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Interspecific Relationships between the Amur Tiger (*Panthera tigris altaica*) and Brown (*Ursus arctos*) and Asiatic Black (*Ursus thibetanus*) Bears

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Abstract—During the years 1992–2013, we studied the relationship between Amur tigers and brown and Asiatic black bears in the Sikhote-Alin Nature Reserve and surrounding areas in the southern part of the Russian Far East. To determine the importance of bears in the diet of tigers, 763 kills were located and identified, and 430 tiger scat samples were collected and analyzed. To detect kills and scat samples, we used radio telemetry and satellite tracking, as well as snow-tracking. Relying on evidence revealed by tracks, as well as radio telemetry, we determined whether bears exploited tiger kills as a food resource and how the two may have interacted at kill sites. Thirty-two Asiatic black bear and 12 brown bear den sites were measured to define properties that might assist in protection from the threat of a tiger attack. We identified 641 instances of marking on trees by both tigers and bears, an indication of the complexity of their relationship. Bears are an important part of the tigers' diet, representing 2.2% of all kills found. Bear remains were found in 8.4% of examined tiger scat. Bears exploited tiger kills after a tiger had left, by usurping a kill, or by "sharing" a kill at alternate times. The occurrence of den properties that provided some protection from tigers was dependent on the den type and location. Evidence of both tiger and bear marking was detected at 50.1% of marked trees. A review of the literature on the relationship of tigers and bears is provided.

Keywords: Amur tiger, brown bear, Asiatic black bear, diet, scavenger, predation

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INTRODUCTION

The range of the Amur tiger in the southern part of the Far East of Russia is inhabited by brown and Asiatic black bears. All three species prefer coniferous-broadleaf and deciduous forests. The significant dimensions and mutual overlap of the habitats of the tiger (Yudakov and Nikolaev, 1987; Goodrich et al., 2010) and two species of bears (Seryodkin et al., 2006), as well as the broad seasonal movements of bears (Seryodkin et al., 2014, 2014a), suggest the simultaneous presence of differently aged individuals of these species on the same territory. Having common habitats, tigers and bears come into contact with each other, as a result of which a complex of relationships is established between these species.

The relationship of the Amur tiger with the brown and Asiatic black bears has not specifically been studied by researchers. In the numerous publications on these species, there are mainly episodic and interrogatory data on this issue collected by different authors in some areas of the Primorskii and Khabarovsk krais, which do not give a complete picture of the nature of the relationship and the mutual influence of the predators on each other (Bromley, 1965; Gorokhov, 1973; Kostoglod, 1977; Khramtsov, 1993; Tkachenko, 2012; etc.). The possibility to complete the picture of the relationships appeared owing to the application of methods of radiotelemetry and satellite tracking along with the traditional methods of studying predators. Such a comprehensive research program, including the tracking of tigers and brown and Asiatic black bears collared with radio and satellite collars, was carried out in the Sikhote-Alin' Biosphere Reserve and its environs (Miquelle et al., 1993; Seryodkin et al., 2011). Analysis of the results obtained and their discussion using previously published information allowed us to explore this topic in more detail.

The Amur tiger has the international status of a specially protected species and needs careful study of its ecology. This is especially true for the issues reflecting the impact of other species on it that are potentially capable of affecting its population. Among them are brown and Asiatic black bears.

MATERIALS AND METHODS

Field observations were carried out in the years 1992–2013 in the Sikhote-Alin' Reserve and its environs, including the Bol'shaya Ussurka River basin (Middle Sikhote-Alin). When collecting the material, methods of studying animals by the traces of their life activity, radiotelemetry (Miquelle et al., 1993; Matyushkin, 2000), and satellite tracking (Miller et al., 2013; Petrunenko et al., 2014; Seryodkin et al., 2014) were used.

In the analysis, we used information obtained from 67 collared individuals, of which 36 were Amur tigers (16 males and 20 females), 14 were brown bears (seven males and seven females), and 17 Asiatic black bears (13 males and four females). All these animals were equipped with radio collars of the MOD-400 or MOD-500 systems (Telonics, Mesa, Arizona, United States) and GPS PLUS satellite collars (Vectronic Aerospace).

The location of the radio-collared animals was determined by the triangulation method on foot and automobile routes, as well as using an AN-2 airplane and an MI-8 helicopter. The maximum radius of reception of the radio signal in the absence of obstacles from an aircraft is 45 km. From the ground in mountain relief conditions, the signal reception distance rarely exceeded 5 km. Satellite collars determined the geographical coordinates using a GPS receiver, then the data were taken by the researchers remotely in the process of radio communication.

Tiger prey, as well as animals that died for other reasons and were scavenged by tigers, were found when visiting predator sites determined by radiotelemetric methods (Miquelle et al., 1993, Miller et al., 2013), especially in the cases when tigers stayed in one place for more than a day. There were also casual finds of victims. The found remains of animals eaten by tigers and other traces of the life activity of tigers were described in detail. If the tiger was not known (accidentally found prey), researchers tried to determine its sex and age by the size of pawprints (Pikunov et al., 2014). The bears who were present at the tigers' prey were registered: the species of the bear was identified, its activities on the prey were determined by the pawprints, the nature of possible relations with the tigers, the time of stay, and the degree of utilization of the prey by both predators were described.

In total, the remains of animals eaten by a tiger were found 763 times, 378 of them during the nonhibernation period of the bears. Of these, 738 animals (370 in the nonhibernation period) were reliably attributed to the prey of tigers, the rest could have been obtained by other predator species or could have been fallen animals before the appearance of the predator. The nonhibernation period for bears was limited to the period from April 1 to November 30, which corresponds to the average time of coming out of the den and entering it for the Sikhote-Alin bears (Bromley, 1965; Seryodkin et al., 2003).

Depending on the way the tiger prey was used by the bear, we identified three situations. The first one consisted in the bear finding the remains of the prey after the tiger, having consumed most of the meat and left it. The second situation occurred when the bear, finding the tiger on the prey, chased it away and took possession of the prey. The third situation identified by us was that neither the tiger nor the bear left the prey and fed on it at the time when one of the predators allowed the other to do so, temporarily relinquishing the prey to another. The duration of the presence of tigers and bears at the sites with prey was determined by the freshness of the traces of their life activity, by visual registration, and in radio-collared animals by using radio facilities.

The scat of predators was found while tracking them and accidently. Four hundred and thirty samples of tiger scat were collected (of which 194 were found in the nonhibernation period for bears). The samples were washed and disassembled into separate components (undigested remnants): hair, claws, bones, etc. The species of the animals the fur of which were found in the scat were determined by their macro- and microstructure: shape, thickness, waviness, color, the pattern of the cuticle ornament, the structure of the core disk (Kisin et al., 1984; Rozhnov et al., 2011). When claws were found, the species of the bear eaten by the tiger was determined, whereas the species identification of bears by hair was difficult, as no differences in the macro- and microstructure of the hair of these two species could be identified (Mukhacheva et al., 2014). For this reason, when using this method in the analysis of the tiger's diet, the two species of bears were united.

To determine the importance of bears in the diet of the tiger, two methods were used. The first method involved the calculation of the proportion of bears of each species among the discovered tiger prey. The second method was based on analysis of the contents of the predator's excrement. To assess the diet of the tiger, the frequency of occurrence of prey species in the excrement of predators was determined, which was calculated by the formula $F_i = N_i \times 100/Nm$, where N_i is the sum of all excrement samples in which the remains are found belonging to a particular species (group of species) of prey, Nm is the sum of all encounters of remains of different species in the processed feces. The last method shows the relative frequency of consumption of prey species and takes into

account all the remains found in the predator's excrement, including those cases when one sample contained the remains of more than one species (Ackerman et al., 1984).

Thirty-two dens of the Asiatic black and 12 dens of brown radio-collared bears were examined. The den type and structure were evaluated in order to determine the protective properties of the winter shelters of bears during their hibernation from the threat of an attack by a tiger. The dens arranged in the hollows of trees with the entrance at the top and those located in niches between stones and in caves with an entrance the dimensions of which did not allow the tiger to enter the chamber (less than 40 cm in height or width) were considered safe.

On the routes with a total length of 170 km, which we covered in the tracks of predators, 641 marking trees were described, as well as the nature of the marks left on them by tigers and bears. All the trees directly adjacent to the tracks were inspected. The following marks were recorded on the trees: tiger urine marks, tiger and bear rubbed spots (identified by their fur), bites, tear marks, and trace marks of bears. The species of the bears that left the marks were not determined.

The previously published information on the relationship of bears and tigers in the Primorskii and Khabarovsk krais was analyzed; the survey material, card files, and Chronicle of Nature of the Sikhote-Alin Reserve in 1954–2015 were used.

RESULTS

Importance of Bears in the Diet of the Tiger

Analysis of data on tiger-eaten animals, the remains of which were discovered by us, showed that bears of both species make up 2.2% of all the animals; 1.2% of them are brown bears, and 1.0% are the Asiatic black bears (Table 1). In the nonhibernation period, these parameters were, respectively, 4.5, 2.4, and 2.1%. Of the nine brown bears that the tigers ate, one was an adult male (the tiger acted in the role of scavenger), one male at the age of 3–4 years (killed by a tiger), six adult females (five of them were prey of tigers), and one bear cub of indefinite sex in the second year of life (killed by a tiger). Of the eight Asiatic black bears that were all prey of tigers, two were adult males, one was an adult female, and five animals were of indeterminate sex (two young and three adults).

Eight times, bears were killed by adult male tigers (tigers killed brown bears five times and Asiatic black bears three times), once a brown bear was killed by a male tiger, the age of which was not determined, three times the bears were procured by adult female tigers (an adult female of the Asiatic black bear, an adult Asiatic black bear of indefinite sex, and a young Asiatic black bear of indefinite sex) and in three cases the sex and age of tigers that killed one brown bear and two Asiatic black bears were unknown. Five bears (three adult female brown bears, one brown bear in the second year of life, and one young Asiatic black bear) were killed by one tiger—an adult radio-collared resident male. An adult tigress ate an adult female brown bear shot by a poacher, and a young male tiger consumed an adult male brown bear killed by another brown bear.

The frequency of occurrence of bear remains in the excrement of tigers was 8.4% ($Nm = 454$). According to these calculations, bears were even more important (16.0%) in the diet of the tigers in the nonhibernation period ($Nm = 206$). In fall, tigers fed on bears more often than in summer and spring: the frequency of occurrence was 24.3 ($Nm = 70$), 16.1 ($Nm = 56$), and 8.6% ($Nm = 81$), respectively.

Obtaining and Eating of Bears by Tigers, Protective Properties of Dens

In four cases, when tigers attacked brown bears (in all cases they were adult female bears), we managed to establish the degree of confrontation of the predators. In two cases, signs of struggle were minor and the tigers quickly killed the female bear. In the other two cases, the struggle was longer and ended with the death of the bears. In July 1997, in the Zabolochennaya River basin, an adult tiger male attacked a female bear. As a result of the fight, soil was upturned and shrubs broken on a forest site of 10×2 m. The place was littered with a lot of patches of bear fur, but there was also tiger fur. The entire battleground with the blood-spattered earth and trees had a length of 30 m. In another case (August 12, 2001), after a pursuit, a tiger attacked an 8- to 10-year-old female bear weighing 150–200 kg on the slope. The animals grappled with each other and rolled down a few meters. On the site of the battle, ground was trampled measuring 10×8 m. After winning, the tiger retreated 15 m to the side to lie down and rest. It had a bleeding wound.

As for the mortality of young brown bears from tigers, we know about one case only. On June 18, 1996, a male tiger killed a bear cub in the second year of life on an animal path. The tiger was frightened off by people no later than an hour after the beginning of eating the prey. The entire time, a female bear and the second cub were sitting in a tree above the hunting spot.

In seven cases it was known how much time it took tigers to dispose of the soft tissues of bears by 90–100%. Twice adult male tigers fed on adult brown female bears for four days, and the adult male ate the brown bear (male) aged three to four years over seven days. Adult male tigers utilized the Asiatic black bears from two days to a week: two days for a bear of two years of age (sex unknown), five days for an adult male and six to eight days for an adult bear of indeterminate sex. The time of eating Asiatic black bears by adult female tigers was determined twice: three days for the adult female and five days for a bear at the age of

Table 1. Importance of bears in the diet of tigers in the Russian Far East

Region and observation period, sample size, source	Relative share in the diet, %			
	two bear species	brown bear	Asiatic black bear	bear species not determined
According to results of tiger's prey				
Sikhote-Alin, 1966–1971, $n = 98$ (Kucherenko, 1972)	6	–	–	6
Sikhote-Alin, 1970–1972, $n = 37$ (Yudakov, 1974)	5.4	–	–	5.4
Primorskii krai, 1958–1978, $n = 690$ (Abramov et al., 1978)	7.3	–	–	7.3
Lazovskii Reserve, 1973–1979, $n = 133$ (Zhivotchenko, 1981)	1.5	0	1.5	0
Khabarovsk and Primorskii krai, the years are not indicated, $n = 131$ (Kucherenko, 1985)	6	–	–	6
Sikhote-Alin Reserve, 1962–1989, $n = 292$ (Smirnov, 1991)	2.4	–	–	2.4
Ussuriiskii Reserve, 1974–1991, $n = 97$ (Poddubnaya and Kovalev, 1993)	6.2	0	6.2	0
Bol'shekhekhtsirskii Reserve, 1992–2000, $n = 11$ (Tkachenko, 2012)	18.2	0	18.2	0
Bol'shekhekhtsirskii Reserve, 2000–2007, $n = 35$ (Tkachenko, 2012)	0	0	0	0
Sikhote-Alin Reserve and environs, 1992–2013, $n = 763$ (present report)	2.2	1.2	1	0
According to the results of analysis of tiger excrement				
Lazovskii Reserve, 1973–1979, $n = 203$ (Zhivotchenko, 1981)	1.5	0	1.5	0
Lazovskii Reserve, 1980–1990, $n = 30$ (Khramtsov, 1993)	16.7	0	16.7	0
Sikhote-Alin Reserve, 1962–1989, $n = 373$ (Smirnov, 1991)	6.4	–	–	6.4
Bol'shekhekhtsirskii Reserve, 1992–2000, $n = 91$ (Tkachenko, 2012)	31.2	5.4	21.5	4.3
Lazovskii Reserve, 2001–2006, $n = 483$ (Kerley et al., 2015)	7.1	–	–	7.1
Bol'shekhekhtsirskii Reserve, 2000–2007, $n = 59$ (Tkachenko, 2012)	1.7	0	0	1.7
Ussuriiskii Reserve, 2008–2009, $n = 90$ (Chistopolova et al., 2010)	5	–	–	5
South-West of Primorskii krai, 2008—2012, $n = 152$ (Kerley et al., 2015)	4.2	–	–	4.2
Sikhote-Alin Reserve and environs, 1992–2013, $n = 430$ (present report)	8.4	–	–	8.4

A dash indicates the absence of data.

Table 2. Nature of the relationship between bears and tigers on tiger prey in the Sikhote-Alin Reserve and its environs for the years 1992–2013

Species of bear	Ate the prey after the tiger left		Took the prey away from the tiger		Shared the prey with the tiger		Nature of relationship not known	
	n	%	*n*	%	*n*	%	*n*	%
Both species	37	57.8	11	17.2	7	10.9	9	14.1
Brown bear	15	41.7	9	25	6	16.7	6	16.7
Asiatic black bear	8	88.9	1	11.1	0	0	0	0
Species not determined	14	73.7	1	5.3	1	5.3	3	15.8

n is the number of cases of one the types of relationships between bears and the tigers on the tiger prey, % is the proportion of cases of this type of relationship of all the cases.

2 years (sex unknown). In another case, an adult tiger (sex unknown) was frightened off from the prey on the fifth day; by this time it had eaten 70% of the brown bear's meat, which weighed 150–200 kg.

All 12 of the dens of brown bears surveyed by us were potentially accessible to the tiger. Of the 32 dens of radiocollared Asiatic black bears, 56% were inaccessible to tigers. These dens included hollows in trees with a high entrance (15 dens) or having the entrance in the butt end part, but continuing into the upper part of the tree (one den), as well as niches in stones with narrow entrances (one) or narrow long burrows (one). The other 14 dens (44%) were potentially accessible to tigers. Among them, there were dens in the form of a ground nest (six dens), dens arranged in the butt end part of trees with an entrance from below (five dens), in niches between stones or in a rock (two), and in the old den of a brown bear (one).

None of the bears hibernating in the described dens was killed by a tiger. But on December 5, 1998, a tiger killed a male Asiatic black bear near its den. It appears that during the attack the bear was not fast asleep and temporarily came out of its den. The bear tried to escape by climbing a poplar, but the tiger jumped up after the bear and pulled it down.

In May 2002, in the Sikhote-Alin Reserve, we observed a case when a tiger discovered the den of a female Asiatic black bear, which was inside with newborn cubs (Seryodkin et al., 2003). It was located in a niche under a large stone on the edge of a placer. The entrance with a height of 35 cm and a width of 41 cm was blocked by stones. The tiger could not penetrate into the den due to the size of its body, so it lay down at the entrance and spent no fewer than 24 hours there.

Visiting of Tiger's Prey by Bears

Traces of the bears' stay at the prey obtained by tigers were found 64 times, which is 17.3% of all the surveyed prey during the nonhibernation period. The real share of tiger prey visited by bears is higher, as we were not able to trace all the prey before their full utilization by saprophages. Brown bears visited tiger victims more often than the Asiatic black bears (36 and 9 times, respectively); in 19 cases the bear species was not determined.

The earliest date of detection of the traces of a bear's stay at a tiger's prey was March 17 (the species of the bear was not determined). For the brown bear, this date is determined as March 25, and for the Asiatic black bear, April 30. In early April 2001, having passed in the tracks of three males of brown bears over 21 km, we found three tiger prey, dug up and eaten by bears over several days before our discovery. All three red deer (*Cervus elaphus*) were killed by tigers in the winter. The latest date of the tiger prey being visited by the brown bear is November 16. In fall, the share of visits of bears of both species was lower (6%) than in spring (18.6%) and in summer (25.4%).

Among the tiger prey that we found, there were 46 red deer, nine wild boars (*Sus scrofa*), four sika deer (*Cervus nippon*), four roe deer (*Capreolus pygargus*), and one moose (*Alces alces*).

Bears visited tiger prey both after the owner left and while the tiger was still by the prey. In a number of cases, it was known how much time had elapsed between the killing of the prey by the tiger and its detection by the bear. In 17 cases, bears were at the prey no later than a day after the tigers procured them; in 25 more cases, within five days. Bears found winter tiger prey under the snow six times in the spring.

In terms of the way in which the prey of the tiger was obtained by a bear, the most typical was the situation when the bears fed on the remnants of the tiger prey after it had already left (Table 2).

In at least 11 cases, bears drove tigers away, finding them at the prey (Table 2). Of them, in eight cases, the brown bears took the prey away from adult tigresses (five radiocollared individuals). In one case, the brown bear took the prey away from a tiger the sex of which was unknown. In one more case, an Asiatic black bear took the prey away from a tigress with cubs. In the latter case, at the end of April, on the day when the red deer was killed by the tiger, a bear roar could be heard repeatedly from the place where the prey lay. The next day, when the researchers approached the

deer, the Asiatic black bear was feeding on its remains and the tigress was far from its prey (established by radio tracking). The prey still had 65% of the meat. The tigers did not return to the prey, while the Asiatic black bear did and was caught. It was an 8- to 10-year-old male in physiologically good condition.

Seven cases were registered when the prey of a tiger had traces of simultaneous or alternating presence of the tiger and the bear (Table 2); in some cases, this was established by means of telemetry. This sharing of the prey was observed five times between brown bears and adult female tigers (four radiocollared individuals), once between a brown bear and an adult male tiger, and once between a bear of an unknown species and an adult tigress.

In at least 11 cases, bears threw forest litter, earth, and branches onto the tiger prey or the remnants. In five of these cases, the bears heaped the litter on the prey that they had just taken away from the tigers; in two cases, after the prey was left by the owner; and in the rest of the cases, the nature of the relationship was not known.

Both brown and Asiatic black bears in some cases dragged the prey away from the place where it was eaten by the tiger. The length of the trails reached 300 m. In some cases, it was not possible to detect large parts of the body of the prey, which may be a consequence of their being dragged by bears over considerable distances. In one case, a tigress, after killing a red deer, went into the den to her cubs, and when she returned, she discovered that her prey had been visited by a brown bear. She dragged the prey 200 meters and crossed the road. Another time, a tiger dragged a red deer 90 meters after the place was visited by an Asiatic black bear and people. After the tiger left the prey, the bears did not always carry away the remains, but often used the same feeding and resting places as the tiger.

The Staying of Tigers and Bears on Carcasses That Are Not Tiger Prey

In the Sikhote-Alin Reserve in the spring of 2001, a malnourished radiocollared male tiger found and ate a brown bear, killed by another brown bear.

Both tigers and bears can stay at the carcass of an animal that is not a prey of any of them. In October 1999, in the Terneiskii district of Primorskii krai, a brown bear found a red deer killed by poachers and covered it with some earth. After this, a tiger fed on the carcass.

Joint Use of Marking Trees by Tigers and Bears

On the routes along which we traveled in the Sikhote-Alin Reserve, marking of trees with traces of marking by both tigers and bears prevailed (50.1%; n = 641). Over a five-kilometer stretch of the animal path along the Khanov Spring, out of 65 marked trees, 42 bore such double marks (64.6%), the remaining 35.4% of the trees had only tiger or only bear marks. Over 2 km of the path along the Kunaleika River, 2/3 of the marking trees were joint ones.

More often than other types of trees, traces of joint marking by tigers and bears could be found on Dahurian larch (*Larix dahurica*) (n = 83), Khingan fir (*Abies nephrolepis*) (n = 75), Siberian silver birch (*Betula platyphylla*) (n = 67), Yezo spruce (*Picea ajanensis*) (n = 40), Korean birch (*B. costata*) (n = 19), and Korean pine (*Pinus koraiensis*) (n = 13). Some trees of these species were used by predators especially frequently and intensely. Such marking trees usually had the whole complex of marks left by tigers and bears on trees.

The Asiatic black bear that we tracked in March approached a tilted birch tree, which had the mark of tiger urine. The bear sat under the tree, studying the mark. It did not mark this tree, although shortly before, it had rubbed against a marking tree without a tiger mark but freshly rubbed by a brown bear.

DISCUSSION

The Importance of Bears in the Diet of Tigers

In the diet of the Amur tigers, bears play a significant role, though not the primary one (Table 1). In the study area, only ungulates are more important than bears: red deer, wild boar, and roe deer (Miquelle et al., 2005; Seryodkin et al., 2012; Mukhacheva et al., 2014). Among the brown bears killed by tigers and found by us, there was only one three- or four-year-old male; the rest were females and a bear cub. The sex of the Asiatic black bears obtained by the tiger, apparently, did not matter for the latter. The presence of bear cubs, probably, makes females more accessible for tigers, because, in protecting their offspring, females are exposed to increased danger.

Some tigers appear to be more likely to kill bears than others; however, only adult males are able to confront a bear. From published sources, only two cases are known when brown bears were obtained by female tigers (Kaplanov, 1948; Bromley, 1965).

Tigers are more likely to eat bears in the fall, probably because it is easier to find the bear, sneak up, and kill it when it is feeding noisily and enthusiastically on fattening feed (Mongolian oak acorns and Korean pine nuts) on the dry forest litter.

Both methods used by us, showing the importance of bears in the diet of the tiger, give a relative estimate, so they need to be compared carefully. The method based on the analysis of the tiger prey, apparently, underestimates the share of bears in the diet of the tiger. Since bears are larger than other prey, then their absolute share in the diet should be higher than their percentage in the total number of animals eaten by the tiger. As can be seen from other studies (Table 1), the presence of bears in the diet of the tiger varies widely

depending on the local conditions and methods of assessment used and, in some cases, can reach 31.2% (Tkachenko, 2012). Even in the same territory, the share of bears in the tiger diet can change significantly from year to year (Poddubnaya and Kovalev, 1993; Tkachenko, 2012).

An opinion exists that the share of bears in the tiger diet increases during a decline in the number of its main prey—ungulates (Bromley, 1965; Rukovskii, 1968; Khramtsov and Zhivotchenko, 1983). According to Kucherenko (1977), the Amur tiger procures, on average, three bears of two species per year and extracts around 3–4% of the populations of the fall livestock of bears. He notes that the weight fraction of bears in the composition of feeds of the tiger reaches 12% and is higher than the frequency of their occurrence, as the average bear is superior in weight to other prey. Similar calculations are given by Smirnov (1991), in whose studies the weight index of the occurrence of bear remains is 1.7 times higher than the quantitative one. Within its range in the Far East, the tiger is the main natural enemy of bears. According to Yudin (1993a), tigers are not the leading factor limiting the number of bears, but they can affect bear populations when they are in a critical condition. The killing of bears by tigers is, probably, beneficial to the populations of the latter, as it eliminates the weakest individuals (Kostoglod, 1977).

In different parts of the range, tigers can attack bears of other species. Thus, on the Malay Peninsula, the tiger's diet includes the Malayan sun bear (*Helarctos malayanus*) (Kawanishi and Sunquist, 2004), and in India, the sloth bear (*Melursus ursinus*) (Biswas and Sankar, 2002; Reddy et al., 2004; Ramesh et al., 2009).

Obtaining and Eating of Bears by Tigers, Protective Properties of Dens

One way for tigers to hunt bears is to kill them during the hibernation period in winter dens. In this way, tigers killed both brown bears (Kaplanov, 1948; Bromley, 1965) and Asiatic black bears (Gorokhov, 1973; Khramtsov and Zhivotchenko, 1981; Yudakov and Nikolayev, 1987; Seryodkin et al., 2003). Bromley (1965) points out that in 1952–1959, 15 cases of attacks by tigers on bears hibernating in dens on the slopes of the Middle Sikhote-Alin were registered, mainly in the early spring and late fall. In the vast majority, it was brown bears. The author notes that the tiger does not always manage to kill the brown bear. The largest bears escape from the claws of the predator and, being expelled from the den, become insomniac bears.

Upon finding a sleeping bear, tigers do not always dare to attack them. In the Pogranichnyi district, the following incident was observed: the tiger (female) retreated, not trying to hunt, from the den of a large brown male bear. The tiger, seeing the sleeping bear in a den of the open type at a distance of 25 m, turned sharply and left, stepping in its own tracks (Yudakov and Nikolaev, 1987).

The dens of the ground type preferred by the Sikhote-Alin brown bears (Bromley, 1965; Yudin, 1993; Seryodkin et al., 2003) are accessible to tigers, but they are usually located on steep slopes, at an altitude of 775 m above sea level (Seryodkin et al., 2003) with relatively high snow cover in places where the presence of tigers in winter is unlikely. Apparently, the location of the den in hard-to-reach places is the main protective mechanism that protects the brown bear from their main enemies in winter: the tiger and man.

The Asiatic black bears, which settle down in tree hollows for the winter, are inaccessible to tigers, if the entrance to the den is not located in the butt end part. But a part of the bears (22% in the Sikhote-Alin Reserve) prefers to winter openly in a small hollow (Seryodkin et al., 2003). Such dens are completely unprotected from tigers and other enemies of the Asiatic black bear. The wintering of Asiatic black bears on the ground must negatively impact the reproductive capabilities of the population, increasing the accessibility of bears to predators, as predators primarily find females with cubs (Abramov, 1972). In the southern regions of Primorskii krai, as well as in places where the defective trees suitable for the hibernation of animals are damaged as a result of felling, forest fires, and in the process of extracting bears from them, the share of ground dens is higher (Abramov, 1972; Abramov and Pikunov, 1976; Yudin, 1993a). Their protective properties, including those from the threat of an attack by a tiger, are much lower. Cases are known of tigers hunting Asiatic black bears in ground dens, which were placed under uprooted trees at the butt end side (Yudakov and Nikolaev, 1987) and in root hollows (Gorokhov, 1973). Khramtsov and Zhivotchenko (1981) report that Asiatic black bears wintering in rocky dens are easily accessible to tigers. In dens located in crevices of rocks or niches between stones, the protective properties depend on the size of the entrance to the den or the presence of additional narrow chambers inside. The small size of the entrance and burrows do not allow the tiger to reach the bear.

Tigers kill most of the bears during their waking period. With the larger and stronger, in contrast to Asiatic black, brown bears, tigers often come into confrontation and they do not always manage to overcome the brown bears. Kostoglod (1981) described a case of an unsuccessful hunting attempt of a tigress with two grown cubs. Gorokhov (1973) reported about two more fights of tigers with brown bears, in which there were no winners.

The brown bear is capable of not only showing resistance to the tiger that attacked it, but also of emerging victorious out of the fight. Of the 45 cases of encounters of tigers with brown bears (Kaplanov, 1948; Sysoev, 1950, 1960; Abramov, 1962; Bromley,

1965; Rakov, 1970; Kucherenko, 1972; Gorokhov, 1973; Kostoglod, 1981; Khramtsov, 1993; our data), the tiger was the initiator in 13 cases, the bear started eight fights, and in the other cases, the attacker was not established. In 51.1% of cases, the fights ended with the death of the bear, in 26.7% with the death of the tiger, and in 22.2% the animals broke up.

The Asiatic black bears, compared with the brown bears, show less resistance during the tiger attacks (Gorokhov, 1973). However, Sysoev (1960) reports about the long struggle of these two predators. The tiger hunts the Asiatic black bears furtively, attacking at random encounters (Gorokhov, 1973). The hunting is usually more successful in small forests, glades, and other places, devoid of large trees, on which the bears often finds salvation (Kucherenko, 1974), as well as when the tiger approaches closely enough so that the bear does not have time to climb a tree. Young bears frequently become the prey of the tiger (Khramtsov, 1993). Eight cases are known when Asiatic black bears tried to escape a tiger in a tree (Bromley, 1965; Gorokhov, 1973; Kucherenko, 1974; Khramtsov, 1983, 1993; Seryodkin et al., 2003). In six cases, they succeeded. In each case, the tiger lay under the tree (for up to two days), guarding the potential prey, with the bear waiting all this time up in the tree. One of the bears, escaping from the claws of a tigress with tattered skin, did not venture to come down for three days after the predator had already left. Two times tigers had time to pull the bears off the trees; both times they broke away and were again stopped on the tree, after which they were killed.

There are cases when tigers stayed with killed bears for 8–10 days (Kaplanov, 1948; Rakov, 1965). After a complete disposal of the bear by the tiger, only the head and the gnawed bones remain. In the excrement of tigers that have eaten bears, their claws and phalanxes often occur (Khramtsov, 1993; our observations). In some cases, the satiated animal eats only the fattiest parts of the body, leaving the greater part of the carcass untouched (Bromley, 1965; Gorokhov, 1973). A case is known in which a tiger, having consumed a female brown bear completely, did not eat its two cubs, which it had previously killed (Kaplanov, 1948).

Visits of Tiger Prey by Bears

Both brown and Asiatic black bears visit the prey of tigers in order to eat it (Gorokhov, 1973; Matyushkin, 1974; Kostoglod, 1981; Khramtsov and Zhivotchenko, 1981; Pikunov, 1991; Khramtsov, 1997). In visiting the prey of tigers, bears can perform the role of commensals, if they use food remnants after the departure of the owner, or that of spongers, if they eat tiger prey before the tigers voluntarily leave the remnants of the prey.

In terms of the way in which bears took hold of tiger prey, significant differences were revealed. Asiatic black bears mostly used the prey after the tigers have left, where brown bears took the prey away from tigers or shared it with them (Table 2). This is, apparently, due to the fact that the Asiatic black bear avoids the tiger to a greater degree than the brown bear.

Tiger prey can be visited by bears during their waking time in all seasons. Pikunov (1991) reports of the fact of a visit by an Asiatic black bear to tiger prey on March 21, immediately after leaving the den. The lower percentage of visits in the fall compared with spring and summer is possibly due to the presence of high-calorie food of plant origin in the fall, which have a fattening value for bears.

In spring, bears have the opportunity to find tiger prey, following in the footsteps the predator left on the snow, so the likelihood of a visit increases. In addition, over the winter, the number of tiger prey accumulate, not having been eaten completely by predators and scavengers that do not hibernate in winter. Bears have access to these stocks of food only after leaving the den. In the spring of 1984, in the Abrek tract of the Sikhote-Alin Reserve, O.Yu. Zaumyslova (personal communication) found two boars eaten by the Asiatic black bear. These animals were killed, but not eaten by a tiger in February. Such spring activity of bears is described for the Mologo-Sheksninskii interfluve by Vishnevskii (1991). The probability of finding prey in summer increases due to the higher temperatures at this time of year. The warmer it is, the greater the distance at which the animals sense the source of the smell (Korytin, 1998).

Bears can visit tiger prey in the winter season as well. This is due to the fact that some individuals of both brown and Asiatic black bears (mainly, males) can sleep in the den in December or January, and wake up in February. Some bears do not lie in the den and lead an active lifestyle throughout the winter. Of the six food remains discovered by Kostoglod during the winter tracking (1981) of an insomniac brown bear in Sikhote-Alin, three were the remains of the prey of tigers.

The species of the prey, apparently, does not matter to the bear, as they ate all the animals found. Bears eat prey almost entirely, including the large bones that tigers do not eat. Tigers often leave the skeleton, skin, head, and meat on the lower parts of the limbs and neck. Bears leave partially gnawed bones of the extremities, the upper and lower jaws, and part of the vertebrae; sometimes they leave the pelvic bones, scapula, and ribs. With a shortage of feed, especially in early spring, bears utilize the carcass more fully. Insomniac bears eat animals completely, including all the bones (Kostoglod, 1976). The duration of the stay of a bear on a tiger victim depends on the extent of its use by the tiger.

Of the 55 cases in which we knew how the tiger prey got to the bear, in 18 cases the tigers did not fully use the carcass themselves: the bears took the victim or

shared it with the tiger. Such relations should lead to an increase in the number of prey obtained by tigers. In the areas with a low density of ungulates, this circumstance can be reflected on tigers more sharply. In the known cases, the prey was relinquished to the bear by female tigers, the lack of food for which can adversely affect the reproductive capacity, as well as the survival of young animals.

Particular attention should be paid to the simultaneous presence of bears and tigers on the prey of the latter. The mechanism of such relations is built on the principles of physical "equanimity": on the equality of physical possibilities (Yudin, 2008). The fact of such a relationship was established in Belarus between the brown bear and the wolf, when both predators one by one went to feed on the corpse of a drowned moose during the night (Lavov, 1993). The tolerant attitude of bears and wolves to each other during their simultaneous presence at dead animals was also noted in Alaska (Murie, 1944; Lent, 1964).

Collisions of bears with tigers at prey sites occur when the tiger protects its prey at the approach of a bear or when a tiger, returning to the remnants of its prey, finds the bear (Gorokhov, 1973; Kostoglod, 1976; Khramtsov and Zhivotchenko, 1981). The outcome of such collisions varies.

The burying of tiger-killed animals is characteristic of the brown bears of Sikhote-Alin (Matyushkin, 1974; Seryodkin, 2011). Apparently, this act provides, first of all, the preservation of the prey from other predators and scavengers (Pazhetnov, 1990). In addition, this promotes a faster course of enzymatic processes (Korytin, 1998).

Dragging of the prey by animals can also be considered as a manifestation of concern for its preservation (Pazhetnov, 1990); the same behavior is shown by predators when they find prey from other animal.

Occasions when several bears (for example, brown bear females with this year's broods) fed on tiger preys are known. We noted one such case. Another example is known from the publication of Gorokhov (1973); Matyushkin (1974) described the case when a Far Eastern red deer corpse gained by a tiger attracted three bears all at once: two Asiatic black bears and one brown bear.

Feeding of Tigers on Bear Prey

Apart from bears feeding on tiger preys, the reverse is also possible. In October 1959, a bear killed an adult tigress in the basin of the Ussuri River, attacking it at the moment when it was eating a wild boar killed by that bear (Rakov, 1965). The feeding of tigers on carcasses of animals that are not their own prey is presumably caused by a lack of a sufficient number of potential prey or the poor physiological condition of the predator. The latter is confirmed by the fact of a tiger in poor condition eating a brown bear carcass killed by another brown bear.

Tigers as a Feeding Object of Bears

There were no cases of an Asiatic black bear eating a tiger. Nevertheless, it is not excluded that bears can feed on the remains of dead tigers.

Brown bears sometimes attack tigers. There were 12 cases of brown bears killing tigers (Sysoev, 1950, 1960; Abramov, 1962; Rakov, 1970; Gorokhov, 1973; Kostoglod, 1981). Six dead tigers were adults, four were cubs, and in two cases the authors did not specify the age. All the tigers were eaten by bears. In years with poor fattening feed, bears become aggressive. In some cases, brown bears can pursue tigers for a long time with success (Kostoglod, 1981).

At a total relatively low number of tigers, the death of some individuals can significantly affect the state of the population. Such fights, however, are more likely to lead to the death of weakened individuals, including traumatized and old animals; therefore, the brown bear will help to eliminate the tigers potentially dangerous to humans (Kostoglod, 1981). The predation of the brown bear is one of the reasons for the mortality of tiger cubs. Of the 14 deaths of tiger cubs detected by Gorokhov (1977) in 1951–1972, three were killed by a brown bear.

Brown bears can eat the tiger remains they found. This explains the brown bear excrement containing some tiger fur found in April 2001 in the basin of the Serebryanka River (Sikhote-Alin Reserve) (our data). In autumn 2009, the remains of an adult radiocollared tigress were found in the basin of the Kunaleika River (Sikhote-Alin Nature Reserve) eaten by a brown bear after her death, which was presumably not associated with predators.

Joint Use of Scent Mark Trees by Tigers and Bears

Amur tigers use trees as a means of intraspecific communication, applying olfactory (urinary spots, scratches) and visual (scuffs) marks (Matyushkin, 1987; Yudakov and Nikolaev, 1987; Yudin and Yudina, 2009; Protas et al., 2010). Bears that live in the range of the Amur tiger also leave marks on trees in the form of bites, scuffs, and scratches, while brown bears mark trees more often than Asiatic black bears (Seryodkin et al., 2014). The marks for tigers and bears can be the same trees usually located along the animal paths used by the animals. In this case, these trees serve not only as intraspecific means of information, but also as means of interspecific communication of animals.

Food Competition of Tigers and Bears

Bears are not competitors of tigers in predation (Seryodkin, 2010). Brown and Asiatic black bears feed mainly on plant feed, which is 78.4 and 94.1% of the

annual diet of each species, respectively (Seryodkin, 2015), while the tiger is a specialized predator. Some competition to the tiger can only be expected from the brown bear in spring, when its predatory activity increases, and the bear can hunt successfully, pursuing wild boars and Far Eastern red deer (Bromley, 1965; Yudin, 1993). Nevertheless, the food chain competition between predators is manifested in the fact that bears use the prey of tigers before the latter voluntarily leave the remnants of such prey.

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