

Sex-Selective Infanticide and Sociality in Brown Bear Populations

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Received May 17, 2023; revised June 12, 2023; accepted June 19, 2023

Abstract—An analytical review of scientific publications containing materials or discussion of the concept of sexually selective infanticide (SSI) in brown bear populations (*Ursus arctos*) is presented. The authors of the SSI concept refer to the idea of sexual selection, which is a rather shaky conceptual basis. The concept was formed largely on the basis of materials obtained during the study of intraspecific relations in lion populations (*Panthera leo*). However, facts regarding the behavioral ecology of the lion, which accumulate relatively quickly, can be interpreted quite ambiguously and even only when applied to this species, the concept of this does not look convincing enough and is obviously unnecessarily anthropomorphic. Infanticide, cannibalism, and their combination are recorded in both lion and brown bear populations. However, the behavioral ecology of these species differs significantly. Brown bear populations are characterized by pronounced seasonality of reproduction; the presence of a reproductive interval in bear females, which can vary significantly in populations with different habitat conditions and varies from 1 to 5 years; and mating patterns than can vary from lax monogamy to panmixia. Multiple paternity is possible within the same litter of cubs of a brown bear. It follows from the review that brown bear populations are characterized by many features of sociality, with the lifestyle of bears being both solitary and group. It is hardly correct to classify the brown bear (and other species of bears) as uniquely asocial. From the analysis of publications on the behavioral ecology of the brown bear, it follows that the application of the SSI concept without significant additions is hardly useful for understanding the intraspecific relations of this species.

Keywords: brown bear, lion, selective infanticide, redundancy, sexual selection, sociality

DOI: 10.1134/S2079086423090098

INTRODUCTION

Analytical reviews of the spread of infanticide among mammals are presented in publications (Hrды, 1979; Ebensperger, 1998; Knörnschild et al., 2011; Lukas and Huchard, 2014). Their authors discuss a number of hypotheses (four or five main ones are named) about the biological significance of infanticide, while turning to the idea of sexual selection (Darwin, 1886). Both among Darwin's contemporaries and subsequently, there was no consensus in assessing the validity of his doctrine of sexual selection. This doctrine never gained the status of a scientific theory, and many publications over a century-and-a-half have observed the descriptiveness of factual materials, as well as the low degree of certainty and the debatable nature of ideas about sexual selection (Morgan, 1936; Mayr, 1968; Schmalhausen, 1969; Lyubishchev, 1973; Grant, 1980; Puchkovskiy, 2013; Panov, 2014; Glutton-Brock and Vincent, 1991). Despite the instability of the conceptual basis in the form of the idea of sexual selection, the idea of sexually selective infanticide (SSI), supported by the results of studies of lion populations, has gained noticeable popularity and has found application in publications devoted to the behavioral ecology of the brown bear (Bellemain et al.,

2005; Ballesteros et al. al., 2021; Ito et al., 2022). In this area of science, the tradition of evolutionary biology of the past two centuries continues (Vorontsov, 1999): having some biological erudition and taking into account the idea of pansélectionism (the idea that everything in surviving biosystems is the result of natural selection (Lyubishchev, 1973; Levontin, 1978), one can use the materials in reference to the biology, for example, of the brown bear, talking about the selection of male bears by female bears and of female bears by males, and cubs by both, not forgetting about gamete competition (Grant, 1980; Bellemain et al., 2005) and about selection for success in reproduction (Mayr, 1968, pp. 168–169; Lukas and Huchard, 2014; Morehouse et al., 2021). For the sake of objectivity, I note that the concept of SSI in relation to brown bear populations is characterized by some researchers as debatable and in need of clarification and development (Puchkovskiy, 2023; Bellemain et al., 2005, 2006; Frank et al., 2017).

The purpose of the article is to present an analytical review of published materials and existing opinions regarding the suitability of the SSI hypothesis for understanding the behavioral ecology and social organization of brown bear populations.

THE CONCEPT OF SEXUALLY SELECTIVE INFANTICIDE

A convenient object that turned out to be accessible for study in natural conditions and whose behavioral ecology, apparently, served as a model for the formation of the concept of SSI, turned out to be the lion *Panthera leo* (Packer and Pusey, 1995). The sexual selection hypothesis proposes that infanticide is a reproductive strategy in which males kill the offspring of competing males to increase their own reproductive investment (Trivers, 1972; Packer and Pusey, 1995). If successful, the male deprives the nursing female of her cubs, as a result of which lactation is interrupted. The female undergoes a hormonal shift, and estrus begins in the coming days. The male (or resident males of the lion pride) gets a chance to mate with this female and contribute his descendants and his genes to the coming generations. This variant of intrapopulation relationships and the sequence of events during reproduction were identified using materials obtained from the study of lion prides (Schaller, 1972; Packer and Pusey, 1995; Grinnell and McComb, 1996). The gain for males is survival as part of a pride, which is ensured by collective hunting, and success in confronting male competitors. The loss of cubs by lactating females apparently pays off with protection and successful hunting when living in a pride. In the SSI concept, the male lion is characterized as a natural breeder, concerned with increasing his own contribution to the pride's gene pool. Interestingly, a relatively early review (Hrdy, 1979) focused on the consequences of male infanticide on female reproductive strategies. However, it is the reproductive strategy of males that is widely known among researchers studying large carnivorous mammals.

The SSI model has found not only supporters, but also opponents, among zoologists. An anonymous article (<https://felidae-g2n.jimdofree.com/panthera/panthera-leo/%D1%81%D0%BE%D1%86%D0%B8%D1%83%D0%BC%D0%BB%D1%8C%D0%B2%D0%BE%D0%B2/> accessed April 27, 2023) provides a useful analytical review of publications on sociality and reproductive characteristics in lion populations that have been studied in sufficient detail. Some clarifications on the biology of this species, mentioned in the review, are significant. Some of them are that not all lions are organized into prides; females in a pride are more philopatric than males; the life of male leaders (breeder) in a pride rarely exceeds 2 years, that is, the elimination (and, accordingly, turnover) of males is very intense; the social organization of different lion populations can vary significantly; and a study of the relatedness of descendants (using molecular biology and radio tracking methods) showed that both male and female lions can mate outside their pride.

Already, from the cited fragments of the review, we can conclude that the concept of SSI, even when

applied to lion populations, is not very convincing and the facts from the behavioral ecology of lions can be interpreted quite differently. In particular, the question arises: is the contribution of breeding males to the gene pool of a pride so significant if the time of their individual leadership is on average 2 years and only very rarely reaches 4 years? Also worthy of attention are the revealed facts of the implementation by females of counterstrategies, which are aimed at counteracting infanticide by male lions (Hrdy, 1979; Ebensperger, 1998). Lionesses who are part of a pride can counteract the invasion of foreign males; in particular, the likelihood of such events can be reduced by the combined roars of adult females (Grinnell and McComb, 1996).

INFANTICIDE IN BROWN BEAR POPULATIONS

Infanticide (killing of cubs) is a practice common to many animal species (Hrdy, 1979; Pusey and Packer, 1994; Ebensperger, 1998) and also recorded in brown bear (*Ursus arctos*) populations (Smirnov, 2017, 2021; Puchkovskiy, 2023; Swenson et al., 2001; Bellemain et al., 2005; Morehouse and Boyce, 2017). Adult males are usually the perpetrators of infanticide, but in rare cases female bears from Kamchatka are capable of such actions (Gordienko, 2012).

I note that the populations of lions and brown bears differ very much in social organization (see below). However, the male brown bear (like the lion) is also portrayed by some authors as a kind of breeder, concerned with the contribution of his own genes to the gene pool of the population (Bellemain et al., 2005, 2006). How appropriate infanticide in this form is for the survival of brown bear populations is a large question. Some foreign colleagues suggest that male brown bears purposefully track and pursue conspecific families, trying to kill cubs (Swenson et al., 2001). It is believed that the death of cubs initiates the inclusion of the estrous cycle in the female bear (Craighead et al., 1969; Swenson et al., 2001; Bellemain et al., 2005; Steyaert et al., 2014). After a few days, she is ready to mate, and the male gets a chance to pass on his genes to the offspring. In my opinion, there is a fair amount of anthropomorphism embedded in the ursine SSI model. Quite a lot of evidence of infanticide is known from different parts of the range of this species, but their significance for the population is the subject of debate (McLellan, 2005; Bellemain et al., 2005; Steyaert et al., 2014). To answer the question of the usefulness/harmfulness of infanticide for the population, further research using genetic monitoring methods and social ethology will be required.

Several main hypotheses have been put forward in scientific publications about the likely significance of infanticide for brown bear populations: intraspecific predation, infanticide as part of the mechanism of intrapopulation regulation, competition for food

resources, SSI, and random anomalies of sociality. There are also variations within these hypotheses. Their evidence today is clearly insufficient; these logical constructions continue to be a topic of discussion among specialists in brown bear biology (McLellan, 2005; Bellemain et al., 2005; Steyaert et al., 2014; *Yellowstone Grizzly* ..., 2017, p. 43; Penteriani et al., 2020; Ballesteros et al., 2021; Ito et al., 2022) and serve as “a kind of simulators for desk office exercises” (Puchkovskiy, 2023, p. 83). For me, it is obvious that infanticide limits the population size to some extent, as well as its influence on the behavior and placement of potential objects of attack on the territory by a strong and aggressive male: cubs and bear families, young or weakened conspecific individuals. A significant evolutionary consequence of the threat of infanticide is the development of various forms of defensive behavior in a mother bear with cubs, which are activated when an adult bear appears (Pazhetnov, 1990a; *Medvedi* ..., 1993; Gordienko, 2012; Ebensperger, 1998). It can also be supposed that the aggressive reaction to people is of the same nature and that the female bear reacts to the approach of a person to the cubs in the same way as to an adult male of her species threatening the well-being of her cubs (Puchkovskiy, 2009).

Such an intimate feature of the behavior of brown bears living in closed (forested) landscapes is accessible to visual recordings only in rare cases; directly and relatively more often it is found in especially favorable (open) landscapes for visual observations. On the territory of the South Kamchatka Nature Reserve, there are 37 cases of attacks by adult males on bear families and two cases of attacks by single adult females on bear cubs (Gordienko, 2012). The author of this study also notes that, in the general mass of observations, large old males (width of palmar callus 22–24 cm) do not show noticeable reproductive activity during the rut, but that aggressive behavior towards cubs, female bears, and young bears in these animals also manifests itself during rut and in the autumn (fattening) period.

Based on individual observations or indirect evidence, the reality of infanticide is recognized for many brown bear populations in Russia (Voronov, 1974; *Medvedi* ..., 1993; Gilyazov, 2011; Danilov and Tirronen, 2011; Smirnov, 2017) and abroad (Stringham, 1980; Bunnell and Tait, 1981; Swenson et al., 2001; Bellemain et al., 2005; *Yellowstone Grizzly* ..., 2017; Penteriani et al., 2020; Ballesteros et al., 2021; Ito et al., 2022). I assume that ideas about the biological significance of infanticide are still being formed mainly due to the possibilities of speculative creativity with the slow accumulation of factual basis. I also admit that infanticide, like cannibalism, is a property not only of individual brown bear populations, but also of the species as a whole. Moreover, infanticide has also been registered in the populations of polar bear *U. maritimus* (Derocher and Stirling, 1990) and Asian black bear *U. thibetanus* (Kolchin, 2019; Tamatani et al., 2021).

So, numerous facts reliably testify that adult males of their population pose a mortal danger to bear cubs (Pazhetnov, 1990a; *Medvedi* ..., 1993; Gordienko, 2012; Stringham, 1980; Bunnell and Tait, 1981; Dahle and Swenson, 2003; McLellan, 2005; Steyaert et al., 2013). Observations by foreign authors have been described indicating that in nature, during the rutting period, a female bear who has lost her cubs due to infanticide can regain readiness to mate after a few days (Craighead et al., 1969; Swenson et al., 2001; Bellemain et al., 2005; Steyaert et al., 2014). However, such a cause-and-effect relationship between these events cannot be considered a mandatory rule for brown bear populations (see below).

CANNIBALISM IN BROWN BEAR POPULATIONS

Cannibalism (intraspecific predation) is common in the animal world (Polis, 1981), including the class of mammals, and among them the order of Carnivora. According to published review (Puchkovskiy et al., 2017), cannibalism of brown bears has been recorded in 11 subjects of the Russian Federation in five federal districts of Russia: Northwestern, Southern, Volga, Ural, and Siberian. Instances of intraspecific predation are recorded in isolated cases, although it is obvious that a significant part of the phenomena of intraspecific biology remains hidden from human beings.

The cannibals usually turned out to be larger animals; in almost all cases, when the gender of the authors of the publications was recorded, these were males. There are known exceptions: the behavior of two female bears in Kamchatka (Gordienko, 2012). shatun bears in the Komi Republic have proven themselves to be cannibals (Neifeld, 2004), as was the only shatun bear discovered in Kirov oblast (Toropov, 1991). In two recorded cases (Murmansk and Tomsk oblasts), adult bears killed and ate cubs (Zhdanov and Pavlov, 1972; Gilyazov, 2011). From a review of generalizing publications, it also follows that, starting from the Yenisei, in Altai-Sayan mountainous country, and further to the east, instances of cannibalism have been recorded in brown bear populations of all Siberian and Far Eastern regions of the Russian Federation (Bromley, 1965; Kucherenko, 1983; *Medvedi* ..., 1993; Chernyavsky and Krechmar, 2001; Smirnov, 2017), including Kamchatka krai (Chestin et al., 2006; Gordienko, 2012). Over the entire observation period (1996–2005), at model sites in the South Kamchatka Federal Reserve, researchers recorded visually and by traces 37 cases of male attacks on bear families (44 bear cubs and five female bears died); twice, single adult females attacked cubs (one yearling was killed and eaten). In five episodes, five medium-sized bears died and were eaten; two of them had two yearlings, and the other three had one yearling each. All female bear cubs that died while protecting were significantly

(2–2.5 times) smaller in size than males (Gordienko, 2012, p. 113).

In the Cantabrian Mountains (Spain), where about 200 brown bears live, a case was recorded of an attack by a male brown bear on a family with a cub of the year during the mating season (Ballesteros et al., 2021). The she-bear tried to protect the cub, but was killed. The attacking male fed on her carcass for several days. In Norway and Sweden, brown bear cannibalism is well known and has been extensively studied (Swenson et al., 2001). In North America, intraspecific predation of brown bears has been studied by many teams of researchers for many years. For example, of 6976 grizzly bear scat collected from the Yellowstone ecosystem from 1975 to 1990, 12 contained grizzly bear remains and ten contained remains of American black bear *U. americanus* (Mattson et al., 1992). Obviously, the presence of fur and other remains in excrement can be a consequence not only of intraspecific predation, but also of eating the corpse of an animal that died from an unknown cause.

Cannibalism of brown and other bear species is regarded by zoologists as an essential part of the mechanism of self-regulation of population size and composition (Polis, 1981; Mattson et al., 1992; Swenson et al., 2001; Miller et al., 2003). Our compatriots also adhere to this theoretical position (Pazhetnov, 1990a; Danilov, 2017; Smirnov, 2017).

The presented review of publications gives grounds to conclude that brown bear cannibalism is widespread within the species' range and can be considered an adaptation of general species significance (Kozhechkin and Smirnov, 2017; Puchkovskiy et al., 2017).

Foreign colleagues published a review of reliable cases of cannibalism among bears around the world (Allen et al., 2022), and the review did not include the results of analysis of excrement. From this work it follows that of the eight species of bears, intraspecific predation is characteristic of four: American black bear, brown bear, Asian black bear, and polar bear. Among these species, the polar bear stands out with an increased frequency of recorded cases of cannibalism. However, this species is the most carnivorous of the four named.

FEATURES OF INTRASPECIFIC RELATIONSHIPS OF BROWN BEAR

So, infanticide, cannibalism, and a combination of these forms of intraspecific relationships are found in populations of lions and brown bears. However, by analogy with lion populations, can we confidently attribute an SSI strategy to the brown bear? The following is a discussion of characteristics of brown bear populations, including those that are uncommon (or only slightly common) in lion populations, but are common (or not uncommon) in brown bear popula-

tions. The sociality of the brown bear is also noticeably different from that of the lion and is discussed in a special section.

Brown bear populations are characterized by a pronounced seasonality of reproduction (Stroganov, 1962; Heptner et al., 1967; Pazhetnov, 1990a; *Medvedi ...*, 1993; Smirnov, 2017; Puchkovskiy, 2023; Couturier, 1954; *Bears ...*, 1994), and the rut occurs during the snowless period, and the birth of cubs occurs during winter sleep in dens.

For lionesses with cessation of lactation (regardless of the reason), the rule is the onset of estrus and the absence of a temporary break in reproduction.

For female bears, the rule (with some exceptions) is the reproductive interval (Puchkovskiy, 2023; *Yellowstone Grizzly ...*, 2017). It is believed that, in central Russia, the female bear participates in rut once every 2 years, although female bears can give birth every year in the more southern parts of the range and in captivity (Geptner et al., 1967; Pazhetnov, 1990a). According to the work of foreign colleagues, the interval between births in North American brown bear populations varies from 1 to 5 years (Stringham, 1980; Ballard et al., 1982; McLellan, 1989), the average values of this indicator being close to 2.5–3 years. In the province of Alberta (Canada), the average interval between litters for female bears is 4.4 years (Garshelis et al., 2005). As follows from the general publication (*Yellowstone Grizzly ...*, 2017), North American brown bears from places with harsher climates and long winters mature later, and the pauses between births of cubs are longer. According to this summary, the average birth interval in North America is 3 years or more. Processing of long-term materials obtained in 20 surveyed territories (Sweden, Alaska, Canada, continental United States) showed that, on average, brown bears give birth to cubs every 3 years (Schwartz et al., 2003). On the island of Hokkaido, birth intervals are usually 2, less often 3, years (Moriwaki et al., 2017). According to expert assessment (Zavatsky, 2004), the same mode of participation in reproduction of female bears of the Western Sayan is the same.

A special example is the relict population of brown bear living in the Apennines (Central Italy), which was thoroughly studied from 2005 to 2014 (Tosoni et al., 2017a, 2017b), and its monitoring continues. The female bears of this population stop feeding their cubs at approximately 1.4 years of age, but the interval between births for female bears is on average 3.7 years! The authors of the study explain the slow rate of reproduction of the Apennine population as being due to long-standing isolation and an assumed high level of inbreeding (Tosoni et al., 2017a, 2017b). A proposal was made (Ciucci and Boitani, 2008) to consider this population a special subspecies *U. a. marsicanus*.

The reproductive interval of female bears in a newly established growing population of bears from Northern Italy (Groff et al., 2017) was 2.12 years.

In Deosai National Park (Pakistan), a relict population of the Himalayan brown bear is being monitored *U. a. isabellinus* (Nawaz et al., 2008), which has been protected since 1993 and has grown by 5% annually since then. As the cited authors suggest, the increase occurred due to reproduction and immigration and the population had very low reproductive characteristics of its own. The average single fecundity of the local population is 1.33 cubs, the start of reproduction of female bears is 8.25 years, the reproductive interval of female bears is 5.8 years, and the period of family life is 4.2 years.

As follows from a brief review of materials on the reproductive interval of brown bear populations, there is no obligatory cause-and-effect relationship between the end of lactation or the period of family life with the onset of estrus.

Various are described patterns of marital relations in brown bear populations. A female bear can mate in one season with one male (Pazhetnov, 1990a; Couturier, 1954), or with several (Stroganov, 1962; Couturier, 1954; Craighead et al., 1969; Schwartz et al., 2003; *Yellowstone Grizzly ...*, 2017). Brown bears of Kamchatka during the rutting period behave in approximately the same way as Yellowstone bears (*Yellowstone Grizzly ...*, 2017), mating with different partners (Nikolaenko, 2003; Gordienko, 2012). In general, many characteristics of the brown bear rut in nature are apparently very variable and are still not fully studied and covered in the literature (Steyaert et al., 2012; Moriwaki et al., 2017). However, there are sufficient reasons to join in the conclusion (Steyaert et al., 2012) that different models of marital relations are possible in brown bear populations: from loose monogamy to polyandry and polygyny, or even a combination of both. The use of DNA analysis methods from materials obtained from brown bear populations in Scandinavia and North America has made it possible to establish that cubs from the same litter can have different fathers (Bellemain et al., 2005; *Yellowstone Grizzly ...*, 2017). A study conducted on the island of Hokkaido showed that, in the local brown bear population, multiple paternity within one litter was recorded with a probability of 14.6–17.1% (Shimozuru et al., 2019). Facts of inbreeding occur with less frequency. The cited authors believe that the dispersal of maturing individuals, especially males, reduces the likelihood of inbreeding and its negative consequences.

SOCIALITY OF THE BROWN BEAR

A number of publications express a fairly definite point of view, according to which the brown bear is classified as a social, solitary species (Geptner et al., 1967; Seton, 1937; Couturier, 1954; Swenson et al., 2001; Støen et al., 2005; Bellemain et al., 2005; Steyaert et al., 2014).

An opposite point of view is also presented, from which it follows that populations of brown bears (as well as other species of bears) are characterized by many manifestations of sociality (Pazhetnov et al., 1999; Kolchin, 2015; Puchkovskiy, 2023; Stonorov and Stokes, 1972; Egbert and Stokes, 1976; Derocher and Stirling, 1990; Gilbert, 1999). A logically coherent scheme for the parcel structure of brown bear communities has been proposed (Pazhetnov, 1990a, 1990b) and supported by many authors (Kudaktin and Chestin, 1993; Yudin, 2011; Smirnov, 2017; Puchkovskiy, 2023): the dominant male is the organizer, in the vicinity of which there are more weak relatives, including adult males. Great importance is attached (Danilov, 2017) to the dynamism of social relations depending on the food supply and the characteristics of the distribution of female bears—with and without cubs.

Indeed, bears spend part of their lives (this part is especially large for males) as solitary animals; however, they also have periods of living together (in a family, a mating group, etc.), and other manifestations of sociality are noted. I am of the opinion (Puchkovskiy, 2009, 2023) that the lifestyle of brown bears is characterized as solitary—family group. The reproduction function is associated with short-term associations of adult animals in rutting groups with very tense relationships between group members, as well as family groups that unite bears for a longer period of a year or more (Chernyavsky and Krechmar, 2001; Smirnov, 2017; Puchkovskiy, 2018, 2023; Egbert and Stokes, 1976; Gilbert, 1999). Mammals tend to create temporary accumulations of individuals (aggregations) in places with favorable conditions (Panov, 2010). With a significant concentration of food resources, bears are also able to show some tolerance for living together in a limited area, forming aggregations (Tirronen, 2010; Smirnov, 2017; Egbert and Stokes, 1976; Gilbert, 1999; Lewis and Lafferty, 2014; Sorum et al., 2023). In conditions of captivity, with a satisfactory food supply, some tolerance and even affection between individual animals is also found (Colmenares and Rivero, 1983a, 1983b). All of the named properties of brown bear populations and the dynamics of their relationships can be considered as examples of a unique level of sociality in populations of this species.

Family groups in brown bear populations are well known (Geptner et al., 1967; Pazhetnov, 1990a; *Medvedi ...*, 1993; Danilov, 2017; Puchkovskiy, 2023; Couturier, 1954; Bears..., 1994; *Yellowstone Grizzly ...*, 2017), bears spend the first years of their lives in them: from 1 to 4. Kinship relationships can also affect the behavior of young animals in the first years of independent life: bear cubs can stay together until the onset of the denning period. We know of examples in which a young female bear with her offspring (young yearlings) stayed close to a mother bear who had cubs of the next generation, and in another case two yearlings stayed together throughout the summer season (with-

out the female bear) in a limited area near our camp. Such tolerant relationships between female bears (mother and daughter) have been confirmed using materials from the European North of the Russian Federation (Danilov, 2017). According to studies conducted in Sweden, it is assumed that female brown bears have two types of territorial relationships: solitary use of territory and group use (Støen et al., 2005). Work done in Finland (using genetic methods and radio collars) showed a positive correlation between the proximity of the individual territories of female bears and the degree of their relatedness (Olejarz et al., 2022).

For male brown bears, an adult female is a factor of integration into rutting groups of two or more individuals (Puchkovskiy, 2018, 2023). Relations between members of such a group are very tense; moreover, with the loss of attractiveness of the female to males (the end of estrus), the rutting group quickly disintegrates. Sources of sufficiently rich food resources can also cause integration and the formation on this basis of more or less close aggregations of bears. The concentration of food in combination with more or less narrow localization and the presence of family relationships are important; an aggregation of bears also establishes its own temporary hierarchy with elements of tolerance, dominance and aggression (Pazhetnov, 1990b; Gordienko, 2012; Smirnov, 2017; Gilbert, 1999). T.A. Gordienko (Gordienko, 2012) gives many examples of observations of bears in Kamchatka; in particular, he describes five samples of active social behavior, a number of behavioral forms that are characteristic of bears when meeting an unfamiliar male of the same high rank, etc. A complete lack of tolerance towards individuals of their own species is characteristic of shatun bears (Stroganov, 1962; Bromley, 1965; Smirnov, 2017; Puchkovskiy, 2021), for which any other animal (of its own or another species) or person is a potential victim.

From review publication (Puchkovskiy, 2023), it follows that the lifestyle of the brown bear reveals significant dynamism in spatial and temporal aspects. Accordingly, social relations in populations of this species show great variability depending on the ecological and geographical differences of regions, the provision of food resources, long-term dynamics of the yield of fattening feeds, and the seasonality of reproduction of brown bear populations.

In natural associations of brown bear individuals, a hierarchy and elements of territorial relations can be traced (indicated above). When kept in captivity, researchers discover the formation of dominance/subordination relationships already in groups of yearling bear cubs (Pazhetnov, 1990a; Pazhetnov et al., 1999). In the Russian literature, the very controversial age category of “pestun” is sometimes used (Middendorf, 1851; Geptner et al., 1967): a nanny bear who supposedly takes care of younger cubs. Not all experts recog-

nize the reality of such a figure in a bear family. However, employees of the Pazhetnov bear cub rescue center based in Tver oblast', in their rich practice of observing bear cubs, noted real examples of the caring attitude of some of them towards bear cubs that are lagging behind in development (Puchkovskiy, 2023).

All of the named properties of brown bear populations and the dynamics of their relationship can be considered as reasons (factors) for maintaining and adaptive self-adjustment of the unique level of sociality of populations of this species. Discussion of the topic gives grounds for the assertion: in brown bear populations, there is a certain level of sociality, which differs from the typical extremes in understanding the sociality of animals of various taxa (Panov, 2010) primarily in its dynamism. Sociality in a similar form is also characteristic of American black bear (Jonkel and Cowan, 1971; Gilbert, 1999; Stringham, 2012), polar (Derocher and Stirling, 1990) and Asian black bears (Yudin, 2011; Kolchin, 2015).

It is generally accepted that male lions distinguish their cubs from the offspring of other males. As far as I know, there is no evidence that male brown bears have the ability to distinguish between their own and other bears' offspring. However, the use of genetic methods in studying populations of this species proves that multiple paternity within a brood is quite possible (noted above).

The biology of the brown bear reveals the interaction of two trends in the spatial organization of populations of this species: disintegration (separation) and integration (Puchkovskiy, 2023). The need for selective use of natural resources (spatial, food, protective, etc.) and avoidance of dangerous factors forces bears to disperse throughout the territory. However, at certain points in time, there is a need to reduce the distance between individuals or even communicate closely as parts of aggregations, family, and rutting groups: a seasonally realized tendency towards integration is revealed. The dynamism of the interaction of these two trends is ensured by communications, which include remote signaling systems (Naumov, 1973; Tembrok, 1977; Pazhetnov, 1990a; *Biologicheskoe signal'noe ...*, 2013).

CONCLUSIONS

Let me remind you about panselectionism: this is a concept according to which everything in the organization of living systems is only adaptive and the result of natural selection (Lyubishchev, 1973; Nelson, 1988; Puchkovskiy, 2013; Gould, 1977; Goldsmith, 1990). In fact, the organization of biosystems at any level includes adaptive, neutral, and even moderately harmful parts (Severtsov, 1939; Lyubishchev, 1982; Shmalhausen, 1982; Kimura, 1985; Lima de Faria, 1991; Puchkovskiy, 1999; Bock, 1980).

The concept of SSI is formulated as a generalization of information about the intraspecific struggle for existence of animals of different classes (Hrdy, 1979), including mammals of several orders (Ebensperger, 1998; Knörnschild et al., 2011; Lukas and Huchard, 2014).

It is supposed that the SSI strategy is characteristic of lion populations, which are the most accessible of all large predatory animals for study and for which significant progress has been made in accumulating knowledge about intraspecific relationships. Central to this concept is the active role of adult males, who kill lion cubs—the descendants of other males—and ensure the reproduction and preservation of their own descendants and, accordingly, their own genes in the population.

A discussion of the features of intraspecific relationships in brown bear populations reveals features of significant originality and differences from intraspecific struggle in lion populations. In its pure form, the “lion” model of SSI does not correspond well to the accumulated knowledge about intraspecific relationships in brown bear populations. In my opinion, the concept of SSI is an example of an anthropomorphic verbal model that needs to be replaced with a more promising concept.

I am inclined to turn to the concept of “redundancy of living systems” (Puchkovskiy, 1998, 1999): a certain excess of cubs in brown bear populations ensures reproduction, restoration of the population after depression, potential for range expansion, etc. In conditions of instability in the production of food resources (or their insufficient availability), this is a food resource for a rainy day. In addition, it is necessary to take into account the cyclical nature of the participation of female bears in reproduction: they give birth to cubs once every 2, 3, or more years, due to which a surplus of males is formed in the population, which is ready for reproductive services during the rutting period. At this time, males are concerned about realizing their reproductive potential, but readiness to reproduce also means increased aggressiveness (an example of qualitative redundancy is Puchkovskiy, 1999) and, as a consequence, infanticide.

The onset of estrus in a female bear, her readiness to mate, and, subsequently, the possibility of a male contribution to the gene pool of the population are elements of reproduction necessary for the survival of the population. However, the idea that the male has a goal-directed orientation towards sexually selective infanticide and the reproduction of his own genes is pure teleology and anthropomorphism. It is also necessary to prove that the killer of the cubs was not their father and that only he will impregnate this she-bear—their mother—since the she-bear does not come into heat immediately, and there can be two or more males in a rutting group. Under natural conditions, there is no guarantee that all cubs (there may be two to four of

them in a family) will carry his genes, since the female bear can mate with other males who are not dominant.

I will add that a significant part of African lion populations live in prides, in which lionesses usually make up the majority among adult individuals (Schaller, 1972; Packer and Pusey, 1995; Grinnell and McComb, 1996; Kotze et al., 2018). Apparently, they do not have a pronounced seasonal pattern of reproduction, which is obligatory in brown bear populations. In the same populations of brown bears in which the phenomenon of shatunism is occasionally detected, during years of lack of food there is a mass appearance and subsequent death of shatun bears, among which the majority are adult males (Formozov, 1976; Smirnov, 2017; Puchkovskiy et al., 2019; Puchkovskiy, 2021). It is likely that, in the coming years, the excess of males in rutting groups will decrease, as will the potential for selective elimination.

From the above-mentioned features of the behavioral ecology of the brown bear, it follows that the concept of SSI is insufficient for understanding the intraspecific relationships of this species.

FUNDING

This work was supported by ongoing institutional funding. No additional grants to carry out or direct this particular research were obtained.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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