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Hymenoptera in the diet of bears in the Russian Far East
Перепончатокрылые в питании медведей на Дальнем Востоке России

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Ключевые слова: бурый медведь, гималайский медведь, *Ursus arctos*, *Ursus thibetanus*, мирмекофагия, муравьи, Formicidae, Vespidae.

Abstract. Social Hymenoptera, primarily ants, are part of the diet of the brown bear (*Ursus arctos* Linnaeus, 1758) and the Asiatic black bear (*U. thibetanus* G. Cuvier, 1823) in various regions. This article presents the results of a study on the regional aspects of the species composition of insects consumed by bears and provides a quantitative assessment of this dietary component across different seasons. The mutual interactions between bears and insects, as well as bear behavior when obtaining Hymenoptera from various types of nests, are also partially addressed. In three regions of the Russian Far East, Sikhote-Alin, Sakhalin, and Kamchatka, bear excrements were collected from 1998 to 2023 to analyze their diet. Insects were extracted from bear excrements and the nests they destroyed to determine species composition. The damage to Hymenoptera nests caused by predators was described, and bear behavior when obtaining ants was observed. At least 29 species of Hymenoptera were observed in the diet of bears, with up to species identified: 19 species of ants, 4 species of wasps, 2 species of bumblebees and 1 species of bees. Among the ants, *Formica* spp. were the most significant (found in 30.5 % of excrements samples containing ants), followed by *Camponotus* spp. (26.0 %), *Lasius* spp. (24.4 %), and *Myrmica* spp. (19.1 %). The frequency of Hymenoptera occurrences in brown bear excrements throughout the active period was 2.6 % on Sakhalin and 13.7 % in Sikhote-Alin. For the Asiatic black bear in Sikhote-Alin, this figure was 21.4 %. The frequency of insect occurrences in bear excrements was highest during the summer. To obtain ants, bears use at least four different methods, depending on the type of ant nest. Most often, they destroy dome-shaped anthills. The influence of bears on Hymenoptera communities is discussed, as well as the role of insects in the diet and life of bears.

Резюме. Общественные перепончатокрылые, в большей степени муравьи, входят в пищевые рационы бурого (*Ursus arctos* Linnaeus, 1758) и гималайского (*U. thibetanus* G. Cuvier, 1823) медведей в разных регионах. Представлены результаты исследования региональных особенностей видового состава поедаемых медведями насекомых, а также количественной оценки данного компонента в их питании в разные сезоны. Частично освещены вопросы взаимного влияния медведей и насекомых, поведения медведей при добывании перепончатокрылых из разных типов гнёзд. В трёх регионах Дальнего Востока России: Сихотэ-Алинь, Сахалин и Камчатка, в 1998–2023 гг. производили сбор экскрементов медведей для анализа их питания, отбор насекомых из экскрементов медведей и разорённых ими гнёзд для определения видового состава; проводили описания повреждений хищниками гнёзд перепончатокрылых, а также наблюдения за поведением медведей при добывании муравьёв. В питании медведей отмечено по меньшей мере 29 видов перепончатокрылых, из которых достоверно определены 19 видов муравьёв, 4 — ос, 2 — шмелей и 1 вид пчёл. Среди муравьёв наибольшее значение имели *Formica* spp. (30,5 % образцов экскрементов с муравьями), в меньшей степени *Camponotus* spp. (26,0 %), *Lasius* spp. (24,4 %) и *Myrmica* spp. (19,1 %). Частота встреч перепончатокрылых в экскрементах бурого медведя за весь активный для них период составила: на Сахалине — 2,6 %, в Сихотэ-Алине — 13,7 %. Для гималайского медведя в Сихотэ-Алине этот показатель составил 21,4 %. В летний период частота встреч насекомых в экскрементах медведей была наибольшей. Для добывания муравьёв медведи используют как минимум четыре способа, которые зависят от типа гнезда. Наиболее часто медведи разрушают купольные муравейники. Обсуждается влияние медведей на сообщества перепончатокрылых, а также роль насекомых в питании и жизни медведей.

Introduction

The brown bear (*Ursus arctos* Linnaeus, 1758) and the Asiatic black bear (*U. thibetanus* G. Cuvier, 1823) inhabiting the Russian Far East are omnivores that play a significant role in the region's ecosystems. Their diets consist predominantly of plant matter and salmon, which they catch along the Pacific coast [Bromley, 1965; Bears…, 1993; Seryodkin, 2017].

Social Hymenoptera, particularly ants, are a common component of the diet of bears both in the Russian Far East [Bromley, 1965; Seryodkin, 2015, 2016] and in other regions [Onoyama, 1988; Reid et al., 1991; Craighead et al., 1995; Swenson et al., 1999; Hwang et al., 2002]. The species composition of Hymenoptera

consumed by bears and their proportional contribution to the diet varies significantly depending on the region [Loskutov, Radchenko, 1991; Noyce et al., 1997; Große, 2003; Yamazaki et al., 2012]. For example, in Sweden, ants comprise only 4–12 % of the total excrements volume [Swenson et al., 1999], whereas in Minnesota, ants account for up to 58 % of the dry mass of bear scat in early July [Noyce et al., 1997].

In Sikhote-Alin, Asiatic black bears are found at the northern limit of their range and, unlike their conspecifics in more southern regions, experience a lower diversity of food resources and are impacted by a relatively cold climate, resulting in a prolonged hibernation period [Kozakai et al., 2021]. How these limiting environmental factors influence the inclusion of Hymenoptera in the diet of Asiatic black bears remains unknown. Furthermore, the role of Hymenoptera in the diet of bears in areas where both species, brown and Asiatic black bears, coexist, and where food competition is likely, has been scarcely studied. It is essential to investigate how the proportion of Hymenoptera in the diet varies depending on the availability and accessibility of other food resources.

In predator-prey systems, mechanisms are required to ensure the sustainability of prey populations. In some cases, insects are known to defend themselves from bears and to rebuild their nests after destruction by predators [Rukovsky, 1987; Bears…, 1993; Swenson et al., 1999; Mordosov, 2006; Zakharov, Zakharov, 2019]. However, the adaptive behaviors of insects under predatory pressure remain poorly understood.

In addition to destroying dome-shaped anthills, bears employ several other methods to access Hymenoptera, including digging up underground nests, gnawing wood, and overturning stones and deadwood [Fujiwara et al., 2013; Seryodkin, 2016].

Comprehensive data on the importance of different types of food, including Hymenoptera, in the diet of bears is important for understanding the conditions necessary for their existence, primarily in terms of food supply. This knowledge can be used for the rational use of bear resources by humans, as well as for preserving the integrity of regional ecosystems and their biodiversity.

The aim of this study is to investigate the role of Hymenoptera in the diet of brown and Asiatic black bears in the Russian Far East. The objectives are to: (1) determine the species composition of Hymenoptera consumed by bears; (2) conduct a quantitative assessment of this dietary component across different seasons; (3) identify the methods employed by bears to obtain insects; and (4) describe the nature of the damage caused to Hymenoptera nests by predators.

Materials and methods

Study area

The study was conducted in three regions of the Russian Far East: Sikhote-Alin (Terneisky, Krasnoarmeysky, Dalnegorsky and Pozharsky districts of Primorsky Krai), Sakhalin (Smirnykhovsky district of Sakhalin Oblast) and Kamchatka (Yelizovsky district of Kamchatskii Krai).

Collection and processing of bear excrements

In Sikhote-Alin, within the Sikhote-Alin State Nature Reserve and its surrounding areas, 482 samples of brown bear excrements and 453 samples of Asiatic black bear excrements were collected between 1999 and 2019. Bear species were identified based on their tracks, which have species-specific characteristics [Pikunov et al., 2004], and through tracking data from animals fitted with radio collars. On Sakhalin, 3,932 samples of brown bear excrements were collected from 2009 to 2013 in the Vostochny Nature Reserve (Table 1).

The excrements samples were collected and thoroughly washed, after which individual components — remains of plants and animals from various species or groups — were separated. Hymenoptera were identified as individual components during the analysis of excrements, including ants (Formicidae), folded-wing wasps (Vespidae), and bumblebees (*Bombus* spp.). A total of 714 components were distinguished in brown bear excrements, 608 in Asiatic black bear excrements from Sikhote-Alin, and 5247 components in brown bear excrements from Sakhalin (Table 1).

Calculation of the frequency of Hymenoptera occurrences in bear excrements

The role of Hymenoptera in the bear diet was assessed by calculating the frequency of occurrence in excrements samples, defined as the proportion of samples containing Hymenoptera remains out of the total number of samples. While this method does not account for the mass or volume fraction of the food components,

Table 1. Characteristics of excrements samples of brown and Asiatic black bears collected in the Russian Far East
Таблица 1. Характеристики выборок образцов экскрементов бурого и гималайского медведей

Region of study (years of collection)	Bear species	Number of samples of excrements (total occurrences of components in excrements)			
		Spring	Summer	Autumn	Total
Sikhote-Alin (1999–2019)	Brown	66 (109)	179 (330)	237 (275)	482 (714)
	Asiatic black	55 (79)	118 (236)	280 (293)	453 (608)
Sakhalin (2009–2013)	Brown	43 (57)	3076 (3958)	813 (1232)	3932 (5247)

it is widely used in zoological studies [Ackerman et al., 1984; Sato et al., 2005; Klare et al., 2011; Seryodkin, Burkovskiy, 2019] as it provides a clear, though not absolute, understanding of the role of individual food components and seasonal variations in diet.

Because the number of samples collected varied by month, the occurrence of Hymenoptera in fecal samples for each season and for the entire active (non-hibernation) period was calculated as the average frequency for each month within the season or period. Based on the hibernation and den-emergence patterns of bears in the studied regions [Seryodkin et al., 2003], the active period was defined as April to November for Sikhote-Alin and May to October for Sakhalin. Differences in the frequency of Hymenoptera occurrences between the excrements of Asiatic black and brown bears in Sikhote-Alin, as well as between brown bears from Sikhote-Alin and Sakhalin, were tested using Pearson's chi-squared test (χ^2). Differences in occurrence frequencies between different taxonomic groups of Hymenoptera were not assessed, as the study's primary focus was the overall contribution of Hymenoptera to the bears' diet.

Description of Hymenoptera nests destroyed by bears

Between 1998 and 2023, 473 nests of social Hymenoptera destroyed by bears were recorded in the Middle Sikhote-Alin, Sakhalin (Vostochny Nature Reserve), and Kamchatka (Kronotsky State Nature Reserve). Of these, 312 involved the destruction of dome-shaped ant nests by bears, while in 78 cases, bears destroyed wood, in 56 cases, they overturned stones, and in 27 cases, they dug nests out of the soil.

Upon discovering destroyed nests, the location, nest type, nesting substrate, and the nature of damage caused by predators to the nest and surrounding environment were documented. Damage caused by bears when extracting nests from tree cavities was measured, and an unsuccessful attempt by wasps to restore a bear-destroyed nest was observed.

Species samples were taken from 36 Hymenoptera nests destroyed by bears for species identification.

Determination of insect species composition

Insects extracted from bear excrements and collected from destroyed nests were preserved in 95 % ethanol. The preservation of insects varied from nearly complete specimens to fragmented parts (e.g., heads, body segments, legs). Based on the degree of preservation, identification was performed at the genus (subgenus) or species level.

Taxonomic identification of Hymenoptera was based on literature [Kupyanskaya, 1990; Radchenko, 2005, 2016; Key to the Insects…, 2007; Radchenko, Elmes, 2010; Zakharov et al., 2013] and comparison with reference specimens from the collection of the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk. All collected materials are deposited at the institute.

Observations of bears foraging for ants

Behavioral observations of brown bears foraging for ants were conducted in the Kronotsky State Nature Reserve (2002–2004) and the Vostochny Nature Reserve (2010). Bears' behavior at 25 ant nests was observed for a total of 160 minutes.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:BABAB53A-1E59-4E55-A2F0-4AB74C701275.

Results

Taxonomic composition of Hymenoptera consumed by bears

At least 29 species of Hymenoptera were identified in the diets of the two bear species studied. These included 19 species of ants (Supplementary, Table S1) from two subfamilies (Myrmicinae, Formicinae), four species of folded-wing wasps from the subfamily Vespinae, and three species from the bee family (Apidae), including two bumblebee species and one bee species. Some samples, however, were identified only to the genus level (wasps, bumblebees) or to both the genus and subgenus (ants).

Ants. The greatest diversity of ants in the bears' diet was found in Sikhote-Alin, with 20 species from four genera and two subfamilies. On Sakhalin, 9 species from three genera and 2 subfamilies were recorded, while Kamchatka had 3 species from two genera and two subfamilies.

The genus *Formica* Linnaeus, 1758 exhibited the highest species diversity (8 species in Sikhote-Alin, 5 species in Sakhalin, and 2 species in Kamchatka) and the greatest number of encounters in excrements and nests destroyed by bears (Supplementary, Table S1). Ants from this genus were found in 30.5 % of excrements samples containing ants. Representatives of two *Formica* Linnaeus, 1758 species (*F. lugubris* Zetterstedt, 1840 and *F. lemani* Bondroit, 1917) were consumed by brown bears across all three regions. In Sikhote-Alin, they were also consumed by Asiatic black bears (Supplementary, Table S1). The genus *Myrmica* Latreille, 1804 was represented by 6 species in Sikhote-Alin, 2 in Sakhalin, and one in Kamchatka. However, their occurrence in the diet was low, making up only 19.1 % of ant-containing excrements samples. Ants of the genus *Lasius* Fabricius, 1804 were recorded in the diets of both brown and Asiatic black bears only in Sikhote-Alin (4 species). Bears in Sikhote-Alin and Sakhalin consumed two species from the genus *Camponotus* Mayr, 1861, but these species occurred frequently in their diet (Supplementary, Table S1).

Wasps. Among the 11 specimens of wasps, 8 were obtained from destroyed nests and 3 from bear excrements. All were classified under the genus *Vespula* Thomson, 1869. In three cases (two from Sikhote-Alin and one from Sakhalin), the wasps were identified as *V. vulgaris* (Linnaeus, 1758). Other species identified

Table 2. The role of Hymenoptera in the diets of brown and Asiatic black bears in the Russian Far East
Таблица 2. Значение перепончатокрылых в рационах бурого и гималайского медведей на Дальнем Востоке России

Bear species	Region	Frequency of encounters in excrements, %			
		Spring	Summer	Autumn	All active period
Brown	Sikhote-Alin	10.3	29.4	0.2	13.7
Brown	Sakhalin	0	5.3	0.2	2.7
Asiatic black	Sikhote-Alin	2.7	55.2	0	21.4

Notes. The total and seasonal numbers of excrements samples and component encounters in excrements (100 %) are provided in Table 1.
Примечание. Общее и посезонное количество образцов экскрементов и встреч компонентов в экскрементах (100 %) указано в таблице 1.

included *V. rufa* (Linnaeus, 1758), *V. flaviceps* (Smith, 1870), and *V. shidai* (Ishikawa, Sk. Yamane et Wagner, 1980), while the remaining 5 samples could not be identified to species. One nest destroyed by a bear belonged to the genus *Vespa*. Except for one instance of *V. vulgaris* collected from brown bear feces on Sakhalin, all wasp samples were collected from Sikhote-Alin. The consumption of wasps by bears was observed once in Sikhote-Alin (a brown bear consuming *V. vulgaris*).

Bumblebees and bees. Two bumblebee nests destroyed by bears in Sikhote-Alin were attributed to *Bombus sporadicus* Nylander, 1848, and *Bombus hypnorum* (Linnaeus, 1758). An additional bumblebee from brown bear excrements in Sakhalin was identified only to the genus level (*Bombus* sp.). In Sikhote-Alin, the remains of 4 nests of the wax bee *Apis cerana* Fabricius, 1793 were found, destroyed by either brown or Asiatic black bears.

The role of Hymenoptera in the diet of bears

The diet of both brown and Asiatic black bears across the studied regions included Hymenoptera, represented by ants, wasps, and bumblebees. The frequency of their occurrence in fecal samples varied by season, ranging from 0 % to 55.2 % (Table 2). When considering the entire active (non-hibernation) period, the frequency of Hymenoptera encounters was significantly higher in Asiatic black bears compared to brown bears in Sikhote-Alin ($\chi^2 = 30.2$; $p < 0.01$). Among brown bears, the frequency was higher in Sikhote-Alin compared to Sakhalin ($\chi^2 = 11.7$; $p < 0.01$).

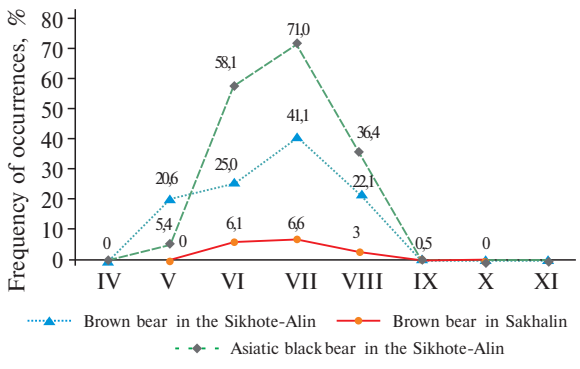

Fig. 1. The role of ants in the diets of brown and Asiatic black bears during the non-hibernation period in the Russian Far East.
Рис. 1. Значение муравьёв в рационах бурого и гималайского медведей во внеберложный период на Дальнем Востоке России.

Among Hymenoptera, ants played the most important role in the bears' diets, being recorded from May to September, with a peak in July (Fig. 1). Ants were less significant in the diet of brown bears on Sakhalin compared to the diets of both bear species in Sikhote-Alin (Fig. 1). The frequency of ant occurrences in Asiatic black bear excrements for the entire active period was 21.4 % (65 occurrences), while for brown bears it was 13.7 % (50 occurrences) in Sikhote-Alin and 2.6 % (170 occurrences) on Sakhalin. Wasps were detected in brown bear excrements once in August (Sikhote-Alin) and three times in September (Sakhalin). Bumblebees were found in samples once in July on Sakhalin.

Bears' foraging behavior for ants

Bears' behavior in searching for anthills during summer indirectly confirms that, over a short period (presumably one day), they consumed ants from multiple species. For instance, in Sikhote-Alin, a single excrements sample of Asiatic black bear in August contained remains of seven ant species from four genera, while a brown bear sample contained five species from three genera. On Sakhalin, one brown bear sample in July contained five species from two genera.

Methods used by bears to obtain ants

Based on activity traces and direct observations, bears employed the following methods to obtain ants: destruction of ant mounds, tearing apart the surface layer of soil, turning over stones, and destroying wood.

Destruction of ant mounds. In some forest and tundra areas along bear trails, up to 10 destroyed dome-shaped nests were noted within 50 m of the route. Minor damage did not cause ants (*Formica* spp., *Lasius* spp.) to abandon their nests, and they subsequently rebuilt the mound. In Kamchatka, brown bears were observed repeatedly moving between familiar anthills, partially raking the mound with their claws and licking the ants (*Formica* spp.) and their brood. Some anthills were subjected to this process multiple times in a single season. Damaged mounds of *F. lugubris* showed depressions up to 50 cm in diameter and 20 cm deep.

Tearing apart the soil surface layer. In mid-July 2002, in the berry tundra of the Kronotskaya river basin (Kamchatka), a female bear with two cubs was observed obtaining *F. lemani* ants. The bears sniffed out the insects' locations, then used their claws to lift a thin layer of soil, turning it over to consume the ants and their brood.

Turning over stones. Bears were observed turning over stones to access ants with nests located underneath. Anthills of this type are characteristic of *Camponotus saxatilis* Ruzsky, 1895 in the Far East region [Kupyanskaya, 1990]. These stones were frequently found on open rocky slopes and ridges.

Destruction of wood. Decaying tree trunks and stumps, often found in old burn areas (Fig. 2), were frequently destroyed by bears to access ants (*C. herculeanus* Linnaeus, 1758), which nest in wood. On Sakhalin, a brown bear was observed destroying a dry windfall tree with its claws and teeth to extract ants.

In Sikhote-Alin, a dry, still-standing Korean pine (*Pinus koraiensis* Siebold & Zucc., 1842) with a diameter of 52 cm was found in September 2000, where a bear had gnawed the wood from the base of the trunk up to a height of 120 cm, with the damaged area being 20 cm wide. By doing so, the bear accessed a cavity containing the nest of *Formica truncorum* Fabricius, 1804. In 2010, another dry Korean pine was found in Sikhote-Alin, where a bear had gnawed a hole through the wood to extract a nest of *Lasius* (*Dendrolasius*) sp. ants from a cavity within the tree (Fig. 3).

Methods of obtaining wasps, bumblebees, and bees by bears

Bears extracted nests of wasps from the genus *Vespula*, depending on the nests' locations. Six nests found in Sikhote-Alin were underground, and the bears dug them out, with excavations reaching depths of up to 35 cm. The nests belonged to *Vespula shidai*, *V. rufa*, and *V. vulgaris* (one of each), while the remaining three nests were of unidentified *Vespula* species. One *V. vulgaris* nest was unsuccessfully rebuilt throughout September after being destroyed by a bear in August; only a small portion of the nest shell was reconstructed using a mixture of soil and materials from the old nest (Fig. 4). Additionally, one nest of *V. flaviceps* was found under a fallen tree, attached to it. The bear overturned the tree and extracted the larvae from the nest. Another *Vespula* sp. nest was located inside a larch tree, and the bear made a hole in the tree, measuring 13 cm wide and 40 cm long, to access the nest.

Two bumblebee nests (*Bombus sporadicus* and *B. hypnorum*) and four bee nests (*Apis cerana*) destroyed by bears were located in tree cavities. The bears chewed through the tree trunks to access the nests, with the thickness of the gnawed wood reaching up to 20 cm.

Fig. 2. Dry tree destroyed by a brown bear while foraging for *Camponotus herculeanus* ants.
Рис. 2. Сухое дерево, разрушенное бурым медведем при добывании муравьёв *Camponotus herculeanus*.

Fig. 3. Fir tree damaged by a bear while extracting ant nest of *Lasius* (*Dendrolasius*) sp.

Рис. 3. Пихта, повреждённая медведем при добывании гнезда муравьёв *Lasius* (*Dendrolasius*) sp.

Discussion

Taxonomic composition of Hymenoptera consumed by bears

The species diversity of ants consumed by bears in the Far East, represented by the genera *Formica*, *Myrmica*, *Lasius*, and *Camponotus* (Supplementary, Table S1), is consistent with observations from other regions. In the Southern Urals, 15 species of ants from the genera *Formica*, *Camponotus*, *Lasius*, *Tetramorium* Mayr, 1855, and *Myrmica* were recorded in the diet of brown bears [Loskutov, Radchenko, 1991]. In Slovenia, brown bears feed on at least 13 species of ants from the genera *Formica*, *Camponotus*, *Lasius*, and *Myrmica* [Große et al., 2003], and in the Central Forest Reserve (Tver Region), 12 species from the same genera were documented in their diet [Ogurtsov, Fedoseeva, 2018]. The predominance of *Formica* and *Camponotus* ants in the diet of bears is a common pattern across various parts of their range [Grenfell, Brody, 1983; Mattson et al., 1991; Swenson et al., 1999; Mordosov, 2006].

The greater number of ant species in the diet of bears from Sikhote-Alin compared to Sakhalin and Kamchatka can be attributed to the longer duration of studies in Sikhote-Alin and the higher species diversity of ants in this region [Annotated Catalog…, 2012].

The selection of particular Hymenoptera species by bears is influenced by the species composition in their habitat, as well as the abundance and accessibility of these insects. The diet of bears in Sikhote-Alin is dominated by ants that build large, conspicuous anthills, which contain substantial amounts of brood [Kupyanskaya, 1990; Berman et al., 2007; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013; Zakharov, 2015]. These large nests, housing colonies of more than 10,000 individuals, include ants from the genera *Formica* and *Lasius*. Two species of *Formica* found in the diet of bears in the Far East, *F. lugubris* and *F. aquilonia* Yarrow, 1955, can have colonies exceeding a million individuals [Kupyanskaya, 1990; Zakharov et al., 2013]. *Camponotus* ants, with medium-sized nests, often build their smaller, more concealed colonies under stones or in wood [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated Catalog…, 2012; Kupyanskaya, Shabalin, 2012].

In addition to wild bee nests (*Apis cerana*), both brown and Asiatic black bears in beekeeping regions of the Russian Far East actively visit apiaries to collect honey from the honey bee (*Apis mellifera* Linnaeus, 1758) [Bromley, 1965].

Fig. 4. Failed attempt by *Vespula vulgaris* wasps to rebuild their nest after it was destroyed by a bear.

Рис. 4. Результаты безуспешной попытки восстановления гнезда осами *Vespula vulgaris* после его разрушения медведем.

The role of Hymenoptera in the diet of bears

Among social Hymenoptera, bears most frequently consume ants, with wasps, bees, and bumblebees being less commonly targeted. The frequency of ant encounters in brown bear excrements can reach 85 % during the summer [Große, 2003; Sato et al., 2005], and up to 96 % for the American black bear (*Ursus americanus* Pallas, 1780) [Noyce et al., 1997]. When destroying anthills, bears consume both adult ants and their brood (larvae and pupae). While larvae begin to appear in ant nests in early May, with egg-laying continuing into the autumn, brood is most abundant during the summer months [Kupyanskaya, 1990]. Consequently, summer is the peak period for ant consumption in both the study area and other regions [Aoi, 1985; Ohdachi, Aoi, 1987; Reid et al., 1991; Noyce et al., 1997; Swenson et al., 1999; Große, 2003; Huygens et al., 2003; Sato et al., 2005]. Studies suggest that the presence of brood influences

bears' preference for ants as a food source [Fujiwara et al., 2013].

Wasps, bees, and bumblebees are included in the bears' diets across different regions during most of the active period, from spring to autumn [Bromley, 1965; Nozaki et al., 1983; Aoi, 1985; Ohdachi, Aoi, 1987; Smirnov et al., 1987; Bears…, 1993; Huygens et al., 2003]. The frequency of wasps and bees encountered in bear excrements rarely exceeds 15 % [Aoi, 1985; Sato et al., 2005]. Bears are primarily attracted to honey in bee nests due to its high energy content, which can lead to significant damage to apiaries. This, in turn, leads to conflicts with beekeepers, who sometimes kill bears to protect their livelihoods, posing a challenge for bear population management in the region.

In our study, the frequency of Hymenoptera encounters in bear excrements was significantly higher in Sikhote-Alin compared to Sakhalin (Fig. 1, Table 2). The diets of brown and Asiatic black bears in Sikhote-Alin are primarily composed of plant-based foods (grass in the summer and oak and pine nuts in the autumn) [Seryodkin, 2015]. The relatively high proportion of insects in the diet may reflect the bears' need to supplement their predominantly plant-based diet with animal protein.

In earlier work by G.F. Bromley [Bromley, 1965] in Sikhote-Alin, the frequency of ant encounters in excrements and stomachs varied seasonally for brown bears, ranging from 9.1 % (April) to 75.0 % (late May), and for Asiatic black bears from 9.1 % (April) to 46.2 % (late May). The highest frequency of wasp and bee encounters for brown bears occurred in July (27.8 %) and for Asiatic black bears in June (23.6 %). The annual diet for brown bears consisted of 29.6 % ants and 4.0 % wasps and bees, while for Asiatic black bears, these figures were 13.3 % for ants and 4.4 % for wasps and bees. Compared to our results, Bromley's study found a slightly higher frequency of Hymenoptera encounters in brown bears and a slightly lower frequency in Asiatic black bears. These discrepancies may be attributed to methodological differences or variations in food availability across study years. For example, following a productive year for Korean pine nuts, bears may feed on these high-calorie nuts throughout the summer and consume fewer insects.

The relatively low importance of ants in the diet of brown bears on Sakhalin, as observed in our study, has also been noted in other regions, such as Yellowstone National Park, USA [Mattson et al., 1991], and British Columbia, Canada [McLellan, Hovey, 1995]. On Sakhalin, bears have access to a wider range of food, including animal prey, reducing the need to consume smaller, less rewarding food items like insects. From June to October, Pacific salmon provide an abundant food source for bears in spawning rivers in our study area [Seryodkin et al., 2012; Seryodkin, 2017].

The proportion of Hymenoptera in the diet decreases sharply in the fall with the availability of high-calorie foods like salmon and nuts, a pattern observed both in our study area [Bromley, 1965; Seryodkin, 2015] and in other regions [Ohdachi, Aoi, 1987; Reid et al., 1991; Bears…, 1993; Swenson et al., 1999; Huygens et al., 2003]. The decrease in Hymenoptera consumption may also be linked to seasonal declines in insect activity, as ants begin preparing for winter by the end of summer. For example, ants in the genus *Myrmica* in the European part of Russia begin moving to winter nests in August and September, where larvae are housed in lower chambers [Zakharov, Fedoseeva, 2005]. Similar patterns are likely to occur in Primorsky Krai, where ant activity peaks from mid-April to October [Kupyanskaya, 1990]. By late September, ants in southern Primorye are already settling in underground winter chambers [Kupyanskaya, 1990], making it more difficult for bears to locate their nests.

As human activity increasingly affects bear habitats, secondary food sources such as Hymenoptera may play a larger role in their diet, particularly in years when primary food sources are scarce. In the Russian Far East, salmon overfishing and the harvesting of Korean pine nuts are undermining the food supply of bears [Seryodkin, Pikunov, 2009; Seryodkin, 2017]. While insects cannot fully replace these crucial food resources, they may help compensate for shortfalls, particularly in years with limited food availability. It has been observed that poor harvests of plant-based foods drive bears to increase their consumption of ants [Zakharov, Zakharov, 2019].

Insect foraging by bears and mutual influence in the predator-prey system

Bears exhibit stereotypical behaviors aimed at obtaining social Hymenoptera [Pazhetnov, 1990; Seryodkin, 2016]. The foraging behavior of predators depends on the type of insect, nest location, and nesting substrate. The ability of insects to restore their nests varies according to the extent of the damage.

Bears frequently locate and destroy ground ant nests [Yurgenson, 1937; Chernyavsky, Petrichenko, 1984; Pazhetnov, 1990; Loskutov, Radchenko, 1991; Swenson et al., 1999; Mordosov, 2006; Seryodkin, 2016; Tirronen et al., 2016], using their keen sense of smell, sometimes detecting these nests from tens of meters away [Rukovsky, Kupriyanov, 1970]. Upon discovering an ant nest, bears typically use their paws to break apart the upper layer (outer mound), exposing the nesting chamber, from which they consume the ant larvae and pupae. In some instances, bears may destroy the entire anthill [Pazhetnov, 1990]. We have identified two additional methods of foraging for ants by bears that have not been previously reported: turning over layers of soil above nesting sections of *F. lemani*, and gnawing nests of *F. truncorum* and *Lasius* (*Dendrolasius*) sp. ants from upright tree trunks.

In central Sweden, brown bears destroy approximately 23 % of anthills annually [Swenson et al., 1999], while in the Lapland Nature Reserve in Russia, this figure reaches up to 40 % [Nasimovich, Semenov-Tyan'-Shansky, 1951]. In northwestern Russia (Vologda Region), of 45 observed anthills, 41 were visited by bears 115 times over four years, resulting in half of the anthills being abandoned by ants [Rukovsky, 1987]. In the Berezinsky Nature Reserve (Republic of Belarus), bears destroyed up to 60 % of *F. polyctena* Forster, 1850 anthills, while leaving *F. exsecta* (Nylander, 1846) nests untouched [Grimal'sky, 1975]. In Eastern Kazakhstan, brown bears dug up 81 (93 %) of 87 anthills [Baidavletov, 1993]. In some areas, bears may destroy up to 100 %

of anthills belonging to preferred species [Pazhetnov, 1990; Loskutov, Radchenko, 1991].

By selectively targeting certain ant species, bears influence the structure of ant communities. Some anthills destroyed by bears are reconstructed by ants, while others are abandoned. Repeated destruction of anthills can lead to adaptive responses, such as the merging of colonies from different nests, including nests of different species, resulting in the formation of mixed colonies [Zakharov, Zakharov, 2019].

During summer, both brown and Asiatic black bears frequently consume multiple ant species (up to seven species) in a single day, suggesting that they actively seek out anthills and their inhabitants. This observation indirectly confirms the importance of ants in the bears' summer diet.

The destruction of wasp, bee, and bumblebee nests by bears usually results in irreversible damage. Bears not only destroy the nests but also damage the surrounding substrate. For instance, when bears gnaw on trees, the resulting hollows become unsuitable for future use by insects.

In their coexistence with social Hymenoptera, bears have developed behaviors focused on locating and obtaining insects and their byproducts. In turn, social Hymenoptera have evolved adaptations to mitigate the impact of predators. In addition to rebuilding nests and merging colonies after destruction [Zakharov, Zakharov, 2019], ants may exhibit aggressive defensive behaviors, such as the use of formic acid by *Formica* species to deter predators [Swenson et al., 1999].

Conclusions

This study demonstrates that the diets of bears in the Russian Far East include representatives from three Hymenoptera families: Formicidae, Vespidae, and Apidae. A total of at least 29 insect species were identified in their diets, with ants from the genus *Formica* being the most commonly consumed, alongside *Myrmica*, *Camponotus*, and *Lasius* species. The proportion of Hymenoptera in the diet was highest for Asiatic black bears in Sikhote-Alin and lowest for brown bears on Sakhalin. The frequency of insect encounters in bear excrements peaked during the summer compared to other seasons. The methods bears used to obtain social Hymenoptera from nests varied depending on the species, nesting substrate, and type and location of the nest.

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Table S1. Species composition and brief ecological characteristics of ants identified in the diets of brown and Asiatic black bears in the Russian Far East

Таблица 1. Видовой состав и краткая экологическая характеристика муравьёв, отмеченных в питании бурого и гималайского медведей на Дальнем Востоке России

Species, genus (subgenus)	Region, bear species	Sample type (number of samples)	Nesting substrate	Nest type [Zakharov et al., 2013]	Size of colony or section*
Subfamily Formicinae					
Camponotus herculeanus (Linnaeus, 1758)	PK[1, 2], SO[1]	Excrements (5), nests (2)	Dying and damaged wood [Kupyanskaya, 1990; Aibek, Yamane, 2009; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Capsule	1×10^4 [Berman et al., 2007]
C. saxatilis Ruzsky, 1895	PK[1, 2], SO[1]	Excrements (12)	Soil, under rocks, occasionally in stumps and damaged wood [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional	4×10^3 (1×10^4) [Kupyanskaya, 1990]
Camponotus spp.	PK[1, 2], SO[1]	Excrements (17)	Soil, under stones, stumps, dying and damaged wood [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional or capsule	4× 103 (1×10^4) [Kupyanskaya, 1990]
Formica aquilonia Yarrow, 1955	PK[2, 3], SO[1]	Excrements (4), nest (1)	Soil [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Zakharov et al., 2013]	Capsule	1 × 105 (1×10^7) [Kupyanskaya, 1990; Zakharov et al., 2013]
F. forsslundi Lohmander, 1949	PK[1]	Excrements (1)	Moss bumps [Zakharov et al., 2013]	Capsule	(1×10^4) [Zakharov et al., 2013]
F. kupyanskayae Bolton, 1995	PK[2]	Excrements (1)	Soil [Kupyanskaya, 1990]	Capsule	No data
F. lemani Bondroit, 1917	PK[1, 2], SO[1], KK_1	Excrements (8), nests (2)	Soil, dying wood (stumps, deadwood), under stones [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013]	Sectional	500–700 (9×10^3) [Berman et al., 2007; Zakharov et al., 2013]
F. lugubris Zetterstedt, 1840	PK[1, 2], SO[1], KK[1]	Excrements (5), nests (4)	Soil [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013]	Capsule	5 × 103 (1×10^7) [Kupyanskaya, 1990; Zakharov et al., 2013]
F. pressilabris Nylander, 1846	PK[1]	Nest (1)	Soil [Kupyanskaya, 1990; Annotated catalog…, 2012; Zakharov et al., 2013]	Capsule	3×103 (3×10^4) [Kupyanskaya, 1990; Zakharov et al., 2013]
F. sanguinea Latreille, 1798	PK[1, 2], SO[1]	Excrements (8)	Dying wood (stumps, logs), soil, occasionally under stones [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013]	Capsule	7×103 (3×10^4) [Kupyanskaya, 1990; Berman et al., 2007; Zakharov et al., 2013]
F. truncorum Fabricius, 1804	PK[1, 2], SO[1]	Excrements (8), nest (1)	Stumps, soil, trunks of dying trees [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013]	Capsule	2×104 (5×10^5) [Zakharov et al., 2013]
F. spp. (*Formica fusca* group)	PK[2, 3], KK[1]	Excrements (5)	Soil, dying wood (stumps, deadwood), under stones [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Imai et al., 2003; Berman et al., 2007; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012; Zakharov et al., 2013]	Sectional or capsule	500–800 (1×10^4) [Kupyanskaya, 1990; Zakharov et al., 2013]

Lasius flavus (Fabricius, 1782)	PK[1, 2]	Excrements (2), nests (4)	Soil, under rocks, occasionally stumps [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Capsule	2–3 × 10^4 (7 × 104) [Zakharov, 2015]
L. umbratus (Nylander, 1846)	PK[1, 3]	Excrements (4)	Soil, under large rocks, dying wood [Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Imai et al., 2003; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional or capsule	2 × 10^4 [Kupyanskaya, 1990; Zakharov, 2015]
L. (*Lasius*) spp.	PK[1, 2]	Excrements (25), nests (2)	Soil, under stones, dying wood (stumps, dead wood, dying trees [Kupyanskaya, 1990; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional or capsule	1 × 10^4 [Kupyanskaya, 1990; Kupyanskaya, Shabalin, 2012]
L. (*Dendrolasius*) spp.	PK[1, 3]	Excrements (1), nest (1)	The trunks of living and dying trees [Kupyanskaya, 1990; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Capsule	5 × 10^5 [Kupyanskaya, 1990; Zakharov, 2015]
Subfamily Myrmicinae					
Myrmica ademonia Bolton, 1995	PK[2]	Excrements (2)	Rotten wood, dry branches, occasionally soil and under stones [Kupyanskaya, 1990]	Sectional	> 1 × 10^3 [Kupyanskaya, Shabalin, 2012]
M. angulinodis Ruzsky, 1905	PK[3]	Excrements (1)	Soil and wood debris, stumps, moss bumps, under stones [Dmitrienko, Petrenko, 1976; Radchenko, 2005; Berman et al., 2007; Radchenko, Elmes, 2010; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional	600–700 (2 × 10^3) [Berman et al., 2007; Radchenko, Elmes, 2010]
M. excelsa Kupyanskaya, 1990	PK[2]	Excrements (1)	Wood [Kupyanskaya, 1990]	Sectional	400–700 [Radchenko, Elmes, 2010]
M. kotokui Forel, 1907	PK[1]	Excrements (1)	Soil, under the stones [Kikuchi et al., 1999; Imai et al., 2003; Radchenko, 2005; Radchenko, Elmes, 2010; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional	> 1 × 10^3 [Kikuchi et al., 1999; Radchenko, Elmes, 2010]
M. kurokii Forel, 1911	SO[1]	Excrements (2)	Dying wood, soil, occasionally under stones, in mossy bumps [Kupyanskaya, 1990; Radchenko, 2005; Radchenko, Elmes, 2010; Annotated catalog…, 2012; Zakharov et al., 2013]	Sectional	400–700 [Radchenko, Elmes, 2010]
M. luteola Kupyanskaya, 1990	PK[2], SO[1]	Excrements (2)	Dying wood (stumps, logs), soil, under stones [Kupyanskaya, 1990; Imai et al., 2003; Radchenko, 2005; Radchenko, Elmes, 2010; Annotated catalog…, 2012]	Sectional	400–700 [Radchenko, Elmes, 2010]
M. ruginodis Nylander, 1846	PK[1, 2]	Excrements (12), nest (1)	Dying wood (stumps, dead wood), soil, mossy bumps [Imai et al., 2003; Radchenko, 2005; Radchenko, Elmes, 2010; Annotated catalog…, 2012; Kupyanskaya, Shabalin, 2012]	Sectional	400–700 (1,2 × 10^3) [Radchenko, Elmes, 2010]
Myrmica spp.	PK[2, 3], SO[1], KK[1]	Excrements (4)	Soil and wood debris, stumps, mossy bumps, under stones [Radchenko, Elmes, 2010]	Sectional	400–700 [Radchenko, Elmes, 2010]

Notes: PK — Primorskii krai, SO — Sakhalinskaya oblast, KK — Kamchatskii krai, 1 — brown bear, 2 — Asiatic black bear, 3 — bear species unknown; * — literature data on the average (and maximum recorded) colony sizes or sections (for species with sectional nests) are provided.

Примечания: ПК — Приморский край, СО — Сахалинская область, КК — Камчатский край, 1 — бурый медведь, 2 —гималайский медведь, 3 — вид медведя неизвестен; * — приведены литературные данные о средней (максимально зарегистрированной) численности семей или населения секций (для видов с секционными гнёздами).