnham and Anderson, 2002; Barton, 2018). AICc weights were calculated, and coefficient estimates with their errors were averaged for models with $\Delta AICc < 2$ (Burnham et al., 2011). Post-hoc comparisons were performed using the Tukey HSD test in the emmeans package (Lenth et al., 2019). All continuous predictors were standardized and checked for collinearity. We used Microsoft Excel, Statistica 13.0, and R 4.1.0 for statistical analysis (Hornik, 2020 R Core Team, 2021). All tests were 2-tailed with a significance level of 0.05.

3. Results

3.1. Social behavior during pairing

The ratio of different types of social contacts on females varied among species and periods. In **domestic cats** the contacts initiated by females towards males during the mating period were mostly aggressive (more than 50% of all social contacts registered during the trials, $N = 19$ for mating season), while during the non-reproductive period the social contacts were mostly affiliative (more than 80% of all contacts, $N = 33$ for non-reproductive season). In the **Eurasian lynx**, the general frequency of female social contacts was very high during both studied seasons as compared with the three other cat species ($13,21 \pm 3,26$ per 1 h). Most of these contacts were affiliative (more than 80%, $N = 12$) for both mating and non-reproductive seasons. In **bobcats** the average frequency of social contacts initiated by the females was the lowest among species ($2,9 \pm 0,75$ per 1 h) during both periods, and most of these contacts were aggressive (more than 60% during the mating

Table 2

Components extracted by principal component analysis from the four variables characterized the frequencies of different types of social behavior of females towards males during the tests for four cat species (*L. lynx*, *L. rufus*, *F. catus*, *P. bengaliensis*). Loadings > 0.75 are marked with bold.

Factor loadings (Varimax raw):	PC 1 "Friendly behavior"	PC 2 "Aggressive behavior"
Affiliative behavior	0,79	-0,09
Aggressive behavior	-0001	0,94
"Identifying" behavior	0,78	0,08
Mating behavior	0,55	0,4
Eigenvalue	1,54	1,07
Percentage of total variance explained	0,38	0,27

season ($N = 12$) and more than 80% ($N = 12$) during the non-reproductive season). During the mating period the **Amur leopard cat** females displayed aggressive and affiliative behavior with the similar frequency ($0,96 \pm 0,24 / 0,51 \pm 0,14$), while during the non-reproductive period all types of social contacts were very rare and mostly aggressive (67%).

The level of the male social activity varied between periods (linear mixed effect models, $B = 0.80 \pm 0.23$, $p = 0.0008$, the male identity was fitted as a random term in the model), but the seasonal dynamics value was different among the species. In domestic cat, bobcat, and Amur leopard cat the frequency of social contacts in males was high during the mating season and decreased significantly in the non-reproductive period (Tukey post hoc test, $p = 0.003$, $p = 0.003$, $p = 0.001$, respectively; Fig. 1), and the decrease was very strong: the average frequency dropped 11 times in bobcat and 19 times in Amur leopard cat. In contrast, in the Eurasian lynx the level of male social activity did not vary between seasons (Tukey post hoc test, $p = 0.9$, Fig. 2).

We extracted principal components from the set of four variables characterizing the social behavior of females towards their partners. Two new variables (components) were obtained using the principal component analysis after Varimax raw rotation: the first component PC1 "friendly behavior" correlated positively with the frequency of affiliative and identifying behavior directed to the male (the factor loadings are greater than 0.75, Table 2). The second component PC2 "aggressive behavior" correlated positively with the frequency of aggressive contacts directed towards the male (the loading = 0.94, Table 2).

3.2. Effects of the level of male social activity on female behavior

The best model for the female "friendly behavior" in cats included the only predictor – the frequency of male social contacts. The cat species and period as well as their interaction did not receive sufficient support in the model selection procedure and did not affect the frequency of the male social contacts significantly (Table 3). The level of male social activity correlated positively with the level of the female "friendly behavior" (Table 3), but the connection was weak (Pearson's $r = 0.14$).

In contrast, the level of female "aggressive behavior" was strongly affected by all analyzed predictors: all fixed terms (male social activity, period, species, and their interaction) received strong support in the model selection procedure and were included in the most parsimonious model. All of them had significant effects on the female "aggressive behavior" (Table 3). The level of female "aggressive behavior" was higher in the mating season than in the non-reproductive period (Tukey post hoc test, $p = 0.05$), and there was strong variation among species in the seasonal dynamics of the female behavior. In domestic cat the female

"aggressive behavior" was very high during the mating season, it was commonly higher than in Eurasian lynx (Tukey post hoc test, $p = 0.07$), bobcat ($p = 0.01$), Amur leopard cat ($p = 0.02$) and it was much higher than in the non-reproductive period ($p < 0.0001$, Fig. 2). In all other species we did not reveal significant differences in the female "aggressive behavior" between the mating and non-reproductive periods ($p > 0.5$, Fig. 2). However, in all species the male social activity had pronounced effect on the female "aggressive behavior": the higher was the frequency of male contacts, the higher was the level of the "aggressive behavior" (Table 3), there was high linear correlation between the variables (Person's $r = 0.48$).

3.3. Effects of behavior on changes in cortisol levels

3.3.1. Changes in cortisol levels in females in response to pairing with a partner

Analysis of the reaction of females to pairing with a partner in four Felidae species at different periods showed significant effects of period and species on the change in cortisol levels after pairing with a partner (Table 4). During the mating period, the fecal cortisol level dynamics in females before and after pairing with a partner was similar in all studied species. A meeting with a partner was accompanied by a rise in cortisol levels (Fig. 3). In the domestic cat cortisol level increased in 1.65 ± 0.36 times, in the Eurasian lynx in 2.02 ± 1.32 times, in the bobcat in 2.12 ± 0.33 times, and in the Amur leopard cat in 2.14 ± 0.50 times. During the non-reproductive period, the reaction of females to a partner varied among species (the factor interaction was significant, Table 4). In female Eurasian lynx and domestic cats, the reaction to meeting was the same as during the mating period: the average ratio of the cortisol level after the test to the female basal level was 2.37 ± 0.36 in the excrements of female domestic cats and 2.27 ± 0.28 in female Eurasian lynx. In contrast, responses of female bobcat and Amur leopard cat to a meeting with a partner during a non-reproductive period differed significantly from those during the mating period ($B = -1.21 \pm 0.48$, $p = 0.01$; $B = -1.01 \pm 0.45$, $p = 0.02$, respectively, Fig. 3): female cortisol levels in feces after pairing with a partner were almost indistinguishable from basal levels (Tukey post hoc test, $p > 0.1$). Cortisol level in bobcat females increased on average 1.18 ± 0.22 times, and in Amur leopard cat females 1.26 ± 0.24 times as compared with basal cortisol levels.

Since there was significant factor interaction and strong among-species variation in cortisol concentrations, we investigated the effects of the female behavior on the change of cortisol level in each period separately and constructed two models.

During the mating period, changes in cortisol levels in females after encountering a mate were significantly affected by the level of "aggressive behavior" of the females (linear mixed effect models, $B = -0.24 \pm 0.11$, $p = 0.03$) (Table 5). Female "friendly behavior" level had no significant effect on the change of cortisol level ($B = -0.24 \pm 0.13$, $z = 1.75$, $p = 0.08$). The species and the frequency of male social contacts had no effect on the response, did not receive sufficient support in the model selection procedure, and were not included in the best models with $\Delta AICc < 2$.

In contrast, during the non-reproductive period, no effect of behavior on the female cortisol level after meeting a mate was detected ($p > 0.1$). Changes in cortisol levels in females feces in response to a meeting with a partner were determined by the species. In bobcat and Amur leopard cat, the change in female cortisol levels in response to mate meeting were significantly lower than in Eurasian lynx and domestic cat ($B = -0.74 \pm 0.35$, $p = 0.05$; $B = -0.76 \pm 0.31$, $p = 0.02$, respectively).

4. Discussion

Our study showed significant differences in social contacts of males and females both among species and between seasons. For two species (Eurasian lynx and domestic cat), we observed a high frequency of interactions during both the mating and nonreproductive periods.

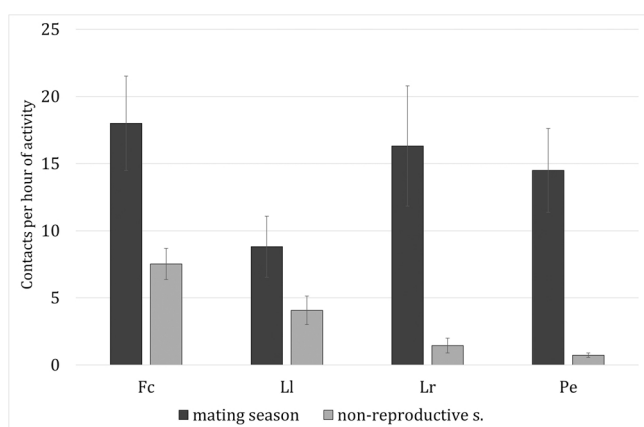


Fig. 1. Frequency of contacts of males in relation to females. The figure shows the averaged values by period and species. Fc - *Felis silvestris* var. *catus*, Ll - *Lynx lynx*, Lr - *Lynx rufus*, Pe - *Prionailurus bengalensis euptilura*.

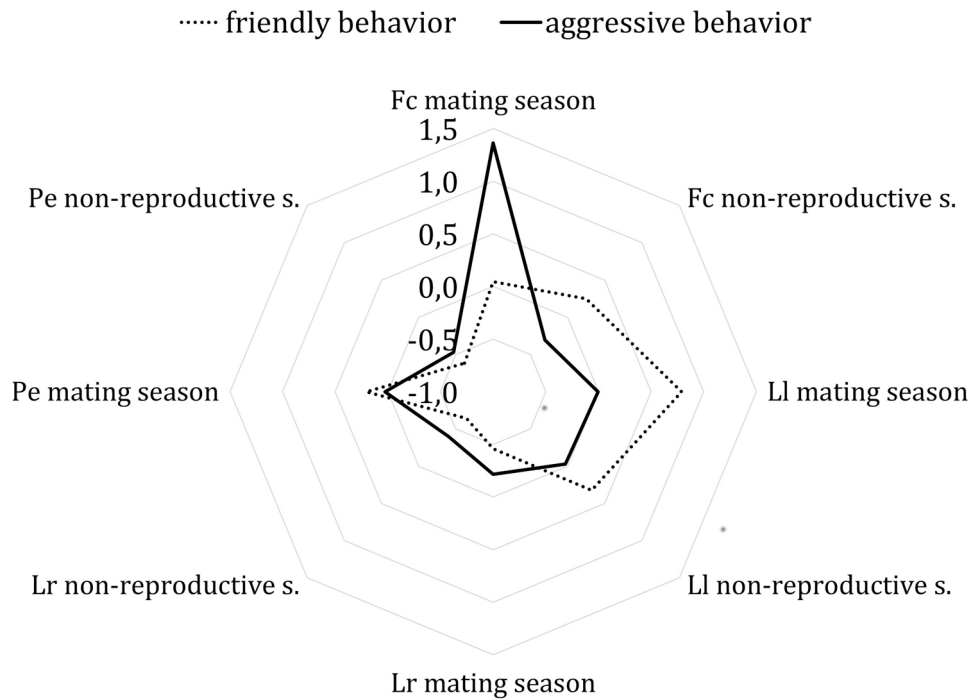


Fig. 2. Projection of behavior of females in relation to their partners by the 2 components: "friendly behavior" and "aggressive behavior". The figure shows the averaged values by period and species. Fc - *Felis silvestris var. catus*, Ll - *Lynx lynx*, Lr - *Lynx rufus*, Pe - *Prionailurus bengalensis euptilura*.

Table 3

Influence of period, species and the frequency of male contacts on the female "friendly behavior" and "aggressive behavior" in a linear mixed-effect model. B and SE correspond to model-averaged parameter estimates and SEs in LMM. Model-averaged parameter estimates B are presented for models with $\Delta AIC_c < 2$. Female identity was fitted as a random term in all models. NR – non-reproductive period. (Fc - *Felis silvestris var. catus*, Ll - *Lynx lynx*, Lr - *Lynx rufus*, Pe - *Prionailurus bengalensis euptilura*.)

Predictors	"Friendly behavior"	"Aggressive behavior"
Intercept	B= 0.10 ± 0.12, p = 0.6	B= 1.2 ± 0.2, p < 0.0001
Frequency of male contacts period	B= 0.15 ± 0.07, p = 0.03	B= 0.31 ± 0.08, p < 0.0001
species	B= -0.01 ± 0.07, p = 0.8	B= -1.38 ± 0.21, p < 0.0001
	Ll: B= 0.12 ± 0.30, p = 0.7	Ll: B= -1.22 ± 0.38, p = 0.003
	Lr: B= -0.18 ± 0.39, p = 0.6	Lr: B= -1.60 ± 0.39, p = 0.0001
	Pe: B= -0.08 ± 0.24, p = 0.7	Pe: B= -1.30 ± 0.34, p = 0.0003
Period* species	Not included in the models with $\Delta AIC_c < 2$	Ll*NR: B= 1.44 ± 0.35, p < 0.0001
		Lr*NR: B= 1.62 ± 0.32, p < 0.0001
		Pe*NR: B= 1.34 ± 0.31, p < 0.0001

However, in the domestic cat, unlike the Eurasian lynx, the character of these interactions differed greatly between seasons (during the mating period interactions were mostly aggressive, and during the nonreproductive period friendly interactions prevailed). In the Amur leopard cat and bobcat, we observed a high frequency of social contacts only during the mating period. During the nonreproductive period, contacts between animals were sporadic. The high frequency of contacts initiated by males was accompanied by a high frequency of female aggressive behavior in all species. The level of female aggressive behavior was positively related to the cortisol level in females. A high level of cortisol in females in response to pairing with males was observed in all species during the mating period. In the nonreproductive period increasing of the females'

Table 4

Effect of period and species on the dynamics of cortisol level after meeting a mate. B and SE correspond to model-averaged parameter estimates and standard errors in linear mixed-effects models. Female identity was fitted in the model as a random term. (Fc - *Felis silvestris var. catus*, Ll - *Lynx lynx*, Lr - *Lynx rufus*, Pe - *Prionailurus bengalensis euptilura*.)

Predictors	Statistics
Intercept	B= -0.21 ± 0.22, p = 0.35
Period	B= -0.40 ± 0.28, p = 0.15
Species	Ll: B= 0.46 ± 0.36, p = 0.2
	Lr: B= 0.50 ± 0.35, p = 0.17
	Pe: B= 0.33 ± 0.36, p = 0.37
Period:Species	Ll: B= -0.17 ± 0.50, p = 0.73
	Lr: B= -1.21 ± 0.48, p = 0.01
	Pe: B= -1.01 ± 0.45, p = 0.02

cortisol level following the encounters with males was observed only in species characterized by a high frequency of interactions during this period.

4.1. Social behavior during pairing

The system of relationships between the sexes is highly variable and depends on many behavioral and biological traits of the species (Clutton-Brock, 1989; Clutton-Brock and Parker, 1995; Birkhead, 2000). In promiscuous species, as a rule, even during the mating season animals do not form long-term social ties (Clutton-Brock, 1989; Birkhead, 2000). However, the pattern of partner relationships even with this mating system can have a significant impact on the reproductive success of an individual. In sexually reproducing species, the choice of a mating partner is thought to be largely determined by how viable their offspring will be (Birkhead, 2000; Erofeeva et al., 2022). However, mate selection in promiscuously breeding species is often difficult. In Felidae with strongly pronounced sexual dimorphism during the mating period, the pattern of interactions is determined by males. They initiate contact with their partner more often and are very persistent in their attempts to

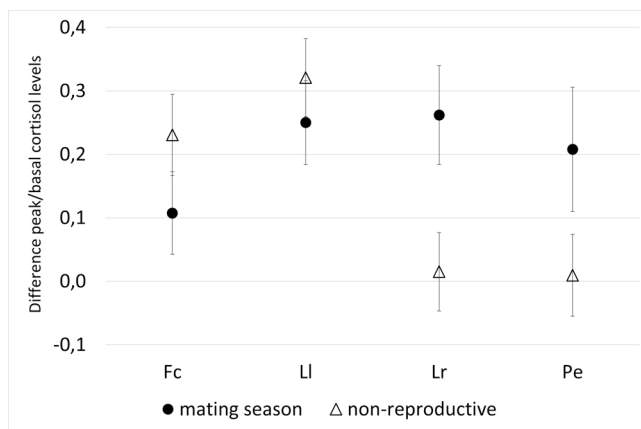


Fig. 3. Reaction of females to mate meeting: logarithm of the difference in cortisol levels before and after mate meeting. Fc - *Felis silvestris var. catus*, Ll - *Lynx lynx*, Lr - *Lynx rufus*, Pe - *Prionailurus bengalensis euptilura*. The values on the graph are presented as logarithmic mean values with the error of the mean ($M \pm SE$).

Table 5

Effects of the species, behavior of the female and her partner during the mating season on changes in cortisol level in female excrement in LMM. B and SE correspond to model-averaged parameter estimates and SEs in GLMM. Female identity was fitted as a random term in all models.

Predictors	Statistics
Intercept	B= 0.09 ± 0.16, p = 0.59
aggressive behavior	B= -0.24 ± 0.11, p = 0.03
friendly behavior	B= -0.24 ± 0.13, p = 0.08

mate with the female. On the contrary, in species with weakly expressed sexual dimorphism, the pattern of relationships is determined by females (Erofeeva and Naidenko, 2020).

Our study showed significant interspecies differences in the social interactions between females and males in felines. In female Eurasian lynx, a species with the lowest sexual dimorphism, we observed the highest frequency of contacts in relation to males. Most of these contacts were friendly. In species with pronounced sexual dimorphism the behavior of females toward males was different from the Eurasian lynx. The female domestic cat was also characterized by a high frequency of contacts with the male, but the type of these contacts differed between periods. During the mating period, we observed mostly aggressive behavior toward the male, while during the non-reproductive period, more friendly contacts occurred. Females of the Amur leopard cat showed friendly and aggressive behavior toward males in the mating period with equal frequency. However, females rarely initiated contacts with males during the non-reproductive period. For bobcat females, we observed an equally low number of contacts with males both during the mating period and during the non-reproductive period.

For all species with pronounced sexual dimorphism biased towards males, we observed a very high frequency of male-to-female contacts during the mating period. Such behavior was accompanied not only by a high frequency of sexual behavior, but also by a high frequency of other social contacts (aggressive, friendly, and identifying) toward the female. Therefore, the overall frequency of contact on the part of the male well characterized his persistence toward the female. The high frequency of contact from males led to a high frequency of aggressive behavior from females. This character of relations between males and females in cats with pronounced sexual dimorphism has been noted before (Erofeeva and Naidenko, 2020). Bobcat is the only species for which we noted severe aggressive interactions (fights, biting) between males and females during the mating season. From the first minutes of pairing, males showed aggression toward the female and only after a thorough

inspection (sniffing) of her territory demonstrated elements of "courtship" toward the partner.

During the non-reproductive period, males made contact with females much less frequently. Such a low number of social contacts during this period can be explained by the specific traits of the spatial organization of the species we studied. Most felines live solitary (Yudakov and Nikolaev, 1987; Poole, 1994; Sliwa, 2004; Grassman et al., 2005). Individuals occupying neighboring territories usually use the home range independently of each other (Poole, 1995). Contacts with conspecifics outside the mating season are rare and short (Seidensticker et al., 1973), most often animals try to avoid contact with their "neighbors" (Horvöcker, 1969).

However, in Eurasian lynx, both in males and females, the frequency of contacts remained on the same level between seasons. In the Eurasian lynx, contacts both during the mating period and the period of low activity of the reproductive system were initiated by females. At the same time, only during the period of low activity of the reproductive system we observed severe interactions (fights) between partners. The social and spatial organization of the Eurasian lynx is very similar to that of most felines. They also lead a solitary lifestyle. However, in contrast to the bobcat and the Amur leopard cat, the Eurasian lynx is prone to monopolization of the home range. At least for this species, there are no described cases of adults of the same or different sexes staying together outside the mating period. At the same time, cases of cohabitation of adult females or a male with a lactating female have been described for the bobcat (Ray et al., 2017). The spatial organization of the Amur leopard cat is poorly studied. For its closest relative, the Bengal cat, who lives in the tropics, the spatial system has been described as weak territoriality and a slight influence of the season on spatial organization (Grassman et al., 2005). It is possible that similar spatial organization is also typical for the Amur leopard cat. At least, it is the only solitary feline species we studied in which unrelated females can be tolerant of each other and peacefully coexist in groups (Pavlova, 2010; our data).

For the domestic cat, the "persistence" of males in other seasons excluding spring may be related to the breeding peculiarity of this species. It is thought that the domestic cat is capable of breeding year-round (Jones and Coman, 1982; Glukhov and Naidenko, 2013). However, in temperate continental climates (as in our experimental station), female domestic cats show seasonality in breeding. Estrus in females can be observed from late February to early October. We conducted experimental pairing during "the low activity of the reproductive system" from late October to mid-November. This is a time in which we have never observed females in estrus. However, male domestic cats are ready to breed almost year-round (Glukhov and Naidenko, 2013). Therefore, even though females were not reproductively active, males demonstrated sexual behavior toward them.

4.2. Effects of behavior on changes in cortisol levels

In our study, a meeting with a partner during the mating season led to a significant increase in the level of cortisol metabolites in the feces of females of all species, regardless of the degree of sexual dimorphism. This reaction of females to the meeting with a mate was expected for species with strongly pronounced sexual dimorphism. It is difficult for females of such species to avoid the persistent "courtship" of larger males (Erofeeva et al., 2018; Erofeeva and Naidenko, 2020). In Felidae, larger males are more likely to mate with females and have higher reproductive success compared to smaller conspecifics (Yamane, 1998; Pörschmann et al., 2010). However, it is often not the choice of the female. This insistence on males exceeding females in body weight can lead to forced mating between females and males in many species (Alcock et al., 1977; Mineau et al., 1983; Rubenstein, 1986; Le Boeuf and Mesnick, 1991). If the female cannot avoid the "courtship" of the male, she allows mating to avoid injury from too intense courtship (Clutton-Brock and Parker, 1995; Birkhead, 2000). In cats during the mating season, males demonstrate pursuit of females and coercion to mate

(Erofeeva and Naidenko, 2020), in some species it may result in the death of the female (Brown et al., 1995). In our experiments, not a single serious injury was recorded in animals during the pairing. At the same time, for females, the risk of being injured by the active "courting" of the male is higher the larger (in relative terms) the male is. When females interact with males, in species with pronounced sexual dimorphism, females are more likely to occupy a subordinate position, rarely initiate aggressive contacts and avoid them first if the male shows aggression (Pavlova, 2010). In the Eurasian lynx, a species with low sexual dimorphism, on the contrary, females more often initiate contacts with males, with friendly behavior and courtship accounting for the main part of these contacts (Erofeeva et al., 2018; Erofeeva and Naidenko, 2020). In our study, during the mating season females were also more persistent in attracting a mating partner than males. Such courtship of females was never associated with aggressive behavior in case of mating partner refusal, which was fundamentally different from the behavior of males when females refused to mate (our study; Erofeeva and Naidenko, 2020). However, despite the completely different pattern of partner interactions, the meeting with a partner during the mating season in the Eurasian lynx also led to an increase in cortisol levels in females in our study.

At the same time, changes in cortisol levels in response to pairing with a partner during the mating season were associated with the aggressiveness of the female. During the mating season, aggressive contacts of females are an integral part of partner interactions. In most felids, females display elements of aggressive behavior immediately after mating (Stehlik, 1983; Naidenko, 1997). However, females demonstrated aggressive behavior not only in the context of sexual behavior, but also in response to highly persistent behavior of males (Erofeeva et al., 2018; Erofeeva and Naidenko, 2020). In our study, males also demonstrated a high frequency of social contacts with females during the mating season, which was accompanied by aggression on the part of females. Regardless of the initiator of contacts in the pair, this character of interactions can be unpredictable for females and require their constant involvement in interactions, which leads to an increase in cortisol levels in females. Such unpredictability of the situation can lead to the activation of HPA in females with the mobilization of the body's protective systems, contributing to the reduction or prevention of possible danger from social conflict with the partner (McCann et al., 2000; Wingfield and Kitaysky, 2002).

In the non-reproductive period, we did not observe an increase in cortisol in response to mating with males in the bobcat and the Amur leopard cat. During this period, the frequency of interactions between partners in these species is extremely low and sporadic. Against the background of the lack of "interest" on the part of males, in females of these species we did not observe any changes in cortisol levels in response to meeting a mate. At the same time, the high frequency of social contacts during the non-reproductive period in the Eurasian lynx and domestic cat was accompanied by HPA activation in response to mating with the male. Such a high frequency of contacts is probably due to the features of the socio-spatial organization and biology of these species. The Eurasian lynx appears to be more inclined to monopolize the home range compared to other solitary felines (Pavlova, 2010; Ray et al., 2017; our data). Probably, the presence of a conspecific on their territory, regardless of the period, leads to a high frequency of interactions between animals and, as a consequence, the activation of HPA. In domestic cats, males are reproductive and capable of breeding all year (Glukhov and Naidenko, 2013) and they actively interact even with reproductively non-active females. This behavior of males can lead to stress in females.

In domestic cat, contacts between conspecifics can occur throughout the year. The domestic cat at high population density is characterized by a social lifestyle in large structured social groups (Liberg, Sandell, 1988; Macdonald et al., 1987; Pontier and Natoli, 1996; Say et al., 1999, 2002). In stable groups, the relationship of individuals does not lead to changes in the activity of HPA (Stavisky et al., 2001). However, in our

study, the domestic cat was kept solitary (like all the feline species we studied), except for the reproduction period and females with kittens. Accordingly, for the domestic cat, as well as for the other feline species studied, the meeting and pairing of unfamiliar individuals was unpredictable and could act as a stressor. In this case, unstable relationships between animals can lead to an increase in glucocorticoid levels.

The reactivity of HPA can be related to the intensity, duration, and nature (physical or mental) of the interactions (Barrett et al., 2002). In our study, the high frequency of interactions in animal pairs was also related to the level of cortisol increase in females in response to pairing with males. In the wild, in most solitary felines, the meeting of conspecifics, even during the reproductive period, is short (Hornocker, 1969; Erofeeva and Naidenko, 2012). At the same time, the animals were paired for a short period of time. In such unstable short-term groups, an encounter with a partner can be stressful, regardless of the severity of sexual dimorphism (Nuñez et al., 2014).

Thus, our study does not support our hypothesis. Despite the fact that sexual dimorphism influences partner relationships, an increase of activity of HPA in response to an interaction with a partner appears to be caused by the biology of the species rather than by the degree of sexual dimorphism. Sexual dimorphism was related to the roles of the partners in the pair. In species with unexpressed sexual dimorphism, females determined the nature of the relationship in the pair. In species with pronounced sexual dimorphism biased towards males, the nature of social relationships was determined by males. However, meeting with a partner led to increased cortisol levels in females not in sexually dimorphic pairs, but in pairs with a high frequency of partner interactions. The frequency of interactions was determined by specific traits of species biology and was likely related to the seasonality of reproduction and the degree of monopolization of the home range.

Our results demonstrated that the meeting with an actively interacting partner can lead to stress in female felines, regardless of the degree of sexual dimorphism. Accordingly, for female felines the choice of a mating partner may be difficult due to the stressful character of the interaction with a partner, even in species in which females initiate contact with the male.

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Data Availability

Data will be made available on request.

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Institutional Review Board Statement

The study was conducted according to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching and approved by the Commission on Regulatory of Experimental Research (Bioethics Commission) of A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (permission no. 21 of 24/04/2018).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.beproc.2023.104876](https://doi.org/10.1016/j.beproc.2023.104876).

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