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Scat composition as an indicator of brown bear diet quality on Iturup Island

Alexey E. Scopin*, Svetlana V. Lipatnikova & Anton A. Polushkin

ABSTRACT. The results of fractional and chemical analysis of adult brown bear scats are presented. Feces were collected on Iturup Island in summer. The bulk of the bear scats was represented by large-sized fractions of fecal particles, that indicates poor food processing and inefficient digestibility of the consumed food. The coefficient of variation (CV) of occurrence of particle fractions in different scat samples varied within 66–152%. The average dMean value of fecal particles for brown bear scats on Iturup Island is 8.34 mm. The highest dMean (4.6–20.9 mm; 10.4 mm on average) were found in the scat samples containing algae, while the lowest (1.2–6.5 mm; 4.3 mm on average) were detected in the samples containing mainly fruits and seeds. Due to the high variability of the mass of different fecal particle fractions, there are tricky statistically to discern the pooled scat samples between the bears roaming on the coasts and in the inland mountainous areas. Among the macronutrients, crude fiber was the main component of the bear scat (23.5% on average, maximum — up to 55.8%). The protein ratio in the scats was from 0.12 to 0.94 (0.41 on average). The fecal samples differed greatly in fat content (up to 18 times). The scat composition of bears consuming high-lipid plant seeds or fish carrion contrasts sharply with the scats which contain only the vegetative parts of plants. No significant statistical differences were found between the mass of separate fecal particle fractions and the nutrient composition of feces. Scat composition can be used as an indicator of brown bear nutrient status and to assess the quality of habitats.

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Состав помета как индикатор качества рациона бурого медведя на острове Итуруп

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РЕЗЮМЕ. Представлены результаты фракционного и химического анализа помета взрослых особей бурого медведя на острове Итуруп, собранные в летний период. Основная масса помета медведя была представлена крупноразмерными фракциями каловых частиц, что говорит о слабой первичной переработке и неэффективном переваривании потребленного корма. Выявлен высокий коэффициент вариации (66–152%) встречаемости отдельных фракций частиц в разных образцах помета. Средний показатель dMean каловых частиц для летнего помета бурого медведя на острове Итуруп составил 8.34 мм. Максимальные показатели dMean (4.6–20.9 мм, в среднем 10.4 мм) отмечены для образцов помета медведей, содержащих водоросли, а минимальный (1.2–6.5 мм, в среднем 4.3 мм) — для образцов, включающих преимущественно плоды и семена. Из-за сильной изменчивости массы разных фракций каловых частиц в объединенных выборках образцов помета нам не удалось выявить значимые отличия между группировками медведя, обитающих на побережьях острова и во внутренних горных районах. Среди макронутриентов основным компонентом помета медведя была сырая клетчатка (в среднем 23.5%, максимально до 55.8%). Протеиновое отношение в образцах помета варьирует 0.12 до 0.94 (в среднем 0.41). Образцы помета сильно отличались между собой по содержанию жира (до 18 раз). Состав помета медведей, потребляющих семена растений с высоким содержанием липидов или рыбные отходы, резко контрастируют с пометом, включающим только вегетативные части растений. Не обнаружено значимых статистических закономерностей между массой отдельных фракций каловых частиц и составом нутриентов в образцах помета. Состав

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помета можно использовать в качестве индикатора обеспеченности бурого медведя питательными веществами и для оценки качества местообитаний.

КЛЮЧЕВЫЕ СЛОВА: *Ursus arctos*, анализ помета, фекальные частицы, макронутриенты, остров Итуруп.

Introduction

The Japanese brown bear (*Ursus arctos yesoensis*) inhabits Iturup Island as part of southern Kuril Islands. Iturup is the northernmost point of distribution of this subspecies of bear. This predator is currently also distributed on Kunashir, Hokkaido and nearby smaller islands (Baryshnikov, 2007; Baryshnikov & Puzachenko, 2009; Hirata *et al*., 2017). The bear is absent on the central islands of the Kuril ridge. The Kamchatka subspecies of the brown bear (*U. a. piscator*) dwells on the northern Kuril Islands: Paramushir and Shumshu islands (Yudin, 1993; Kostin & Eremin, 2004; Baryshnikov, 2007).

The ecology of Asian populations of brown bear has been studied quite well, especially on the islands of Sakhalin (Benkovsky, 1972; Vshivtsev, 1972; Voronov, 1974) and Hokkaido (Inukai & Kadosaki, 1987; Kadosaki & Inukai, 2000; Amano *et al*., 2006). In particular, the feeding ecology of the brown bear has been investigated in detail in Japan, where this predator lives in variety of landscapes: from the sea coasts and agroecosystems to forested mountain areas (Aoi, 1985; Sato *et al*., 2004, 2005; Sato, 2009; Narita *et al*., 2011; Matsubayashi *et al*., 2014; Kishimoto *et al*., 2017; Shirane *et al*., 2021). According to the type of foraging, the Hokkaido brown bear is a typical omnivorous mammal with a predominant consumption of different plant material, including about 60 species of edible plants (Aoi, 1985; Ohdachi & Aoi, 1987; Sato, 2009). The features of foraging activities of the bear on the southern Kuril Islands is less known. There are few published papers representing fragmentary descriptive-naturalistic information about bear feeding (Velizhanin, 1970, 1974; Voronov, 1972,1974; Perovsky, 1988, 1991; Tumanov, 2017).

Various mammologists over a long period of research have established that each group of this predator on a particular island of the Kuril Archipelago is a specific population with its own unique ecological and morphological characteristics (Yudin, 1993; Baryshnikov & Puzachenko, 2009). The Kuril ridge is elongated in a meridional direction and each island has a diverse flora and fauna, so there are probably inter-island differences in the composition of the brown bear's diet. However, there is no real data that clearly confirms this assumption. There is no data on the dynamics of the composition of its diet throughout the entire season of the predator's activity. The currently available information on bear foraging and nutrition on Iturup was obtained only through short-term visual observations of the trophic activity and as a result of assessing the composition of a few samples of scats (Velizhanin, 1970; Tumanov, 2017).

Scat analysis is one of the main non-invasive methods for studying the nutrition of brown bear (Bromley, 1965; Pazhetnov & Pazhetnova, 1987; Boltunov, 1993; Sato *et al*., 2004; Naves *et al*., 2006; Kobayashi *et al*., 2012; Kishimoto *et al*., 2017; Shirane *et al*., 2021). However, using feces to reveal dietary diversity may have limitations due to a large number of potential plant and animal food items on Iturup Island. Ultimately, it is quite difficult to conduct a detailed analysis of the composition of the bear's diet.

Forage material of different origin and structure is processed and absorbed by the bear's digestive system to varying degrees, that is reflected in the size of undigested particles in the feces. Therefore, by analyzing the composition of scat particles, we can speak about the digestive efficiency (Hume, 2005). The composition and consistency of bear scats can vary greatly throughout the year, also depending on the sex, age, and physiological state of the animal (De Cuyper *et al*., 2021, 2023). In turn, the diverse range of available forage sources and the pronounced spatial, temporal and individual variability of feeding of these carnivores (Bojarska & Selva, 2012) suggest the presence of a wide nutritional niche. This niche is an ecological adaptation of the brown bear to the settling of diverse habitats with different food sources (Coogan *et al*., 2018). High heterogeneity of dietary nutrient profiles influencing the feeding behavior allows us to outline the interactions between the structural and chemical composition of scats and the features of food preferences in a local area. Therefore, analysis of chemical components of the scats can determine the current balance of nutrients of forage vegetation that is important for maintaining the sustainability of the predator population.

To assess the possibility of the use of feces as an object of data collection during non-invasive control over the predator population, we set the goal to evaluate the characteristics of the utilization of the food supply and processing of prey items by analysis of the fractional composition and nutritional components of bear scats. These characteristics reflect the variability of the diet, physiological adaptations to the nutrient niche, and serve as indicators in assessing the quality of available forages in different habitats that shows ecological specificity of different populations and certain groups of this predator within its range.

Materials and methods

Iturup is the largest island of the group of southern Kuril Islands (over 200 km long). It has a rather complex hilly-mountainous terrain formed by volcanic activity. The main landscape is made up of steep slopes of

lava flows and landscapes of volcanic plateaus covered with a variety of vegetation. The main types of vegetation are communities of stone birch (*Betula ermanii*) with alder (*Duschekia fruticosa*) and bamboo (*Sasa kurilensis*, less often *S. makinoi, S. shikotanensis*) at altitudes up to 750 m, and at higher altitudes — the Siberian dwarf pine (*Pinus pumila*) with alder (*Duschekia maximowiczii*) and shrubby willows *(Salix hidakamontana, S. hidewoi, S. nakamurana*) (Ganzey, 2010). After massive logging and fires, bamboo (*Sasa* sp.) became widespread on the island, which can reach a height of over 2 m and form pure thickets over large areas that prevents reforestation. Other plant communities include areas with fir (*Abies mayriana*) in the Kuibyshev Bay area, oak forests (*Quercus crispula*) in the valley of the Kurilka River, and various plant associations with maple (*Acer mayrii, A. ukurunduense, A. tschonoskii*) in the Goryachiye Klyuchi area in the central part of the island (Urusov & Chipizubova, 2000). The Iturup has a developed network of lakes, rivers, and streams. In the floodplains, tree-like willows and tall grass vegetation are common. Wild rose thickets occupy a significant area in the coastal zone. There are 872 species of vascular plants growing on Iturup (Barkalov, 2009), many of which act as potential food items for herbivorous and omnivorous animals.

Fresh fecal samples from brown bear were collected along linear survey routes with a total length of 80 km. A total of 39 scats were sampled from August 15 to September 9, 2022, in the central and northern parts of Iturup Island: (1) **Kur.** The outskirts of the Kurilsk city in the floodplain of the Kurilka river in 2 km from the coast (n = 4, 15 Aug.). The biotope is tree-like willow thickets (*Salix udensis, S. taraikensis, S. caprea*) with birch (*Betula platyphylla*) and alder (*Alnus hirsuta*). The tree canopy is dominated by *Petasites japonicus*; (2) **GK.** The area around the Goryachie Klyuchi village in the floodplain of the Blagodatnaya river in 4–5 km from the coast (n = 6, 16 Aug.). The main habitat is pure thickets of bamboo (*Sasa* sp.) with patches of other plant communities, where willows (*Salix* sp.), alder (*Duschekia* sp.) and larch (*Larix kamtschatica*) dominate among trees; (3) **Tor.** The area of coast of Tornaya (N 45.3222° E 148.4°) and Parusnaya bays (n = 8, 18 Aug. and 3 Sept.) of the Sea of Okhotsk. In Parusnaya Bay, forbs are common, often with *Leymus mollis* that domi-

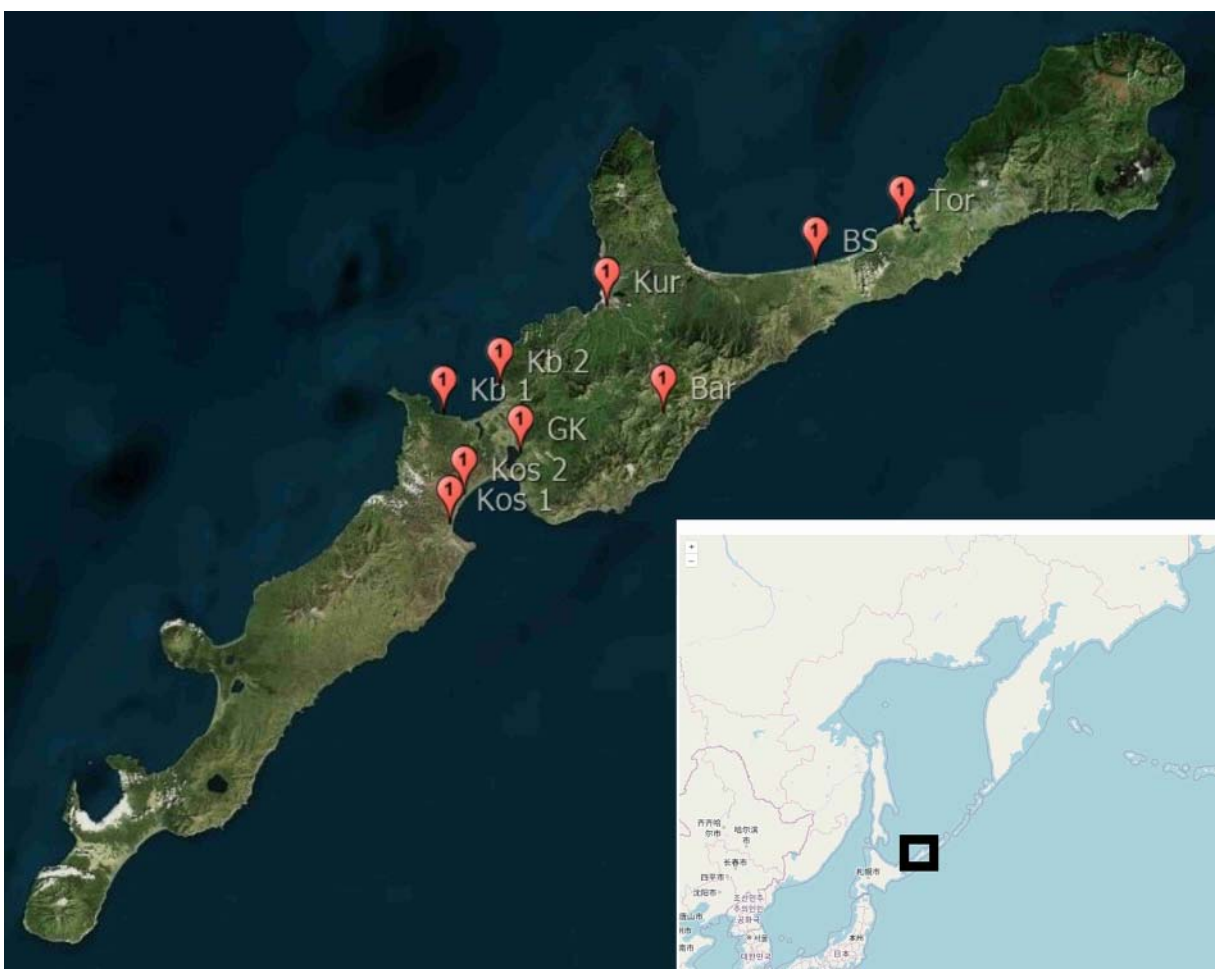

Fig. 1. Brown bear scat sampling locations on Iturup Island.

nate on the coastal sand dunes. The plant communities with areas covered wild rose (*Rosa rugosa*) meet often in the shore of Tornaya Bay; (4) **BS.** The Belye Skaly territory (n = 12, 18 Aug. and 1–3 Sept.). These are sandy and rocky areas along the Sea of Okhotsk coast covered by forb-grass communities; (5) **Kb**. Coast of the Okhotsk Sea near Kuibyshevsky Bay (n = 2, 29 Aug. and 4 Sept.). Larch forests with patches of meadow herbs and clumps of bamboo are distributed here. There is a waste dump from a fish processing plant; (6) **Kos.** The Pacific coast around Kasatka Bay (n = 5, 17 Aug.). The vegetation is represented by extensive forb communities. Beaching of marine animals and algae are common here; (7**) Bar**. The upper zone of the Baransky volcano in 5 km from the Pacific coast (n = 2, 23 Aug. and 9 Sept.) at an altitude of about 900 m. The alpine-type vegetation is dominated. There are vast areas of thickets of pure bamboo, dwarf alder and pine (Fig. 1).

The collected scats were attributed to scores 3 and 4 according to the existing classification (De Cuyper *et al*., 2021). In the field, the surface of the scat pieces was treated with 50% ethyl alcohol, and subsequently the samples were frozen at –20°C until they were analyzed. For the fractional analysis, the fecal samples (n = 30) were thawed and soaked in water for 48 hours in the laboratory. The soaked samples were sifted through sieves (10, 7, 5, 3, 2, 1, 0.5, 0.25, 0.1, 0.05, 0.025 mm), separated into fractions and food items were identified. The material from each sieve and the sediment containing fractions smaller than 0.025 mm were evaporated and dried to an absolutely dry state. The dMean value was calculated for each scat sample (Fritz *et al*., 2012). The maximum length of fecal particles varies widely (from 5 to 120 mm). Therefore, the maximum length of plant fragments found in this particular sample was used as an upper limit in calculating the dMean. The fractional profiles of the scats were constructed using arithmetic means and medians.

The composition of macronutrients in bear scats (BS: n = 3, Kos: n = 4, Kur: n = 1, GK: n = 6, Kb: n = 2, Tor: n = 8) and plant parts most often found in these scats (n = 4: brown algae (*Fucus* and *Laminaria*), seeds of *Rosa rugosa*, shells of dwarf pine (*Pinus pumila*), berries of *Sorbus sambucifolia*)) were analyzed. The content of crude protein by the Kjeldahl method, crude fiber (cellulose+hemicellulose) by the Henneberg–Stohmann method and fat by the von Soxhlet method were determined in the scats in accordance with the state standards of the Russian Federation (Dulepinskikh *et al*., 2022). The results of the chemical analysis were expressed as percentages based on dry matter (DM). The protein ratio was calculated for each sample: protein/fat + crude fiber. Graphical representation of the outcomes is made using right-handed triangles (Raubenheimer, 2011; Coogan *et al*., 2014; Coogan & Raubenheimer, 2016; Machovsky-Capuska *et al*., 2016). The total composition of fat, protein and fiber is taken as 100%. Mathematical processing of the results was carried out using the Statistica 64 program.

Results

While comparing different samples the fractional analysis of bear scats revealed a strong variation in the mass of each size fraction. Often, the DM mass was similar between separate adjacent fractions. However, fecal particles were more often concentrated only on sieves of a certain size. Occasionally, these particles did not sediment on some size sieves, i.e., a few fractions were absent in some analyzed samples. According to average values, the minimum mass was noted for fractions of 0.05 and 0.025 mm (Fig. 2, Table 1), which indicates a low ability of the bear to digest the consumed food that does not promote the formation of small fecal particles. Therefore, when assessing the intensity of food processing by this predator, the main attention should be paid to the scat fractions consisting of large food fragments, which are most effectively destroyed during chewing. The large fractions make up half or more of the DM mass of bear scats (Fig. 2). However, the difference between separate scat samples is quite large. The coefficient of variation (CV) of DM in different fractions in the scat profile ranged from 66.4 to 152.0% (Table 1). At the same time, the fluctuation of the values of these coefficients has no clear connection with the trend of decrease or increase in fecal particle size along the profile. The minimum values of the CV of particle mass were found for the following fractions: 5, 3, 2 mm and sediment (Table 1).

When comparing the fractions in pairs, no statistically significant differences in DM mass (dependent samples according to the t-test) were found between sieves of 7 vs. 5 mm, 1 vs. 0.5 mm, 0.25 vs. 0.1 mm, 0.05 vs. 0.025 mm (Table 2). Between the remaining adjacent sieves, the differences in DM mass of the fractions were significant (Table 2). Thus, in further studies of bear scats, sieves of sizes 7, 1, 0.25, 0.05 mm can be omitted from the line of different-sized sieves and not used in the fractional analysis.

There are differences in the proportion of certain particle fractions from different territories when constructing the fractional profiles of feces based on average data (Fig. 2). In terms of the mass of large fractions in the profile, the variability between different collected samples is higher than in terms of the mass of small fractions. This is evident at comparing the arithmetic mean and median DM mass of the fractions (Fig. 2). The fractional profile of the pooled scat samples based on the median demonstrates a lower occurrence of the proportion of the largest particles (compared to the arithmetic mean) and a more frequent representation of particle fractions of 2–3 mm (Fig. 2). However, basically, the constructed profiles based on the data of the arithmetic mean and median are close, especially when comparing groups of small-sized particle fractions. Similar proportion of the DM mass of small-sized particles of the scat fractional profile in different samples is the result of the functioning stability of the digestive system (the rate of passage of food through the gastrointestinal tract and the time of enzymatic processing of

Table 1. The proportion of fecal fractions (%) of the brown bear scats from coastal and inland regions of Iturup Island (differences between territorial groups of samples are not significant)

.

	Statistical indicator	Size of sieves						
		10 mm	**7 mm**	**5 mm**	**3 mm**	**2 mm**	**1 mm**	**0.5 mm**
Coastal ecosystems (*n* = 18)	M±m	11.48±3.02	9.38±1.95	9.25±1.46	20.23±3.03	9.04±1.70	5.32±1.19	5.23±0.84
	Min–Max	0–36.02	0–31.00	0.58–20.94	8.02–50.6	1.31–30.86	1.18–23.09	0.74–12.92
Interior mountain ecosystems (*n* = 12)	M±m	27.51±9.23	10.69±2.66	10.29±2.02	17.72±3.95	8.31±1.84	3.76±1.21	4.57±1.83
	Min–Max	0–89.9	0–26.7	2.13–25.67	0.83–37.43	0-16.63	0–15.6	0–22.81
The pooled sample (*n* = 30)	M±m	17.89±4.28	9.90±1.56	9.67±1.17	19.23±2.38	8.75±1.24	4.70±0.86	4.97±0.87
	Std.Dev.	23.42	8.53	6.42	13.02	6.78	4.72	4.77
	Coef. Var.	130.87	86.09	66.39	67.75	77.57	100.53	96.10

	Statistical indicator	Size of sieves					dMean, mm	
		0.25 mm	**0.1 mm**	**0.05 mm**	**0.025 mm**	**Sediment**		
Coastal ecosystems (*n* = 18)	M±m	12.02±2.91	8.91±2.36	0.42±0.11	0.51±0.15	8.20±1.23	6.55±1,31	
	Min–Max	0.58–39.66	0.37–29.6	0–1.33	0–2.00	2.23–20.15	1.21–18.51	
Interior mountain ecosystems (*n* = 12)	M±m	4.19±1.74	4.90±1.63	0.71±0.33	0.80±0.27	6.56±1.80	11.01±2.74	
	Min–Max	0-21.99	0–17.02	0–4.25	0–2.84	0.25–19.15	1.11–26.61	
The pooled sample (*n* = 30)	M±m	8.89±1.99	7.30±1.58	0.53±0.15	0.63±0.14	7.54±1.02	8.34±1.38	
	Std.Dev.	10.88	8.67	0.81	0.77	5.60	7.57	
	Coef. Var.	122.42	118.68	152.2	121.84	74.27	90.84	

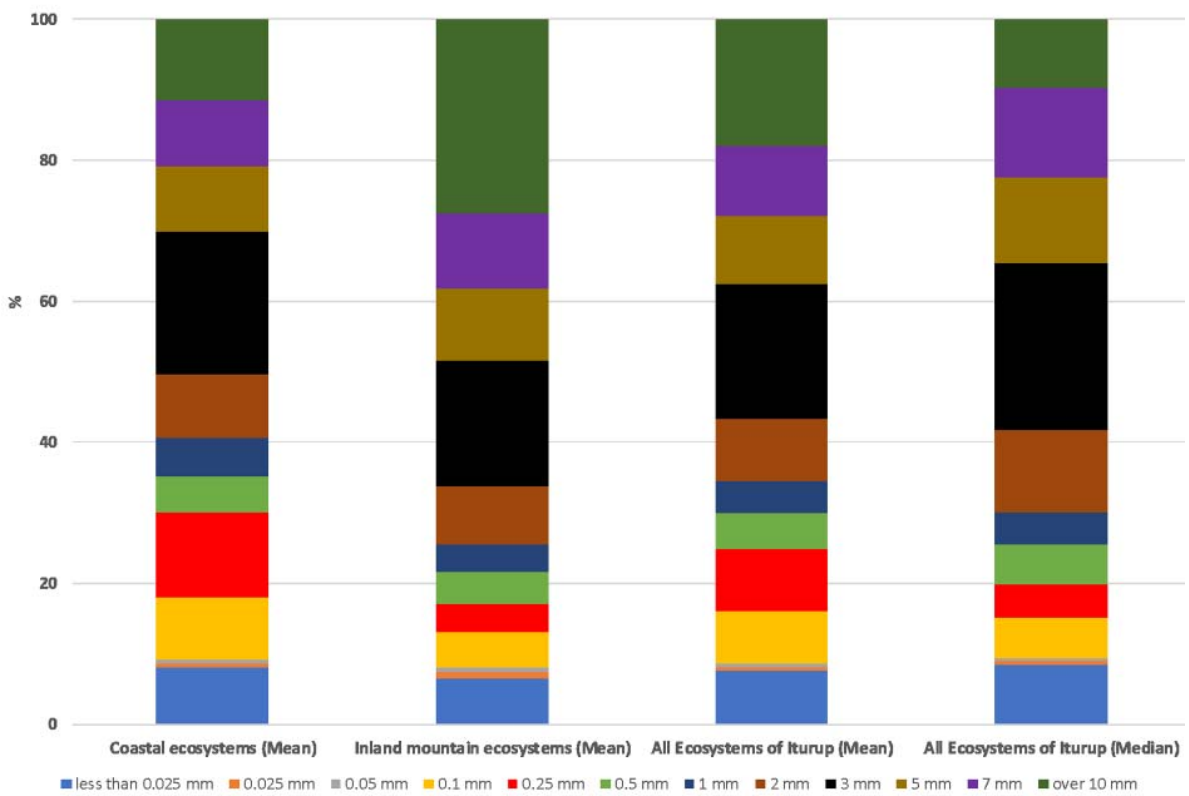

Fig. 2. Fractional profile of bear scats in coastal and inland regions of Iturup Island.

Table 2. The reliability of differences by *t*-test for dependent samples between different particle fractions of the Iturup bear scats (* marked differences are significant at $p < 0.05$).

	10 mm vs 7 mm*	7 mm vs 5 mm	5 mm vs 3 mm*	3 mm vs 2 mm*	2 mm vs 1 mm*	1 mm vs 0.5 mm	0.5 mm vs 0.25 mm*	0.25 mm vs 0.1 mm	0.1 mm vs 0.05 mm*	0.05 mm vs 0.025 mm	0.025 mm vs Sediment*
t	2.088762	0.161277	–4.26808	4.795890	4.073917	–0.338459	–2.13987	0.689392	4.480891	–1.13183	–7.13421
df	29	29	29	29	29	29	29	29	29	29	29
p	0.045617	0.872994	0.000192	0.000045	0.000327	0.737456	0.040908	0.496056	0.000107	0.266980	0.000000
Confidence –95%	0.166502	–2.76851	–14.1381	6.010946	2.016611	–1.91094	–7.66990	–3.11659	3.680306	–0.270409	–8.89739
Confidence +95%	15.81150	3.242509	–4.97789	14.94972	6.082722	1.368271	–0.173438	6.285924	9.861027	0.077743	–4.93261

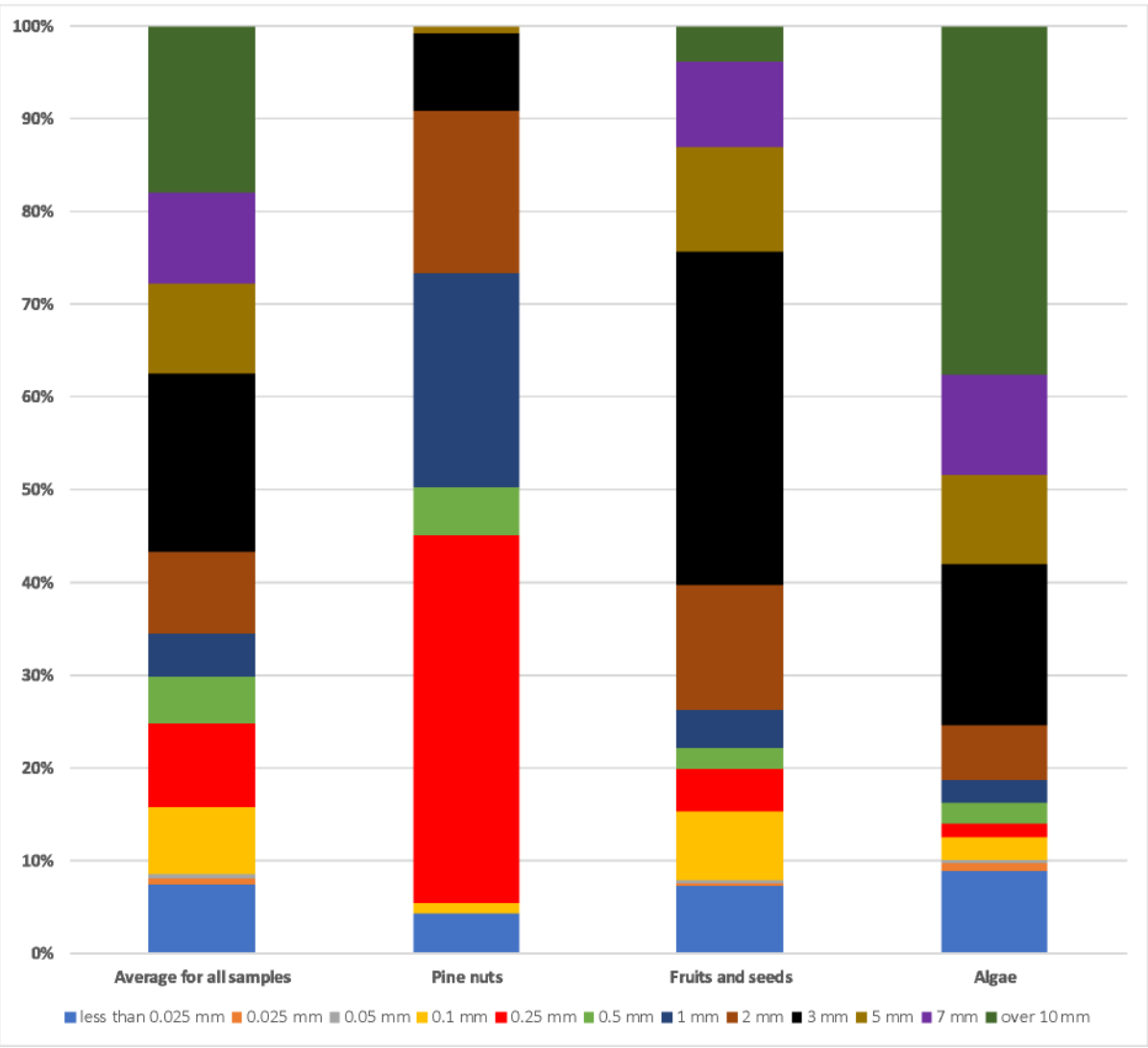

Fig. 3. Fractional profile of different bear scats from Iturup Island, constructed on the basis of average data in each group of samples with predominance of certain plant items.

Table 3. Regression equations of the dMean value and the proportion of a certain fraction of particles in brown bear scats (* data are significant at $p<0.05$).

Dry mass of fecal particle fraction on sieve (x)	Regression equation	Coefficient of determination
10 mm	dMean = 3.2622+0.2836*x	$R^2 = 0.769$*
7 mm	dMean = 2.4901+0.5903*x	$R^2 = 0.442$*
5 mm	dMean = 5.8372+0.2585*x	$R^2 = 0.048$
3 mm	dMean = 13.5523-0.2713*x	$R^2 = 0.218$*
2 mm	dMean = 14.9808-0.7598*x	$R^2 = 0.463$*
1 mm	dMean = 12.5888-0.9056*x	$R^2 = 0.319$*
0.5 mm	dMean = 12.2163-0.7811*x	$R^2 = 0.242$*
0.25 mm	dMean = 10.5536-0.2494*x	$R^2 = 0.128$
0.1 mm	dMean = 11.4743-0.4296*x	$R^2 = 0.241$*
0.05 mm	dMean = 9.7919-2.7289*x	$R^2 = 0.086$
0.025 mm	dMean = 10.6327-3.6467*x	$R^2 = 0.136$*
sediment	dMean = 14.1875-0.7755*x	$R^2 = 0.329$*

Table 4. dMean values (mm) of brown bear scats in different areas of Iturup Island.

Location	n	dMean±SE	Min–Max	Std.Dev.	Coef. Var.
Kur	4	13.46±5.26	4.89–26.61	10.52	78.18
GK	6	8.02±3.48	1.11–20.88	8.51	106.19
Tor	5	7.19±2.42	1.22–13.44	5.41	75.29
BS	6	7.40±2.38	2.32–17.76	5.82	78.74
Kb	2	2.24±1.03	1.21–3.28	1.46	64.96
Kos	5	6.63±3.13	1.35–18.51	7.00	105.54
Bar	2	15.07±9.65	5.43–24.73	13.65	90.50
Average for coastal ecosystems	18	6.55±1.31	1.21–18.51	5.76	85.10
Average for inland mountain ecosystems	12	11.01±2.74	1.11–26.61	9.50	86.26
Average for all samples	30	8.34±1.38	1.11–26.61	7.57	90.84

Table 5. dMean values (mm) of the brown bear scats with various food components.

The main component of feces	*n*	dMean±SE	Min–Max	Std.Dev.	Coef. Var.
Pine nuts	1	1.35	–	–	–
Fruits and seeds	6	4.28±0.77	1.21–6.49	1.85	43.25
Algae	5	10.40±3.46	4.61–20.88	7.75	74.53
Mixed composition of plant items*	18	9.50±1.99	1.11–26.61	8.45	88.88

Table 6. Protein. crude fiber and fat of the Iturup bear scats (% of DM; n = 24).

Nutritional components	Mean±SE	Median	Min–Max	Std.Dev.	Coef. Var.
Protein	9.63±0.86	8.35	4.3–18.8	4.29	44.53
Crude fiber	23.45±2.23	22.87	7.58–55.8	10.94	46.67
Fat	3.98±1.01	2.49	1.43–26.02	4.95	124.41

digesta), adapted to the destruction of food fragments at approximately the same level in different individuals of this predator.

The fractional profile of fecal particles is primarily determined by the composition of the diet. If there are a large number of pine nut shells in scats, the main part of the profile is made up of particles from 0.25 mm and 1 mm sieves. If berry and seed remains predominate in the scats, the main part of the scat profile is made up of particles from 3 mm sieves; and if algae are the basis in the scats, then a significant proportion of the profile is represented by particles larger than 10 mm and the maximum proportion of DM of the smallest fractions. On average, in the pooled samples of the bear scats on Iturup, fecal particles from 3 and 10 mm sieves prevail (Fig. 3).

The results of the calculations of dMean values between scat samples collected in coastal and inland areas of the island demonstrate differences due to uneven occurrence of fecal particle fractions of a certain size (Table 1). The scats from mountainous areas inside the island contained, on average, more large fractions (especially over 10 mm), and the dMean was correspondingly higher. In feces from coastal ecosystems,

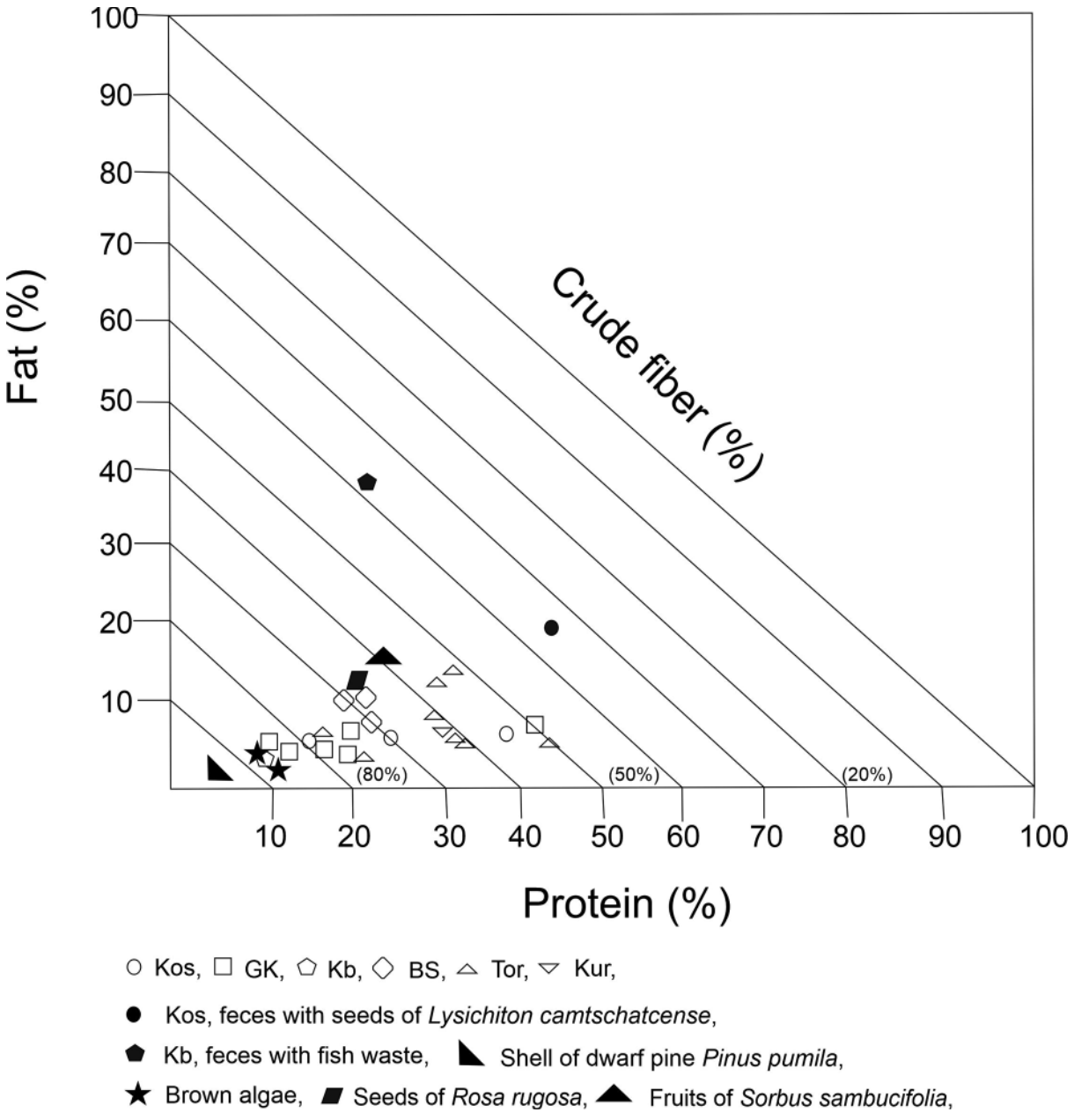

Fig. 4. The proportions of protein, fat, crude fiber for samples of bear scats and food plant objects in different locations of Iturup Island graphically represented as icons within different sections of the right-angled mixture triangle.

particle fractions from 0.25 to 3 mm predominated. However, the differences of dMean found between the pooled samples from coastal and mountainous areas are insignificant due to the strong variability of the composition in these samples. The proportion of DM of each fraction between the samples can vary 2–3 times. Therefore, to obtain statistically significant differences between habitats where bears concentrate for foraging, samples of fresh feces are required from $n = 100$ or more, which is technically difficult to implement, since bears do not use latrines, and the distribution of scats within habitats is often random.

The size of large particles in the scat primarily determines the dMean value. When analyzing the pooled samples, a positive correlation was noted between dMean and fecal particles from 10, 7, and 5 mm sieves, and a negative correlation was found with the particles of smaller size (Table 3). However, the dMean shows a wide range of data, but the range of extreme values is similar for different territorial sites and is most likely determined by the biological characteristics of the predator with its inherent type of digestion (Table 4). For the pooled samples, the average dMean for summer bear scats on Iturup was 8.34 mm. The CV of the dMean is within 65–105% (Table 4). The CV of the dMean in different samples is lower than the CV of the DM mass of separate particle fractions.

The fecal samples we collected had a complex mixed composition, predominantly of plant origin, and only a few samples consisted mainly of algae, berries, and seeds (Fig. 3, Table 5). The average dMean value was highest for scats consisting of algae, and lowest for ones consisting of fruits and seeds (Table 5). The CV of the dMean value was lower in samples consisting of fruits and seeds, which is associated with a more uniform small-sized fraction of these food items. This is also confirmed by the analysis of the composition of separate fractions (Fig. 3). The different level of destruction of certain ingested food and unevenness in the rate of passage of particles through the gastrointestinal tract are observed that is manifested in the formation of a specific fecal fractional profile.

As a result of zootechnical analysis, it was established that the contents of fresh scats contain a sufficiently large amount of nutrients (Table 6). This is largely due to the fact that high-calorie food quickly passes through the gut: it is ineffectively chewed and does not have enough time to be fully digested and absorbed. Nevertheless, the average share of protein, fat and fiber in feces is usually lower than in some groups of feed preferred by bears. In particular, the protein and fat content in rowan berries is 10.4% and 6.6%, respectively, and in rose seeds — 13.6% and 8.4%, respectively, which is significantly higher than the average content of these macronutrients in the scats with these plant items.

We have found out that the largest mass fraction of DM is crude fiber, and fat is represented by a minimal fraction for most of the samples. However, the differences in the concentration of these nutrients between samples can be very significant, that is determined by the pronounced individual preferences of the predator and the changing current daily diet. Therefore, the difference between the minimum and maximum values in the different samples for protein content was 4.0 times, for crude fiber — 8.5 times, and for fat — 18.5 times. This is also confirmed by the high level of the CV presented for all these components (Table 6). The protein ratio in the pooled sample group varies very widely — from 0.12 to 0.94 (on average 0.41±0.05) with the CV of 54.4%. The protein content correlates only with the fat content ($R^2 = 0.324$, at $p < 0.05$).

The distribution of the scat samples in the space of nutrients within the right-hand triangle allows us to demonstrate some patterns. The overwhelming majority of the analyzed samples are concentrated in the area of high crude fiber concentration (Fig. 4). The maximum fiber content is presented in the samples of algae (37% of DM) and dwarf pine shells (64% of DM), and, consequently, in the scat samples containing these components. The concentration of crude fiber in rowan berries is 24% of DM. Therefore, bear feces containing berries and seeds have less fiber. In contrast, feces including of *Lysichiton camtschatcense* seeds have a higher fat concentration, which significantly distinguishes the scat with these seeds from the other samples and brings them closer to the scat containing fish waste (Fig. 4). Thus, using the right-hand triangle, it is possible to divide the fecal samples into groups according to the presence of nutrients in them: samples containing mainly plant components and samples containing the animal remains.

Bear scats contain unequable concentrations of protein, fat and crude fiber in different territories. We were unable to identify reliable statistical differences between fecal samples from the surveyed landscapes. In the spatial field of the triangle, different samples diverge (Fig. 4), that ultimately allows us to characterize the food quality of bear habitats by the analysis of nutrients in the scats. For example, feces from the Tornaya bay and Kurilka river locations do not contain high concentrations of fiber. Here the bears consume a significant amount of protein food of animal and/or marine origin. On the contrary, in the ecosystems of the Goryachiy Klyuchi mountain range, the presence of bear feces with a high crude fiber content indicates the prevalence of poorly digestible plant foods in the diet. The samples from Kosatka bay are distributed over different areas of the right-hand triangle (Fig. 4), that indirectly demonstrates a high diversity of forages in this area and, as a result, the widest range of trophic preferences is realized with a free choice by a bear of easily accessible food. A similar picture is observed when analyzing the protein ratio. In some territories, low protein ratio values were noted (Kuibyshev bay — 0.25 (on average), Goryachiye Klyuchi — 0.30, Belye Skaly — 0.33). It specifies that the bear predominantly uses plant food with a low protein content. Within other landscapes, there is a higher protein ratio value (Tornaya bay — 0.48, Kosatka — 0.55, Kurilsk — 0.49),

which confirms the exploitation of high-protein food in these coastal habitats by this predator.

We have not found a statistical relationship between the concentration of macronutrients and the dMean value (as well as DM mass of separate fractions) in the scats. Only a weak, non-significant relationship (a kind of trend) has been discovered between the dMean value and the fat content: the higher the dMean, the less fat in the sample. It is possible that smaller fecal fractions contain more fat components than undigested large particles. The multi-component composition of various feeds consumed by bears, containing different proportions of fat, as well as different digestibility and assimilation of certain ingredients, make it difficult to find a clear statistical relationship between the macronutrient composition and the fractional scat profile.

Discussion

The density of bears in the surveyed area was 1.29–1.38 individuals/1000 ha. This high density of predators is indirectly indicated by their increased moving and feeding activities. A large number of tangled bear paths in various plant communities creates great difficulties in collecting the feces and its assessment if they belong to specific individuals. However, it can be assumed that the collected scats belong to adult bears, since 90% of all encountered predator tracks in the survey locations had a forepaw width from 12 to 16 cm (Polushkin & Scopin, 2025).

The Japanese subspecies of brown bear can be considered as one of the most herbivorous compared to the populations from the continental part of Eurasia. On Iturup, plant foods make up to 95% of the diet of this predator in the summer: from edible plants such as *Allium ochotense*, dwarf pine nuts, various berries (rowan, rose, etc.) to various types of forbs and even hard roots of bamboo *Sasa* sp., which dominates the vegetation (Velizhanin, 1970). However, the obvious trophic preference of the brown bear is mainly observed for berries and nuts, as the most attractive objects containing more nutrients (Boltunov, 1993). A similar diet of the brown bear was noted on the neighboring island of Kunashir (Perovsky, 1991).

In contrast to the standard analysis of the composition of food items in feces, there are few studies on the determination of the physical structure and chemical composition of scats, the assessment of macronutrient energy and the application of the nutritional geometry method for wild carnivorous mammals (e.g. Steyaert *et al*., 2012; Elfstrom *et al*., 2014; Remonti *et al*., 2016; Gazzola & Balestrieri, 2020; Abd El-Wahab *et al*., 2022; De Cuyper *et al*., 2023; Balestrieri *et al*., 2024). Although using the physicochemical characteristics of feces we can indirectly assess the nutrient status of diet of a particular animal and estimate the quality of its habitats.

The chemical composition of the food components certainly determines the high nutritional value of feces. The bear dental system is not perfect for chewing and grinding feed. Coupled with this is the fast passage of food through the gastrointestinal tract: 3–8 hours (Tsunamoto *et al*., 2024), and in exceptional cases — up to 48 hours (Pazhetnov & Pazhetnova, 1987). As a result, many food components are excreted intact and the digestibility of various nutrients is reduced (Pritchard & Robbins, 1990). At the same time, denser and harder digesta particles can remain in the gut of the bear longer (Pazhetnov & Pazhetnova, 1987). The time for food to pass through the bear gastrointestinal tract increases at feeding on animal carcasses and, on the contrary, the gut retention time is lower and excretion accelerates at digestion of berries (Elfstrom *et al*., 2013), since the digestibility of meat is higher than that of berries (Pritchard & Robbins, 1990). The increase of fiber in the diet enhances the rate of food passage through the gut (Elfstrom *et al*., 2013). For this reason, most seeds are not digested and are successfully excreted intact with feces, and subsequently these seeds easily germinate. Thus, undamaged seeds retain their nutritional value and caloric content while present in feces. As a result, the Japanese brown bear acts as a key endozoochorous animal — seed disperser (Tsunamoto *et al*., 2024).

The fractional scat profile is determined by the food particle size as a result of the oral processing and digestion of forages. The physical and chemical properties of the food objects have a significant impact on the degree of their processing and transformation by the digestive system. Strong individual variability in the qualitative composition of the bear scats makes it difficult to obtain reliable differences between samples collected in the coastal and inland areas of Iturup Island.

The reasons for the variation of the dMean value and the DM mass of certain fractions are the feeding of bears on a variety of foods over short periods of time, as well as the wide movements of these predators from the coasts into the interior of the island and back. That obscures the influence of the forage quality from small mosaic-like habitats on the characteristics and composition of the feces. Even in the inner parts of Iturup, bear scats contain remains of marine animals and algae, which indicates the active movement of predators across the island over a significant distance. Individual home ranges of brown bears often overlap, that is especially typical for island populations (McLoughlin *et al*., 2000). On Sakhalin Island, brown bears make the longest migrations in the summer, and the greatest overlap of their individual home ranges was observed in August during the period of active consumption of plants (Seryodkin *et al*., 2017). The annual home range of the brown bear in Hokkaido is usually within 28–43 km^2 (Mano, 1994; Sato *et al*., 2008). It is many times larger than the area of certain foraging biotopes. High density of brown bears forces them to move longer distances to reduce intraspecific competition for available food resources.

The strong scatter of the dMean value specifies a pronounced omnivory and directed trophic selectivity of the bear. A certain individual can show strong vari-

ability in the choice of a particular food, even within the daily diet. The lower trophic selectivity and selected food objects are relatively uniform in structure, the dMean will be a more stable value with a much smaller CV in the pooled samples.

The consistency of feces depends on the homogeneity of the particle composition and those in turn on the forage features. Large consumption of grasses or animals with bones and feathers leads to the formation of harder and denser feces in bears (De Cuyper *et al*., 2021). Our fecal samples had scores of 3–4 (according to the scale of De Cuyper *et al*., 2021), that indicates a heterogeneous diet composition. High content of large food fragments containing cellulose improves feces quality (Wichert *et al*., 2002). Bear feces become liquid at abundant feeding on salmonids (De Cuyper *et al*., 2021), which we have not observed in any of the samples found. We were able to find a few fragments from fish skeleton only in some scats. A similar fact is described for Sakhalin Island, where in the summer before the mass entry and spawning of salmonids into the rivers, fish remains were found in no more than 15% of bear scats (Benkovsky, 1972). Only in the tundra zone of Chukotka (at the northern limit of the brown bear's distribution, where the biomass of potential plant food is strictly limited) in the summer bear scats can contain up to 50–60% of animal items (Chernyavsky & Krechmar, 1993).

On average, the concentration of fiber in the feces of wild Scandinavian bears is about 25% of DM, but, in some individuals, it can reach 50% of DM in the spring (De Cuyper *et al*., 2021), that is probably due to the consumption of a large share of grasses and the lack of alternative feed. In the Iturup bears, the average fiber content was similar and amounted to an average of 23.5% of DM, although in some areas (Kb, GK) this value was higher. Probably, a fairly stable level of fiber consumption in the diet is a species-specific trophic feature of this predator. DM digestibility efficiency decreases with an increase in the concentration of fiber in the diet (Pritchard & Robbins, 1990).

On Iturup, we noted algae in large quantities in the bear scats, that predetermines the presence of increased concentrations of fiber in these samples. The consumption of algae by the bears is associated with the high density of their population, that is the consequence of the deficit of common easily accessible food. In the summer, the frequency of occurrence of bear footprints in different natural ecosystems of Iturup varies from 0.5 to 3.0 fresh tracks per 1 km (our data), while in Kamchatka — from 0.5 to 3.7 tracks per 10 km of the linear route (Krivenko *et al*., 2019). Due to the sparse density in other populations of the Pacific region, consumption of algae by a brown bear was recorded much less frequently. For example, in Kamchatka and Sakhalin, algae consumption was noted only in the spring not annually, after the bears emerged from their dens, when there was an acute shortage of alternative feed (Kostin & Eremin, 2004; Gordienko *et al*., 2006). For the Hokkaido bears, algae consumption was not indicated at all due to the fact that the Japanese islands have a fairly high abundance of other, more nutritious forages, including agricultural crops such as corn and sugar beets (Sato *et al*., 2004, 2005; Narita *et al*., 2011; Hata *et al*., 2017; Sakiyama *et al*., 2021).

The Far Eastern brown bear has been observed to actively consume food of animal origin only during short periods of time: gathering of different food items on the coast after leaving dens, foraging during the autumn migrations of salmonids, as well as a local trophic connection between this predator and anthropogenic food waste, including from the processing of raw materials in the fishing industry (Yudin, 1993).

In most of species range, the brown bear easily switches to consuming animal food when available. In mainland populations of this predator, ungulates represent important food resources that can be available as a source of protein throughout the year (Yudin, 1993). In Hokkaido, brown bears significantly increase a prey share in their diet with an increase of density of sika deer (*Cervus nippon*) (Kobayashi *et al*., 2012). These island bears also eat a large number of various insects (Kadosaki & Inukai, 2000; Kishimoto *et al*., 2017; Shirane *et al*., 2021; Tomita & Hiura, 2021). We have not found insect fragments in the collected scats. Most likely, the consumption of insects by bears largely depends on the characteristics of the habitat, season, and weather conditions of the current year. In Hokkaido, for example, it was shown that brown bears actively ate cicadas in larch communities, since it was difficult for bears to get food among densely growing bamboo and there were significantly fewer insects there (Tomita & Hiura, 2021). On the contrary, on Iturup, dwarf bamboo thickets are the main type of vegetation, so these habitats are poor feeding sites for the carnivore and it has to stick to and concentrate in azonal landscape complexes — along rivers and coasts, where there is a greater diversity of tall-grass forage vegetation.

Possibly, due to the lack of alternative prey, bears on Iturup consume more salmon fish compared to the Hokkaido population that was established by the stable isotope analysis of bone tissue (Matsubayashi *et al*., 2016a, b). In general, brown bears eat animals in certain intervals of their annual activity when it is necessary to restore body mass lost during winter starvation (Barboza *et al*., 2009). Although some individuals of bears on the southern Kuril Islands, possibly due to food shortage and insufficient fat accumulation, may not hibernate at all (Perovsky, 1988; Klitin, 1998).

The protein content is one of the key indicators in the bear's diet. The optimal proportion of protein is about 17% of DM, and the predator can regulate its intake in the process of free foraging by consuming a variety of diets in a short period of time (Erlenbach *et al*., 2014). That is, the protein content in the feces will indicate the availability of protein food for different individuals of bears at certain periods of their annual activity. However, it should be kept in mind that the increased content of proteins in the bear feces is associated not only with its abundant presence in the forage

ingredients, which do not have time to be fully digested and assimilated. This is also due to the targeted excretion of nitrogen from the body when its required level of needs is exceeded, that is, the main share of nitrogen in the feces is metabolic fecal nitrogen (Barboza *et al*., 2009). In addition, the increased proportion of plant foods with a high content of tannins and other protein-precipitating compounds that form joint irreversible complexes in the intestine can contribute to an increase in the concentration of nitrogen in the feces under certain conditions (Mould & Robbins, 1981; Hobbs, 1987; Verheyden *et al*., 2011).

Indirectly, the body's demand for feed protein is judged by the protein ratio. It has been found that from spring to autumn, the protein ratio value in the bear feces decreases. That indicates a gradual dominance of diets with less protein consisting mostly of plant-based feeds by autumn (De Cuyper *et al*., 2023). In our investigation, a simpler protein ratio (the ratio of protein to fats and fiber) is used, which averages 0.38 for the pooled sample, while for the Scandinavian bear, this ratio is based on the data from the publication (De Cuyper *et al*., 2023) averaged 0.82 for spring, 1.09 for summer, and 0.48 for autumn. Thus, outside the period of active salmon consumption the level of protein intake by the bear on Iturup was significantly lower than that of the European brown bear. The CV of this indicator in our study was 54.1%, while for the Scandinavian bear, the CV of the protein ratio varied greatly — from 28 to 80% depending on the season (De Cuyper *et al*., 2023).

The concentration of fecal fat is a measure closely related to the components of the food consumed. The proportion of fat in feces increases with enlarging a share of animal prey and plant seeds in diet. The fat in scat can be partially lost due to oxidation (especially unsaturated lipids) and the formation of calcium or magnesium soaps, but for carnivores this is less typical, unlike the droppings of ungulates (Robbins, 1983).

We have not found a significant relationship between the fractional profile and the composition of macronutrients in the bear feces, so the weak fragmentation of the feed is likely not to affect the digestibility and assimilation of components of the food digesta due to ineffective digestive processing and a rapid rate of its passage through the gut. This is confirmed by the experiments on dogs, in which no dependence of the digestibility of proteins and fats on the size of food particles was found (Abd El-Wahab *et al*., 2022). Nevertheless, the digestibility of macronutrients may depend on the specific types of feed, since with a reduce in the plant (especially starch-containing) food particles, the gelatinization process is intensified, that can ultimately lead to an increase in nutrient digestibility in carnivorous mammals. It has been established that in dogs consuming a rice diet, the particle size of the feed does not affect the digestibility of dry matter, fat and protein, but the efficiency of digestibility of corn and sorghum grains depends on the size of the ingested particles (Bazolli *et al*., 2015).

We have found a high degree of variability of the macronutrient concentration in the analyzed scats. The predominance of fiber, proteins or fats in food items is immediately reflected in the chemical composition of feces. It can be assumed that the Japanese subspecies of the brown bear has a high selectivity in their diet, which, as was previously established, may depend on the sex, age of the animals, the ability to effectively hunt a specific prey, and social relationships within the territorial group of this predator (Jimbo *et al*., 2020). Therefore, heterogeneity in scat quality will be found in different individuals within a population.

The qualitative and quantitative composition of diets of the island brown bear may directly depend on the landscape type, microhabitat and available forage in it (Ohdachi & Aoi, 1987; Jimbo *et al*., 2020). Thus, the composition of feces can be used for forage diagnostics of the habitats. Based on the distribution of chemically diverse scats, we have identified the territorial confinement of the collected samples: feces containing more protein are more common in the coastal zone, and ones with more fiber are in the interior of the island. Heterogeneity in the distribution of potential food resources (especially berries and fish) is reflected in the concentration of bears in certain landscapes. However, the naturally high abundance of this predator on the island and increased intraspecific competition for food resources in small optimal habitats force bears to move very widely, which smooths out the degree of aggregation of the feces distribution with certain nutrient composition. For this reason, we were unable to obtain significant statistical differences between the bear scat groups collected on the coasts and inland of Iturup Island. In Hokkaido, it was also found that the presence of feces containing pine nut fragments in different island locations in late summer confirms the fact of active brown bear movement between the coasts and interior subalpine ecosystems (Shirane *et al*., 2021).

Conclusion

The brown bear population on Iturup was formed using a variety of plant foods. There are no populations of wild ungulates or native small mammals on this island. Invasive rodents inhabit impassable bush thickets and are poorly available as food for the bear. Given the current high density of bears on Iturup at insufficient supply of available forages, the brown bear is forced to eat an unusual food, in particular algae. The main natural source of animal food for the brown bear in the short autumn period is salmon fish. However, the time periods of consumption of animals by this predator and the level of its piscivory on Iturup have not yet been assessed. We have not found any insect remains in the bear scats. The deficit of animal prey and abundance of alternative forage sources on the island stimulates bears use marine waste and visit the garbage dump in anthropogenic areas.

The fractional and chemical profiles of the scat reflect the individual trophic selectivity of the brown bear, since its diet on the island is based on hard and difficult-to-digest food, mainly of plant origin. The

high variability of the scat composition is confirmed by the large value of CV of the occurrence of different fractions of fecal particles. The greatest variability between samples is noted in relation to the mass of large fractions of fecal particles, the composition of which was determined by the proportion of algae and coarse plant parts. The mass of small fractions of fecal particles is a more stable indicator showing the efficiency of the digestive system.

Carnivorous mammals are characterized by rapid passage of the digesta through the gut and weak transformation of large and coarse food fragments by chewing, grinding and digesting, so the composition of feces can act as an indicator of the fractional and chemical composition of the food consumed. The share of certain macronutrients in scats increases following the increase of these nutrients in the bear diet. This is especially noticeable in relation to fat-containing food ingredients from fish and seeds of some plants.

Analysis of the brown bear scat allows us to diagnose its feeding preferences in the specific periods of time in certain habitats, which is especially important in conditions of high interannual, intraseasonal and individual variability of diets and heterogeneity of nutritional quality of food objects. The averaged data on the quality composition of scats in certain areas should demonstrate the response of the brown bear population group to the feeding situation in the current period. Fecal samples collected in different territories of Iturup Island have specific ratios of protein, fat and fiber. In particular, a scat often contains more protein in the coastal zone. Despite the fact that habitats with high diversity and abundance of available and nutritious food promote the aggregation of brown bears there, we cannot identify significant differences in the pooled scat samples between the coastal and mountain ecosystems of the island in terms of either the composition of fecal particle fractions or the chemical profile of macronutrients. This is most likely due to the wide spatial movements of brown bears across the island, which do not strictly adhere to certain landscapes in the summer in search of food, following a strategy of consuming abundant forage in areas where it is easily accessible. However, the more homogeneous in structure and less diverse the food items, the more unique the chemical and fractional fecal signatures will be. Therefore, to obtain significant differences in the composition of bear feces between habitats and landscapes, large quantity of scat samples within a year is needed.

The brown bear population on Iturup Island has distinctive trophic relationships with forage vegetation confirming the high ecological and behavioral plasticity of this predator and its high adaptability to consuming a variety of available forages.

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References

Abd El-Wahab A., Chuppava B., Zeiger A.L., Visscher C. & Kamphues J. 2022. Nutrient digestibility and fecal quality in Beagle dogs fed meat and bone meal added to dry food // Veterinary Sciences. Vol.9. No.4. P.164. DOI: 10.3390/vetsci9040164

Amano T., Masuda R. & Mano T. (eds.). 2006. [Introduction to Bear Study]. Hokkaido: Hokkaido University Press. 274 p. [in Japanese].

Aoi T. 1985. Seasonal change in food habits of ezo brown bears (*Ursus arctos yesoensis* Lydekker) in northern Hokkaido // Research Bulletin of Teshio Experimental Forest, Hokkaido University. Vol.42. No.4. P.721–732.

Balestrieri A., Gigliotti S., Caniglia R., Velli E., Zambuto F., De Giorgi E., Mucci N., Tremolada P. & Gazzola A. 2024. Nutritional ecology of a prototypical generalist predator, the red fox (*Vulpes vulpes*) // Scientific Reports. Vol.14. P.e7918. DOI: 10.1038/s41598-024-58711-6

Barboza P.S., Parker K.L. & Hume I.D. 2009. Integrative Wildlife Nutrition. Berlin-Heidelberg: Springer-Verlag. 342 p.

Barkalov V.Yu. 2009. [Flora of the Kuril Islands]. Vladivostok: Dalnauka. 468 p. [in Russian].

Baryshnikov G.F. 2007. [Mammals. The bear family (Ursidae)]. (Fauna of Russia and neighbouring countries. Vol.1. Iss.5. New Series. No.147.) St.-Petersburg: Nauka. 542 p. [in Russian].

Baryshnikov G.F. & Puzachenko A.Yu. 2009. Craniometrical variability in insular populations of brown bear (*Ursus arctos*, Carnivora) from Hokkaido, Sakhalin and South Kurils // Proceedings of the Zoological Institute RAS. Vol.313. No.2. P.119–142 [in Russian].

Bazolli R.S., Vasconcellos R.S., de-Oliveira L. D., Sa F.C., Pereira G.T. & Carciofi A.C. 2015. Effect of the particle size of maize, rice, and sorghum in extruded diets for dogs on starch gelatinization, digestibility, and the fecal concentration of fermentation products // Journal of Animal Science. Vol.93. No.6. P.2956–2966. DOI: 10.2527/jas2014-8409

Benkovsky L.M. 1972. [Some materials about the ecology of the Sakhalin bear] // [Ecology, Morphology, Protection, and Use of Bears]. Moscow: Nauka. P.10–13 [in Russian].

Bojarska K. & Selva N. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors // Mammal Review. Vol.42. No.2. P.120–143.

Boltunov A.N. 1993. [Nutrition of brown bears in the mountains of southern Russia] // [Bears of Russia and Adjacent Countries — Sate of Populations]. Moscow: Central Forest State Reserve. Vol.1. P.44–62 [in Russian with English summary].

Bromley G.F. 1965. [Bears of the Southern Far East]. Moscow–Leningrad: Nauka. 120 p. [in Russian].

Chernyavsky F.B. & Krechmar M.A. 1993. [Brown bear (*Ursus arctos* L.) of the tundra zone of Chukotka] // [Bears of Russia and Adjacent Countries — State of Populations].

Moscow: Central Forest State Reserve. Vol.2. P.75–88. [in Russian with English summary].
Coogan S.C.P. & Raubenheimer D. 2016. Might macronutrient requirements influence grizzly bear-human conflict? Insights from nutritional geometry // Ecosphere. Vol.7. No.1. P.e01204. DOI: 10.1002/ecs2.1204
Coogan S.C.P., Raubenheimer D., Stenhouse G.B. & Nielsen S.E. 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis // PLoS ONE. Vol.9. No.8. P.e97968. DOI: 10.1371/journal.pone.0097968
Coogan S.C., Raubenheimer D., Stenhouse G.B., Coops N.C. & Nielsen S.E. 2018. Functional macronutritional generalism in a large omnivore, the brown bear // Ecology and Evolution. Vol.8. No.4. P.2365–2376. DOI: 10.1002/ece3.3867
De Cuyper A., Clauss M., Lens L., Strubbe D., Zedrosser A., Steyaert S., Muñoz Saravia A. & Janssens G.P. J. 2021. Grading fecal consistency in an omnivorous carnivore, the brown bear: abandoning the concept of uniform feces // ZooBiology. Vol.40. No.3. P.182–191. DOI: 10.1002/zoo.21593
De Cuyper A., Strubbe D., Clauss M., Lens L., Zedrosser A., Steyaert S., Verbist L. & Janssens G.P.J. 2023. Nutrient intake and its possible drivers in free-ranging European brown bears (*Ursus arctos arctos*) // Ecology and Evolution. Vol.13. No.5. P.e10156. DOI: 10.1002/ece3.10156
Dulepinskikh L.N., Sycheva L.V., Yunusova O.Yu. & Popov A.N. 2022. [Zootechnical Analysis of Feed]. Perm: IC Prokost. 91 p. [in Russian].
Elfstrom M., Davey M.L., Zedrosser A., Muller M., De Barba M., Stoen O.-G., Miquel Ch., Taberlet P., Hacklander K. & Swenson J.E. 2014. Do Scandinavian brown bears approach settlements to obtain high-quality food? // Biological Conservation. Vol.178. P.128–135. DOI: 10.1016/j.biocon.2014.08.003
Elfstrom M., Støen O.-G., Zedrosser A., Warrington I. & Swenson J.E. 2013. Gut retention time in captive brown bears *Ursus arctos* // Wildlife Biology. Vol.19. No.3. P.317–324. DOI: 10.2981/12-121
Erlenbach J.A., Rode K.D., Raubenheimer D. & Robbins Ch.T. 2014. Macronutrient optimization and energy maximization determine diets of brown bears // Journal of Mammalogy. Vol.95. No.1. P.160–168. DOI: 10.1644/13-MAMM-A-161
Fritz J., Streich J. W., Schwarm A. & Clauss M. 2012. Condensing results of wet sieving analyses into a single data: a comparison of methods for particle size description // Journal of Animal Physiology and Animal Nutrition. Vol.96. No.5. P.783–797. DOI: 10.1111/j.1439-0396.2011.01183.x
Ganzey K.S. 2010. [Landscapes and Physiogeography Division of Kuril Islands]. Vladivostok: Dalnauka. 214 p. [in Russian].
Gazzola A. & Balestrieri A. 2020. Nutritional ecology provides insights into competitive interactions between closely related *Martes* species // Mammal Review. Vol.50. No.1. P.82–90. DOI: 10.1111/mam.12177
Gordienko V.N., Enns M.H. & Gordienko T.A. 2006. [Brown bear feeding on vegetation in the southern regions of Kamchatka] // [Kamchatka Brown Bear: Ecology, Conservation, and Sustainable Use]. Vladivostok: Dalnauka. P.103–115 [in Russian].
Hata A., Takada M. B., Nakashita R., Fukasawa K., Oshida T., Ishibashi Y. & Sato Y. 2017. Stable isotope and DNA analyses reveal the spatial distribution of crop-foraging brown bears // Journal of Zoology. Vol.303. No.3. P.207–217. DOI: 10.1111/jzo.12479
Hirata D., Mano T., Abramov A.V., Baryshnikov G.F., Kosintsev P.A., Murata K. & Masuda R. 2017. Paternal phylogeographic structure of the brown bear (*Ursus arctos*) in northeastern Asia and the effect of male-mediated gene flow to insular populations // Zoological Letters. Vol.3. P.e21. DOI: 10.1186/s40851-017-0084-5
Hobbs Th.N. 1987. Fecal indices to dietary quality: a critique // The Journal of Wildlife Management. Vol.51. No.2. P.317–320.
Hume I.D. 2005. Concepts of digestive efficiency // Starck J.M. & Wang T. (eds.). Physiological and Ecological Adaptations to Feeding in Vertebrates. Enfield-Plymouth: Science Publishers Inc. P.43–58.
Inukai T. & Kadosaki M. 1987. [Brown Bear: Nature of Hokkaido]. Hokkaido: Hokkaido Shimbun. 353 p. [in Japanese].
Jimbo M., Ishinazaka T., Shirane Y., Umemura Y., Yamanaka M., Uno H., Sashika M., Tsubota T. & Shimozuru M. 2022. Diet selection and asocial learning: natal habitat influence on lifelong foraging strategies in solitary large mammals // Ecosphere. Vol.13. No.7. P.e4105. DOI: 10.1002/ecs2.4105
Kadosaki M. & Inukai T. 2000. [Brown bear]. Hokkaido: Hokkaido Shimbun. 377 p. [in Japanese].
Kishimoto Y., Takahashi Sh., Ohara M. & Sato Y. 2017. Entomophagy by brown bears in the Urahoro region, eastern Hokkaido, Japan // Bulletin of the Historical Museum of Urahoro. Vol.17. P.13–18 [in Japanese].
Klitin A.K. 1998. [Notes on the brown bear of Sakhalin and the Kuril Islands] // Bulletin of the Sakhalin Museum. No.5. P.271–280 [in Russian].
Kobayashi K., Sato Y. & Kaji K. 2012. Increased brown bear predation on sika deer fawns following a deer population irruption in eastern Hokkaido, Japan // Ecological Research. Vol.27. No.5. P.849–855. DOI: 10.1007/s11284-012-0962-4
Kostin A.A. & Eremin Yu.P. 2004. [Brown bear (*Ursus arctos*) on Sakhalin and the Kuril Islands] // Bulletin of the Sakhalin Museum. No.11. P.366–375 [in Russian].
Krivenko V.G., Valentsev A.S., Gerasimov Yu.N., Kirichenko V.E., Tkachenko E.E. & Kuznetsov A.V. 2019. [Game Animals of the Kamchatka Krai (state of resources, protection and rational use)]. Petropavlovsk-Kamchatsky: Kamchatpress. 227 p. [in Russian].
Machovsky-Capuska G.E., Senior A.M., Simpson S.J. & Raubenheimer D. 2016. The multidimensional nutritional niche // Trends Ecology & Evolution. Vol.31. No.5. P.355–365. DOI: 10.1016/j.tree.2016.02.009
Mano T. 1994. Home range and habitat use of brown bear in the southwestern Oshima Peninsula, Hokkaido // Bears: Their Biology and Management. International Conference on Bear Research and Management. Vol.9. No.1. P.319–325.
Matsubayashi J., Morimoto J., Mano T., Aryal A. & Nakamura F. 2014. Using stable isotopes to understand the feeding ecology of the Hokkaido brown bear (*Ursus arctos*) in Japan // Ursus. Vol.25. No.2. P.87–97.
Matsubayashi J., Otsubo K., Morimoto J. O., Nakamura F., Nose T. & Tayasu I. 2016a. Feeding habits may explain the morphological uniqueness of brown bears on Etorofu Island, Southern Kuril Islands in East Asia // Biological Journal of the Linnean Society. Vol.119. No.1. P.99–105. DOI: 10.1111/bij.12798
Matsubayashi J., Tayasu I., Morimoto J. O. & Mano T. 2016b. Testing for a predicted decrease in body size in brown

bears (*Ursus arctos*) based on a historical shift in diet // Canadian Journal of Zoology. Vol.94. No.7. P.489–495. DOI: 10.1139/cjz-2016-0046

McLoughlin Ph.D., Ferguson S.H. & Messier F. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations // Evolutionary Ecology. Vol.14. P.39–60.

Mould E.D. & Robbins Ch.T. 1981. Nitrogen metabolism in elk // Journal of Wildlife Management. Vol.45. No.2. P.323–334.

Narita R., Mano T., Yokoyama R. & Takayanagi A. 2011. Variation in maize consumption by brown bears (*Ursus arctos*) in two coastal areas of Hokkaido, Japan // Mammal Study. Vol.36. No.1. P.33–39. DOI: 10.3106/041.036.0104

Naves J., Fernandez-Gil A., Rodriguez C. & Delibes M. 2006. Brown bear food habits at the border of its range: a long-term study //Journal of Mammalogy. Vol.87. No.5. P.899–908.

Ohdachi S. & Aoi T. 1987. Food habits of brown bears in Hokkaido, Japan // Bears: Their Biology and Management. International Conference on Bear Research and Management. Vol.7. P.215–220.

Pazhetnov V.S. & Pazhetnova S.I. 1987. [The speed of passage of a single food portion through the digestive tract of a brown bear] // [Ecology of Bears]. Novosibirsk: Nauka. P.108–112. [in Russian].

Perovsky M.D. 1988. [Bears of Kunashir Island] // Okhota i Okhotnichie Khozyastvo. No.2. P.12–13 [in Russian].

Perovsky M.D. 1991. [Morphology and ecology of the bear of Kunashir Island] // [Bears in the USSR]. Novosibirsk: Nauka. P.233–242. [in Russian].

Polushkin A.A. & Scopin A.E. 2025. Assessment of the occurrence of brown bear (*Ursus arctos*) tracks on Iturup Island // [Current Problems of Biogeography of the Far Eastern Region of Russia]. Khabarovsk: BF Biosfera. P.159–164 [in Russian].

Pritchard G.T. & Robbins Ch.T. 1990. Digestive and metabolic efficiencies of grizzly and black bears // Canadian Journal of Zoology. Vol.68. No.8. P.1645–1651.

Raubenheimer D. 2011. Toward a quantitative nutritional ecology: the right-angled mixture triangle // Ecological Monographs. Vol.81. No.3. P.407–427.

Remonti L., Balestrieri A., Raubenheimer D. & Saino N. 2016. Functional implications of omnivory for dietary nutrient balance // Oikos. Vol.125. No.9. P.1233–1240. DOI: 10.1111/oik.02801

Robbins Ch. T. 1983. Wildlife Feeding and Nutrition. San Diego, New York et al.: Academic Press. 343 p.

Sakiyama T., Morimoto J., Matsubayashi J., Furukawa Y., Kondo M., Tsuruga H., Mano T. & Nakamura F. 2021. Factors influencing lifespan dependency on agricultural crops by brown bears // Landscape and Ecological Engineering. Vol.17. P.351–362. DOI: 10.1007/s11355-021-00446-x

Sato Y. 2009. Brown bear *Ursus arctos* L., 1758 // Ohdachi S.D., Ishibashi Y., Iwasa M.A. & Saitoh T. (eds.). The Wild Mammals of Japan. Kyoto: Shoukadoh. P.232–234.

Sato Y., Aoi T., Kaji K. & Takatsuki S. 2004. Temporal changes in the population density and diet of brown bears in eastern Hokkaido, Japan // Mammal Study. Vol.29. No.1. P.47–53.

Sato Y., Kobayashi Y., Urata T. & Takatsuki S. 2008. Home range and habitat use of female brown bear (*Ursus arctos*) in Urahoro, eastern Hokkaido, Japan// Mammal Study. Vol.33. No.3. P.99–109.

Sato Y., Mano T. & Takatsuki S. 2005. Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan // Wildlife Biology. Vol.11. No.2. P.133–144.

Seryodkin I.V., Paczkowski J., Borisov M.Y. & Petrunenko Y.K. 2017. Home ranges of brown bears on the Kamchatka peninsula and Sakhalin Island // Contemporary Problems of Ecology. Vol.10. No.6. P.599–611.

Shirane Y., Jimbo M., Yamanaka M., Nakanishi M., Mori F., Ishinazaka T., Sashika M., Tsubota T. & Shimozuru M. 2021. Dining from the coast to the summit: salmon and pine nuts determine the summer body condition of female brown bears on the Shiretoko Peninsula // Ecology and Evolution. Vol.11. No.10. P.5204–5219. DOI: 10.1002/ece3.7410

Steyaert S.M.J.G., Hutter F.J., Elfstrom M., Zedrosser A., Hacklander K., Le M.H., Windisch W.M., Swenson J.E. & Isaksson T. 2012. Faecal spectroscopy: a practical tool to assess diet quality in an opportunistic omnivore // Wildlife Biology. Vol.18. No.4. P.431–438. DOI: 10.2981/12-036

Tomita K. & Hiura T. 2021. Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear *Ursus arctos* // Wildlife Biology. No.4. P.wlb.00886. DOI: 10.2981/wlb.00886

Tsunamoto Y., Tsuruga H., Kobayashi K., Sukegawa T. & Asakura T. 2024. Seed dispersal function of the brown bear *Ursus arctos* on Hokkaido Island in northern Japan: gut passage time, dispersal distance, germination, and effects of remaining pulp // Oecologia. Vol.204. No.3. P.505–515. DOI: 10.1007/s00442-024-05510-5

Tumanov I.L. 2017. [Brown Bear on the Islands of the South Kurils]. Saint Petersburg: OOO IPK Biont. 160 p. [in Russian].

Velizhanin A. 1970. [Bears of Iturup] // Okhota i Okhotnichie Khozyastvo. No.4. P.12–13 [in Russian].

Verheyden H., Aubry L., Merlet J., Petibon P., Chauveau-Duriot B., Guillon N. & Duncan P. 2011. Faecal nitrogen, an index of diet quality in roe deer *Capreolus capreolus*? // Wildlife Biology. Vol.17. No.2. P.166–175. DOI: 10.2981/10-111

Voronov V.G. 1972. [Brown bear of the islands of Sakhalin region] // [Ecology, Morphology, Protection, and Use of Bears]. Moscow: Nauka. P.22–24 [in Russian].

Voronov V.G. 1974. [Mammals of the Kuril Islands]. Leningrad: Nauka. 162 p. [in Russian].

Vshivtsev V.P. 1972. [Some information about the brown bear of the Sakhalin region and adjacent territories] // [Ecology, Morphology, Protection, and Use of Bears]. Moscow: Nauka. P.29–32 [in Russian].

Urusov B.M. & Chipizubova M.N. 2000. [Vegetation of the Kuril Islands: Questions of Dynamics and Origin]. Vladivostok: RAS. 302 p. [in Russian].

Wichert B., Schuster S., Hofmann M., Dobenecker B. & Kienzle E. 2002. Influence of different cellulose types on feces quality of dogs // Journal of Nutrition. Vol.132. No.6. P.1728S–1729S.

Yudin V.G. 1993. [Sakhalin and the Kuril Islands] // [Bears: Brown Bear, Polar Bear, Asian Black Bear]. Moscow: Nauka. P.403–419 [in Russian with English summary].