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Lynx's strictly seasonal breeding complex makes its reproduction different from other felids

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ABSTRACT. Most of the felids are tropical nonseasonal breeders, but northern species have adapted to seasonal climate by reproductive seasonality pronounced to a different degree. We review what is known about the reproductive seasonality in felids. The *Lynx* genus includes the most northern felids — Eurasian and Canada lynx, and also Iberian lynx, and bobcat. Specific seasonal adaptations in lynx reproduction act as a unique Strictly Seasonal Breeding Complex expressed to a different extent among lynx species. This complex includes hormonal and gonadal seasonality, monoestric cycle, and unique persistent corpora lutea. We suggest that adaptation to strictly seasonal breeding is very advantageous in a lynx environment. Still, together with other features of lynx biology, we suppose that it could act as one of the prerequisites for sibling aggression development. However, this hypothesis is preliminary and only aims to consider possible interactions of species-specific reproductive features of lynx.

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Комплекс строго сезонного размножения уникален для рысей

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РЕЗЮМЕ. Большинство кошачьих — виды с несезонным размножением, но у северных видов кошачьих важной адаптацией к сезонному климату стало сезонное в той или иной степени размножение. В данной статье мы рассмотрим вопросы сезонности размножения кошачьих. К роду *Lynx* относятся самые северные кошачьи — евразийская и канадская рыси, а также пиренейская рысь и красная рысь. Сочетание специфических характеристик размножения рысей формирует комплекс, важный для строго сезонного размножения, выраженного в разной степени у разных видов рысей. Этот комплекс включает гормональную сезонность и сезонность в функционировании половых желез, моноэстральный цикл размножения, уникальные долго функционирующие желтые тела в яичниках. Мы предполагаем, что особенности, связанные со строго сезонным размножением у рысей, не только являются важной адаптацией в северных широтах, но и, возможно, в совокупности с другими особенностями биологии рысей могут выступать одной из предпосылок развития внутривыводковой агрессии. Однако эта гипотеза является предварительной и лишь рассматривает возможные пути взаимодействия различных видоспецифичных характеристик размножения рысей.

КЛЮЧЕВЫЕ СЛОВА: рысь, размножение, сезонность, сиблицид, внутривыводковая агрессия, персистентное желтое тело.

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> "Lynx is the only group of felines who are the family generally tropical and subtropical that has carried out a deep breakthrough in the northern latitudes"
>
> (Matyushkin & Vaisfeld, 2003)

Spontaneous sibling aggression is a puzzling characteristic of cub development in the lynx genus (Sokolov *et al.*, 1994; Vargas *et al.*, 2005; Antonevich & Naidenko, 2007; Antonevich *et al.*, 2009). The genus *Lynx* includes four species: the Eurasian lynx (*Lynx lynx*), the Canada lynx (*Lynx canadensis*), the bobcat (*Lynx rufus*), and the most endangered felid species of the world, the Iberian lynx (*Lynx pardinus*) (Kitchener *et al.*, 2017). Sibling aggression occurs in half of the litters in Eurasian lynx (Sokolov *et al.*, 1994) and almost all the Iberian lynx litters (Vargas *et al.*, 2005; Antonevich *et al.*, 2009), it leads to siblicide in some cases. Such aggression was found also in bobcats (Antonevich & Naidenko, 2013). Sibling aggression is well-studied in birds. In some species of birds, siblicide is obligate and almost nonsensitive to any regulation. According to the obligate siblicide understanding one of the siblings acts as the parent's insurance for the risk of reproduction attempt failure (Insurance Egg (Insurance offspring) Hypothesis (Forbes, 1990). Usually, this type of aggression has specific prerequisites in the reproductive biology of the species (long nestling period, high competition, small clutch size, and inability to repeat reproduction (Forbes, 1990; Antonevich & Naidenko, 2007)). Although for facultatively lethal aggression there are several hypotheses explaining how siblicide could evolve, always considering the strong benefits of fighting for sibling competition. Food amount hypothesis (Mock *et al.*, 1987), Prey Size Hypothesis (Mock, 1985), Brood Reduction Hypothesis, and Bet-hedging Hypothesis (Forbes, 1991; Mock & Lamey, 1991) explain different pathways of regulation of aggression. Mostly, they suggest that siblicide evolved to adjust the number of offspring to the available resources at the stage when parental investment is not big to prevent bigger losses. In particular such reproductive features, as the ability of birds to lay eggs asynchronously and of different quality contributed significantly to the possibility of birds to use such a regulation system. However, reproduction in mammals is different than that in birds. Siblicidal aggression is quite rare in mammals. The spotted hyaena (*Crocuta crocuta*) — is a species with sibling aggression well documented and studied. Sibling aggression in hyenas is explained by the Food amount hypothesis, but also it became possible due to the species-specific features that can be considered prerequisites for sibling aggression evolution and siblicide development. Spotted hyenas have an enormous duration of lactation (Hofer & East, 1993) and a highly competitive social structure, that leads to the decreased effective population size and thus enables fast fixation of adaptive mutations (Hofer & East, 2008). All these features are connected with species-specific masculinization of spotted hyenas (Frank *et al.*, 1991; Frank, 1997). The unique combination of hyaena biology and physiology makes it outstanding from other mammals.None of these features are present in lynx biology. None of the hypotheses from birds is fully applicable to lynx as well (Antonevich & Naidenko, 2007) detailed discussion in (Antonevich *et al.*, in prep) and alternative hypotheses could be suggested according to mammalian development of behavior (Antonevich *et al.*, 2019).

Whatever way sibling aggression is adaptive for lynx, as far as we know it is unique for lynx among felids. The important question is what unique features of lynx reproduction contributed to sibling aggression evolution in lynx, and were absent in other felids that did not develop sibling aggression.

Here we aimed to suggest specific features in lynx reproductive biology that could act as prerequisites for the evolution of sibling aggression in this genus. To do that we chose to analyze reproductive features that differentiate the lynx genus from the other felids and tompare differences among lynx species with what is known regarding sibling aggression in these species.

Seasonality

Lynx belongs to felids (Kitchener *et al.*, 2017). Most of the felids are tropical and subtropical, they live in conditions that allow them to raise cubs during most of the year favoring reproduction through the whole year (Nowell & Jackson, 1996). They have no seasonal changes in reproductive hormones in males and females as fishing cat (*Prionailurus viverrinus*) (Santymire *et al.*, 2011) or maintain all-year high levels of androgen production as margay (*Leopardus wiedii*), tigrina (*L. tigrinus*) males, even if they increase in the breeding season (ocelot (*L. pardalis*) (Morais *et al.*, 2002)). Some felids increase sperm production during the preferred season but maintain it throughout the year (ocelot, margay, and tigrina males (Morais *et al.*, 2002). Follicular activity in many felids, like lions (*Panthera leo*), leopards (*Panthera pardus*), pumas (*Felis concolor*), margays, ocelots, tigrinas, jaguars and fishing cats are not influenced by season (Brown, 2011).

Northern felids, living in high-latitude seasonal environment, have to give birth and raise cubs during the short summer season when conditions are favorable. Northern species have adapted by reproductive seasonality pronounced to a different degree. Tigers (*Panthera tigris altaica*), European wildcats (*Felis silvestris*), Pallas' cat (*Otocolobus manul*) (Swanson *et al.*, 1996), snow leopards (*Panthera uncia*), domestic cats (*Felis silvestris catus*), Amur leopard cat (*Prionailurus bengalensis euptilura*) (Naidenko, 2019) and lynx are more or less seasonal (Brown, 2006; 2011). Tigers tend to seasonality such as preferred breeding season (Kerley *et al.*, 2003) and some but inconsistent seasonal changes in estradiol (Graham *et al.*, 2006). Tiger male testosterone increases to the breeding season but is not associated with sperm quality features. Tigers have no seasonal sperm quality changes (Byers *et al.*, 1990). In European wildcat females' estradiol and progesterone metabolite levels decrease out of the breeding season, but testosterone level in males does not change (Piñeiro *et al.*, 2020). Amur leopard cat and domestic cat have pronounced changes in testosterone levels, but only some features of sperm quality change to the breeding season (Naidenko, 2019). A few species have complete reproductive seasonality. Pallas' cat lives in a highly seasonal climate in such unfavoring winter conditions that cats lose about 30% of their body mass by the end of the winter (Naidenko *et al.*, 2014). Their sperm quality features change and testosterone drops during a non-breeding season (Swanson *et al.*, 1996), and females have seasonal anestrus (Brown *et al.*, 2002). Snow leopards also live in harsh conditions and breed seasonally (Johansson *et al.*, 2021). Females' reproductive activity is seasonal (Schmidt *et al.*, 1993; Kinoshita *et al.*, 2011), and so do males' sperm quality and hormones as well (Johnston *et al.*, 1994).

The *Lynx* genus includes the most northern felids — Eurasian (EuL) and Canada lynx (CaL) (Matyushkin & Vaisfeld, 2003; Poole, 2003). They are fully adapted to live in high latitudes in severe and seasonal climate (Andrews *et al.*, 2019). Iberian lynx (IbL) also lives in a highly seasonal environment. Bobcats (Bc) live in less seasonal conditions (Nowell & Jackson, 1996). Breeding in Eurasian, Iberian and Canada lynx is seasonal (EuL (Kvam, 1991), IbL (Palomares *et al.*, 2005) and CaL (Poole, 2003)), but is not in the bobcat (Bc (Crowe, 1975; Hansen, 2007)). Ovarian activity is seasonal in CaL (Fanson *et al.*, 2010b), EuL (Jewgenow *et al.*, 2006a; Erofeeva *et al.*, 2014), IbL (Pelican *et al.*, 2009), but nonseasonal in Bc (Brown, 2006). Such seasonality is supported by seasonal testosterone changes in males of EuL (Jewgenow *et al.*, 2006a; Jewgenow *et al.*, 2006b), CaL (Fanson *et al.*, 2010a) and moderate seasonality in IbL (Pelican *et al.*, 2009). Testosterone level does not change seasonally in Bc (Gañán *et al.*, 2009). Sperm quality changes seasonally in EuL (Göritz *et al.*, 2006; Jewgenow *et al.*, 2006a; Erofeeva *et al.*, 2014), but sperm quality unexpectedly was found to be non-seasonal in CaL (González *et al.*, 2019) and IbL (although measured out of the breeding season, so results are inconclusive (Gañán *et al.*, 2010)). Bc can have seasonal changes in spermatogenic activity but not necessarily and they can breed throughout the year (Gañán *et al.*, 2009)

Sperm quality

Teratospermia is highly prevalent within Felidae, with the lowest sperm quality found in the puma and lynx lineages — ejaculates with 76% (63–94%) and 79% (63–98%) abnormal sperm, respectively (Andrews *et al.*, 2019). All four lynx species have a low percentage of normal sperm: EuL (Göritz *et al.*, 2006; Jewgenow *et al.*, 2006a; Erofeeva *et al.*, 2014), IbL (Gañán *et al.*, 2010), Bc (Gañán *et al.*, 2009), CaL (González *et al.*, 2019). Morphologically abnormal sperm are rarely involved in the fertilization process (Pukazhenthi *et al.*, 2006; Erofeeva *et al.*, 2017). Being so critically low, the percentage of morphologically normal sperm is one of the factors that determine reproductive success in lynx males — EuL (Naidenko *et al.*, 2007b; Erofeeva & Naidenko, 2012) as well as other sperm quality features — IbL (Gañán *et al.*, 2010). We can suppose that low sperm quality in lynx makes the initial part of reproduction — conception, more difficult and increases the value of each breeding event, although this hypothesis needs to be tested.

Induced or spontaneous ovulation

Most of the fields are induced ovulators, but not all (Andrews *et al.*, 2019). Spontaneous ovulation occurs, at least occasionally, in the lion, leopard, Pallas' cat, fishing cat, and regularly in the clouded leopard (*Neofelis nebulosa*), margay and domestic cat (Brown, 2011). Strictly induced or rare spontaneous ovulations are found in the tiger, puma, snow leopard, cheetah (*Acinonyx jubatus*), tigrina, ocelot and lynx (EuL, IbL, CaL). Differences occur not only across species but also between individuals within a species (Brown, 2011). EuL (Painer *et al.*, 2014) and CaL (Fanson *et al.*, 2010b) can ovulate spontaneously.

Estrous

In most of felids, females are polyestric — exhibiting multiple estrous events throughout the year or breeding season. Tigers, cats, clouded leopards (Brown, 2011) leopards (de Haas van Dorsser *et al.*, 2007), puma, ocelot, caracal (*Caracal caracal*), bay cat (*Catopuma badia*), panthera (Andrews *et al.*, 2019), Pallas' cat, snow leopard (Schmidt *et al.*, 1993), but not lynx. Lynx (EuL, IbL, CaL) are the monoestric species with a long time from conception to conception (Göritz *et al.*, 2009; Fanson *et al.*, 2010b). In lynx, there is a seasonal pattern of estrogen excretion, with baseline concentrations increasing during the breeding season, regardless of whether mating or pregnancy ensues (Brown, 2011; Jewgenow *et al.*, 2014). On a few occasions, a second estrus is observed about 1–2 months after the end of the breeding season (IbL — Jewgenow *et al.*, 2014; Iberian Lynx Conservation Breeding Center, Spain personal communication, EuL — Naidenko, 2006; Painer *et al.*, 2014). However, there are no data on lynx births after these estruses. This strict monoestric cycle is supposed to be ensured by persistent corpora lutea. However, bobcats are polyestric (Crowe, 1975; Jewgenow *et al.*, 2014)

Persistent corpora lutea (CL) and elevated progesterone

Lynx females have a unique feature — persistent corpora lutea (CL). It retains in all four lynx species for a long period (Fanson *et al.*, 2010b). Non-pregnant luteal phases were described in many felid species, but they typically persist for about half the duration of pregnancy (Andrews *et al.*, 2020). In lynx species CL and elevated progesterone (P4) concentration can persist for two years and both pregnant and non-pregnant luteal phases are long (Pelican *et al.*, 2009; Fanson *et al.*, 2010b; Jewgenow *et al.*, 2014; Painer *et al.*, 2014). It is suggested that in particular in EuL, IbL and CaL CLs induce a monoestrous condition which results in highly seasonal reproduction, makes repeated gestation impossible and supports strict seasonality (Göritz *et al.*, 2009; Pelican *et al.*, 2009; Fanson *et al.*, 2010b; Painer *et al.*, 2014). However, BC also has persistent CLs that regress so slowly that they never completely disappear (Duke, 1949; Crowe, 1975; Göritz *et al.*, 2009; Jewgenow *et al.*, 2014). Intraluteal P4 concentrations in BC are in the same range as described for CLs obtained from non-pregnant EuL, but its level decreases with increasing CL age; a relationship that was not found for the EuL (Jewgenow *et al.*, 2014). Persistent luteal activity develops to a lesser extent in BC than in other lynxes.

However, there is an alternative hypothesis suggesting that persistent CLs in lynx species are required to maintain pregnancy through their functional use due to the luteal insufficiencies without support from persistent CLs from preceding seasons (Woshner *et al.*, 2001; Jewgenow *et al.*, 2014) although this idea has not much evidential support.

Seasonality and adaptations

Lynx species have a unique combination of reproductive features expressed to a different extent (Table). Physiologically persistent CL is a unique feature of the lynx genus, whereas other features are present in different felids. Nevertheless, none of the felids have such a complex of reproductive features providing a strictly seasonal breeding complex (SSBC). Seasonality itself has a strong impact on animal ecology (Boyce, 1979), it has an important evolutionary pressure affecting the life history, behavior, and reproduction of animals. Seasonality can affect reproductive strategies and patterns of reproduction (McNamara *et al.*, 2004), in particular, seasonality is supposed to be related to induced ovulation in carnivores other than felids (Larivière & Ferguson, 2003). A complex of environmental factors supporting seasonal breeding, low population density, and large individual home range provided environmental selection pressures that favored the evolution of delayed implantation in mustelids (Ferguson *et al.*, 2006). Seasonality in lynx is supported by the Strictly Seasonal Breeding Complex that allows to adjust cubs' birth to the best season. It also ensures that males and females are strictly synchronized and thus enables them to meet at an appropriate moment for breeding. Synchronization is especially important because home ranges can be large (EuL Breitenmoser & Haller, 1993; Linnell *et al.*, 2001), and sperm quality is very low out of the breeding season in lynx. Lynx living in the far north have to raise their cubs during a shorter window of favorable conditions and they create even higher reproductive synchrony (Mattisson *et al.*, 2022) than in the southern part of the range. Such strict seasonality allows lynx to minimize thermal stress on neonates and to raise cubs in the most productive period. Reproduction is costly for female lynx, especially under unfavorable conditions (Nilsen *et al.*, 2010). Adjusting reproduction to resource peaks allows to acquire fitness benefits of higher density of resources during the period of energetically demanding period of lactation (Mattisson *et al.*, 2020). Decreasing time away from the vulnerable cubs, lynx also decreases the risks of their predation (Mattisson *et al.*, 2022). The timing of birth is crucial to match a critical period — weaning with a period rich in resources (Mattisson *et al.*, 2020). Such strictly scheduled breeding, low sperm quality and inability to repeat reproduction together with large home ranges increase the value of each breeding event.

Variability and adaptations

At the same time, seasonal environment is very variable. Lynx reproduction is sensitive to the availability of food resources and age in CaL (Poole, 2003) but in the moment of conception it is hard to predict how many resources will be available to weaning — the most competitive period. Litter size in lynx varies from 1 to 4 cubs in EuL (Schmidt, 1998; Gaillard *et al.*, 2014), up to 5 cubs are not rare in IbL (Palomares *et al.*, 2005), and CaL (Poole, 2003), 6 cubs can be in a litter of Bc (Parker & Smith, 1983). In variable environment optimal litter size that lynx would raise can strongly change between breeding cycles of CaL (Poole, 2003). Reproductive success in lynx is strongly related to prey abundance (IbL (Palomares *et al.*, 2005), CaL (Poole, 2003; Nilsen *et al.*, 2010; Walton *et al.*, 2017), BC (Hansen, 2007)) and cub survival is much more sensitive to prey abundance then survival of adults (CaL (Aubry *et al.*, 1999). At the same time lynx (except BC) have a breeding period perfectly adjusted to the particular period and even if resources are over-abundant lynx are not able to repeat breeding season due to the short environmentally favoring period and physiological restrictions. Such inflexibility should make it difficult to adjust reproductive investment according to the changing recourses.

Lynx can slightly adjust the terms of the breeding season to particular latitudes and climate (Mattisson *et al.*, 2022). Surprisingly, litter size at birth is not adjusted to maternal conditions or environment in EuL and IbL (Palomares *et al.*, 2005; Gaillard *et al.*, 2014) but is highly changeable in CaL. There is no correlation between the number of cubs born or the number of breeding females and the population size of the European rabbit (*Oryctolagus cuniculus)*, the main prey of the IbL (Palomares *et al.*, 2005). The inability to match the number of offsprings to available resources (such as EuL and IbL demonstrate) may force the overproduction of the offsprings (Kozlowski & Stearns, 1989) and the development of a litter reduction system (Forbes, 1991). In particular, the long nestling period that ex-

Table. Reproductive features related to seasonal breeding in lynx and some other felids. The Table is based on the references, reviewed in the main text. Most of the felids are non-seasonal breeders, and several of the most studied species are in the Table representing existing patterns.

Species	Seasonal breeding	Ovarian seasonality	Testosterone seasonality	Sperm quality seasonality	Teratospermia	Main ovulation type (I-Induced,S-Spontaneous)	Cyclicity (poly/mono-oestric)	Persistent CL	Continuously elevated P4	Sibling aggression
Eurasian lynx (*Lynx lynx*)	yes	yes	yes	yes	yes	I	mono	yes	yes	yes
Iberian lynx (*Lynx pardinus*)	yes	yes	yes	inconclusive	yes	I	mono (oligo)	yes	yes	yes
Canada lynx (*Lynx canadensis*)	yes	yes	yes	no	yes	I	mono	yes	yes	?
Bobcat (*Lynx rufus*)	no	no	no	slightly	yes	I	poly	yes	contradictory	yes
Snow leopard (*Panthera uncia*)	yes	yes	yes	yes	no	I	poly	no	no	not
Pallas' cat (*Otocolobus manul*)	yes	yes	yes	yes	no	I	poly	no	no	no evidence
Tiger (*Panthera tigris altaica*)	preferred breeding season	inconsistent	increase	no	no	I	poly	no	no	no
European wildcat (*Felis silvestris*)	preferred breeding season	yes	no	n/a	no	S	poly	no	no	no
Lion (*Panthera leo*)	no	no	no	no	no	I+S	poly	no	no	no
Puma (*Felis concolor*)	no	no	n/a	n/a	yes	I	poly	no	no	no evidence
Fishing cat (*Prionailurus viverrinus*)	no	no	no	n/a	no	I+S	poly	no	no	no evidence
Margay (*Leopardus wiedii*)	no	no	no	no	no	I	poly	no	no	no evidence

cludes the possibility of repeated reproduction and increases the value of each breeding event is known as one of the prerequisites for the evolution of siblicidal sibling aggression in birds (Gonzalez-Voyer *et al.*, 2007; Morandini & Ferrer, 2015). In mammals, siblicidal aggression is rare but still can be a very effective mechanism to adjust litter size to the current situation (Drummond, 2006). Gaillard (Gaillard *et al.*, 2014) argues that newborn lynx cubs are small to adult lynx size, so reproductive allocation at birth is small and such a low reproductive effort should allow lynx females to adjust, at a low cost, their litter size to the environmental conditions. The same adult-newborn ratio can be found in Suidae and they have siblicidal sibling aggression also (Sowls, 1974; Fraser & Thompson, 1991). However, lynx cubs fight not at the birth, but more than a month later.

In lynx sibling aggression happens before or at the start of the cubs transition from milk to meat (Naidenko, 2006). After parturition females foraging behavior is centered on a natal den for the first 6–8 weeks of the cubs' lives (Schmidt, 1998; Nilsen *et al.*, 2012; Gaillard *et al.*, 2014; White *et al.*, 2015). Most fights in captivity occur at 6–8 weeks of cubs' lives when a female changes her foraging behavior to normally active. It happens right before the maximal female payoff for their feeding (Langer, 2008) but close to the moment of weaning when an actual situation with resources will determine the number of cubs that can survive. It is not surprising since siblicide should balance between cubs' survival and the costs of cohabiting (Osorno & Drummond, 2003). In facultatively fighting EuL trajectory of cubs' growth rates can determine whether will they fight or not. At least among triplets fights occur in litters with initially high growth rates that decline after the first month and do not happen in litters with initially low growth rates that do not decline to the age of fight (Antonevich *et al.*, 2012). Food recourses in captivity are not limited, but this relation between growth rates and fight occurrence provides evidence that sibling fights if not caused are still triggered by the signs of resource insufficiency (Antonevich *et al.*, 2012). Siblicide is facultative even in obligately fighting the Iberian lynx. Siblicide is supposed to help females save energy for future reproduction, regulating litter size before the moment of maximal competition facultatively when it is needed (Mock & Parker, 1997). At this period lynx females in the wild leave cubs three times a day for several hours and start to move cubs every 5–33 days using 1–4 den per month (Schmidt, 1998). Whereas in captivity females separate fighting cubs (Antonevich *et al.*, 2009), in the wild females are not necessarily close to the litter and able to intervene in the fight, so the mortality rate can be higher.

Adaptiveness of siblicide

Since siblicide is the reduction of the number of siblings, the closest relatives, sharing the same genes, it is evolutionary disadvantageous by default. So it is expected that if such a phenomenon evolved, benefits would overweight costs from the potential reduction of gene carriers (Trivers, 1974). For this reason, the vast majority of siblicide studies aim to find the adaptiveness of sibling aggression.

Alternatively, sibling aggression could evolve as a side effect of the development of another type of behavior during this period, as was suggested for sibling scramble competition in domestic cat (Hudson *et al.*, 2013; Hudson & Hauber, 2014). Although, unfortunately, to the moment, no such appropriate behavior is known. In particular, sibling aggression unlikely evolved as a side effect of predatory behavior due to the differences in brain regions responsible for the regulation of those types of behavior (Gregg & Siegel, 2001). However, sibling aggression remained in different lynx species and was not eliminated by the selection despite of the costs. In sum, the main way to explain the existence of sibling aggression to the moment is to consider its adaptiveness related to sibling competition.

Contradictory data

It was found that kittens from litters of two had a higher probability of surviving than kittens from litters of three or four (EuL (Gaillard *et al.*, 2014; Mattisson *et al.*, 2022)) although the particular age when initial litter size was measured varied a lot (1–6 weeks (White *et al.*, 2015). In most lynx litters fights happen around 6-8 weeks, but in some litters, fights occur as early as four weeks (Antonevich *et al.*, 2009; Antonevich *et al.*, in prep) so it is impossible to extract cases when this litter size was measured before sibling aggression, and cases when this litter size refers to the post aggression period. So we cannot estimate if sibling aggression had a role in maintaining optimal litter size — twin. Finally, in IbL females typically raise 2 cubs to ages older than 3 months (when cubs can hunt with their mother), 75% of cubs survive and then mortality decreases (Palomares *et al.*, 2005) and the same litter size was the most prominent to the winter in CaL (Aubry *et al.*, 1999) and EuL (Jedrzejewski *et al.*, 1996). For EuL mortality measured till independence was around 50% and it is the highest during the first months of life (Jedrzejewski *et al.*, 1996). Our data on the captive population IbL revealed that aggression is earlier and has a higher probability of siblicide in twins than in larger litters (Antonevich *et al.*, in prep). One of the reasons for such contradictory results regarding optimal litter size could be parent-offspring conflict (POC) when the offspring's optimal litter size and parents' optimum are different (Trivers, 1974). A smaller number of littermates does not necessarily decrease competition; on the contrary, fewer competitors mean that each cub has a larger share of available resources, making the fitness gained by the winner more valuable. Therefore, the benefits of sibling aggression are most significant in twins (Antonevich *et al.*, in prep).

Lynx evolution

Both IbL and EuL have sibling aggression leading to siblicide. Similar sibling aggression with similar levels of siblicide (14% of litters in EuL (Antonevich *et al.*, 2009) and 9.2 % in IbL (Antonevich *et al.*, in prep) are not surprising. IbL and EuL lynx are sister species that diverged around 1–1.7 million years ago (Johnson, 2004; Johnson *et al.*, 2006; Boscaini *et al.*, 2015; Abascal *et al.*, 2016). They both passed through a series of severe bottlenecks. Such a decrease in effective population size could cause fixation of adaptive (to the moment) reproductive features. Once appeared, a mutation (or several) that caused sibling aggression in lynx could be even more adaptive in a period of harsh conditions. The most drastic population decline affected both Iberian and Eurasian lynx 700–100 thousand years ago and separated them. But later during the period of milder climate, ranges expanded causing interbreeding of Eurasian and Iberian lynxes. Although the subsequent period of progressive cooling re-isolated both lynx species, genetic interchange did not cease until recently (Abascal *et al.*, 2016). Moreover, IbL had another, the last, and the most harsh population decline that led to a demographic bottleneck in recent history (Simón *et al.*, 2012) and it is proven to cause various mutations fixation (Johnson, 2004). IbL has a harder variant of sibling aggression, fights are obligate and more harsh than in EuL (Antonevich *et al.*, 2009), but siblicide rates are higher in EuL than in IbL (Antonevich *et al.*, in prep). Although based on our captive populations we can not exactly estimate and compare real numbers of mortality in the wild.

There are some questions raised by this hypothesis. The BC has sibling aggression (Antonevich & Naidenko, 2013), but only part of the SSBC (Table). However single case of observed sibling aggression in BC does not allow us to conclude if this aggression leads to siblicide. At least bobcat breeders in the USA do not claim siblicide as a problem accompanying sibling aggression that they reported in some but not all litters (Lynn Culver, personal communication). So BC being the closest among lynxes to ancestral lynx would probably have the same reproductive complex in its ancestral form, including mild sibling aggression. Another explanation can be post-speciation gene flow. CaL and BC (like EuL and IbL) had genetic interchange (Koen *et al.*, 2014), so if CaL had sibling aggression as the SSBC, Bc could get it through occasional interspecific hybridization. Although for CaL behavioral data are lacking, including information regarding fights.

CaL also has SSBC and lives in conditions favoring strictly seasonal breeding. So CaL should have sibling aggression, if not as hard as IbL, but at least stronger than the BC has. Divergent selection between CaL and Bc confirms the adaptations that CaL has to seasonality (Prentice *et al.*, 2020). Unlike EuL and IbL, CaL adjusts their reproductive activity to changing conditions (Poole, 2003; Reynolds *et al.*, 2017), but it is not clear if it takes place only prenatally or postnatally as well e.g. through the siblicide. Anyway, the existence of such fights in CaL litters needs further investigation.

Sibling aggression is unique in mammals and we expect that it can evolve under the unique combination of important factors. Various factors that influence cost-benefit balance could contribute to sibling aggression development in lynx (Naidenko *et al.*, 2007a; Antonevich *et al.*, 2012; 2019).

We suggest that the complex of reproductive features related to nonflexible seasonality in lynx could contribute as one of those factors. Such reproductive strategy could foster the development of additional ways to adjust reproductive efforts, facilitating sibling aggression evolution to serve this function in a critical period of development. The are gaps in the knowledge of Pallas' cat and snow leopard reproductive biology, we also lack information regarding sibling aggression in Canada lynx. Further investigation of these species is necessary to test our hypothesis.

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