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Trophic adaptations of the red fox *Vulpes vulpes* on Urup Island (Kuril Archipelago)

Alexey E. Scopin*, Svetlana V. Lipatnikova & Tatiana G. Shikhova

ABSTRACT. We have studied the composition of scats in the free-ranging population of the red fox *Vulpes vulpes* on Urup Island during the population depression of the island's key prey — the brown rat *Rattus norvegicus caraco*. The scat samples were collected on the northern and southern points of the island. We determined the occurrence of certain food components and biomass of the different-sized fractions of the faecal particles after sieving. Vertebrates make up a small part of the red fox`s diet, both in terms of occurrence and biomass of the remains in the scats. The occurrence of the micromammals is less than 20%. Bird remains occur in the scats twice as high especially in the northern part of the island, where there are forest communities. Insects and crustaceans have the greatest occurrence and the bulk of the biomass in the faecal fragments. This demonstrates the importance of coastal and tidal habitats for the red fox. The berries of wild shrubs are often found in the scats. The discrete mean (dMean) of faecal particle size is 2.47 ± 0.12 mm for all samples. The dMean value is determined by the proportion of the largest faecal particle fraction. The proportion of the smallest size fraction of particles reliably correlates with the fraction of insect biomass. The negative correlation is found between the proportions of the biomass of insects and crustaceans, and between the proportion of crustaceans and the proportion of plant items in the scats. In the period of reduction and absence of some foods in local island sites, the red fox switches to alternative forages easily, confirming its dietary plasticity and opportunistic omnivory. The importance of certain food items in the fox nutrition and the ecological significance of this mesopredator in the ecosystems of Urup Island have been discussed.

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KEY WORDS: red fox, scat analysis, diet, faecal particle size, Urup Island.

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Трофические адаптации лисицы *Vulpes vulpes* на острове Уруп (Курильский архипелаг)

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РЕЗЮМЕ. Исследовали состав кормовых объектов у свободноживущей популяции лисицы *Vulpes vulpes* на острове Уруп в период депрессии численности единственного мелкого млекопитающего острова — серой крысы *Rattus norvegicus caraco*. Образцы помета были собраны на северной и южной оконечности острова. Проводили идентификацию кормовых объектов в помете и определяли процент их встречаемости. Оценивали биомассу размерных фракций помета после просеивания. Установлено, что позвоночные животные составляют малую часть рациона лисиц, как по встречаемости, так и по биомассе остатков в помете. Встречаемость млекопитающих составила менее 20%. В два раза выше была встречаемость в помете остатков птиц, особенно в северной части острова, где имеются лесные сообщества. Наибольшая встречаемость и основная часть биомассы в помете лисиц принадлежит насекомым и ракообразным. Это подчеркивает важность для лисиц прибрежных и приливно-отливных местообитаний. Часто встречаются в помете лисиц остатки ягод кустарников. Дискретный средний размер частиц (dMean) в помете лисиц по всем образцам составил 2.47 ± 0.12 мм. Величина dMean определяется долей наиболее крупной фракции частиц в помете. Величина наименьшей фракции частиц в помете достоверно коррелирует с долей биомассы насекомых. Обнаружена отрицательная корреляция между пропорциями биомассы насекомых и ракообразных в помете, и между долей ра-

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кообразных и долей плодов растений. При недостатке и отсутствии на локальных участках острова определенных кормов лисица переходит на использование других источников пищи, подтверждая свою диетарную пластичность и оппортунистическую всеядность. Обсуждаются вопросы о важности определенных кормовых объектов в питании лисиц и экологическом значении этого хищника в экосистемах острова Уруп.

КЛЮЧЕВЫЕ СЛОВА: лисица, анализ помета, питание, размеры частиц в помете, остров Уруп.

Introduction

The native area of the red fox (*Vulpes vulpes* L., 1758) encompasses many landscape zones of the Northern Hemisphere (Heptner *et al*., 1998; Sillero-Zubiri, 2009). Due to its ecological plasticity this carnivorous mammal inhabits many different biotopes, including urban territories (Doncaster *et al*., 1990; Uraguchi, 2018). The usage of a wide dietary diversity was one of the reasons for the success of the origin of red fox populations after the introduction to new locations. The striking example is the translocation of the red fox into Australia, where it had a huge impact on the abundance and composition of the fauna and influenced the extinction of many aboriginal species (Saunders *et al*., 2010).

The Kuril archipelago is part of the native range of the red fox. At present, it is accepted that the subspecies *Vulpes vulpes schrencki* Kishida, 1924 inhabits Hokkaido and Sakhalin Islands and *Vulpes vulpes splendidissima* Kishida, 1924 dwells on the North and Central Kuril Islands (Sillero-Zubiri, 2009; Uraguchi, 2009, 2018). The taxonomic status of the red fox on Urup Island is unclear, as there is a complex history of the origin of its population. The Urup fox is believed to have intermediate morphological characters between these two subspecies (Voronov, 1974).

Urup Island has an oceanic origin: it has always been isolated and did not possess any land connections and bridges with the mainland (Urusov & Chipizubova, 2000). Apparently, the red foxes penetrated by the ice floes from the mainland and large islands (from Kamchatka, Sakhalin, and Hokkaido) to many islands of the Kuril Archipelago (Velizhanin, 1970; Voronov, 1974; Kostenko *et al*., 2004), where they could subsequently survive in isolation, and in the presence of a sufficient supply of food sources form stable populations. On islands that are too small in area, the populations of the red fox sometimes sharply decrease due to a lack of foods, and carnivores become extinct (Voronov, 1974).

The historical chronicles reported on permanent habitation of red foxes on the Kuril Islands. The red foxes had long been hunted by indigenous Ainu people (Sokolov, 2014). The red fox on Urup Island was first mentioned at the end of the 18th century (Shelekhov, 1793). In the 19th century, about 110 red foxes were harvested annually on this island, and a maximum of 368 individuals per year (Golovnin, 1862; Sergeev, 1947). In the middle of the 20th century, about 250 foxes were yielded on this island annually (Kuznetsov, 1949).

The fur was of great economic importance in the past centuries. The active domestication and breeding of the wild foxes began in America and then in other countries at the end of the 19th century (Walter, 1914; Generozov, 1916; Isto, 2012). Subsequently, the domesticated foxes were introduced into nature, where they interbred with wild foxes, changing the gene pool of these native forms. The introduction of American silver foxes on the northern Pacific islands was more common (Voronov, 1974). The Russian-American company imported alien foxes to ecosystems of the Kuril Islands in the 19th century, and the Japanese breeders did it again in the 20th century (Ishino, 1925; Klumov, 1960; Kostenko *et al*., 2004). It is unknown what color morphs of red foxes were introduced to Urup Island (Ishino, 1932), but melanistic variants of foxes were brought to Hokkaido only in 1941 (Sioto, 1946). Until 1945, four Japanese fur husbandry farms operated on Urup Island, located at different parts of the island: the Takotan (Reid Otkrytyi), Natasha, Novokurilskaya, and Aleutka bays (Kuznetsov, 1949; Gridyaeva *et al*., 2016). The release of captive foxes into the wild led to the origin of the hybrid population of a carnivore on this island (Fig. 3).

The density of red foxes is uneven for many Kuril Islands that is largely determined by the low diversity of the main potential prey — small mammals. At the beginning of the 20th century, in order to maintain the fox populations, the Japanese introduced the root vole *Alexandromys oeconomus* Pallas, 1776 on the Kuril Islands, and in some of them it successfully survived (Voronov, 1982). There are no native micromammals on many islands, including Urup, and the red foxes are forced to consume the marine plant-animal waste and carcasses of sea mammals thrown ashore (Voronov, 1974). For this reason, the density of the fox is always higher in the coastal zone.

Long existence of fox populations on some of the Kuril Islands is associated with the high abundance of the brown rat *Rattus norvegicus caraco* Pallas, 1779, which entered the islands at the time of active marine mammal hunting (Voronov, 1982; Kostenko *et al*., 2004). Although it is possible that the Ainu could also have brought rats to the islands (Kostenko, 2002). In some years, rat populations can reach high density, concentrating along the coasts and floodplains (Kostenko *et al*., 2004). It is known from historical chronicles that a huge number of rats have always been observed on Urup Island (Shelekhov, 1793; Voronov, 1974).

For the first time, the forage composition of the red fox on Urup Island was investigated in the middle of the last century during the peak of the rat density (Shmeleva, 1958). Subsequently, a comparative analysis of fox diets for some other neighboring islands (Iturup, Paramushir, Sakhalin) was also carried out (Shmeleva, 1963; Berzan, 1990). However, in recent decades, Urup rat population has sharply decreased, and they are thriving only in local areas of the island (near residential and abandoned buildings), so it is not known what food sources the fox population now has.

In the absence of small mammals, the red foxes can affect bird populations in the Kuril Islands. Canids that recently got on some islands have led to a sharp decrease or disappearance of many ground-nesting birds and significantly reduced the area of seabird colonies (Kostenko *et al*., 2004). The smaller the island is, the more noticeable the impact of land mammal predators on populations of birds is. A particularly striking example of the complete destruction of seabird colonies was noted after the introduction of Arctic foxes *Vulpes lagopus* L., 1758 on the Islandhir Islands, where the proportion of birds in the diet of predators reached 97% (Voronov, 1982; Kostenko *et al*., 2004), a similar negative effect of mesocanids on avifauna was recorded on the Commander and Aleutian Islands (Ilina, 1950; Murie, 1959; Bailey & Kaiser, 1993).

Invertebrates and plants can also take on the role of alternative prey for canids on the islands of the North Pacific. The hardness and low digestibility are the main constraints that prevent mammals from consuming these food materials. Therefore, the efficiency of the predator's processing of a forage can be of decisive importance. It is known that mesocarnivores are able to exist for a long time and maintain a positive energy balance on a diet of invertebrates (Carbone *et al*., 1999). The success of survival on a non-meat diet largely depends on the thoroughness of the mastification of the feed, which contributes to better assimilation and absorption of nutrients in the intestinal tract of mammals (Moore & Sanson, 1995). Indirectly, the efficiency of digestion can be determined by analysis of the physical structure of the scats, namely by the estimation of the ratio of faecal particles of different sizes. It should be expected that the proportion of large particles in the scats will increase in individuals existing on the forages that include highly fibrous parts of plants and recalcitrant substances (bones, chitinous exoskeletons, shells, feathers). The same approach is classic for the understanding of nutrition processes in herbivorous mammals (Clauss *et al*., 2002). Currently, the assessment of the size fractions of digesta particles and the forming of faeces is carried out for carnivorous mammals under experimental conditions (De Cuyper *et al*., 2017, 2018). However, there are not any comparative studies of the composition of the particles from scats in the different populations of carnivores in wild, although this direction is quite promising in ecological studies of trophic strategies of vertebrates under various environmental conditions.

The aim of our study was to assess the diet of the red fox on Urup Island in the period of low abundance of rodents and the efficiency of processing the ingested foods by sieving scat analysis and also to consider the degree of potential trophic influence of a predator on the biodiversity of the island's ecosystem.

Study area and methods

Characteristics of the survey territory

Urup Island is a continuous monolithic chain of mountain ranges of volcanic origin. It is located in the group of the Central Kuril Islands. In the old Russian Geographical Classification, this island has number 18 (Sergeev, 1947). The territory of the island is 1427.6 km^2 with a coastline length of 282 km and a maximum height is 1328 m asl (Kolokol Volcano) (Ganzey, 2010). The island has a heterogeneous surface: highly rugged terrain, rocky coastal cliffs, steep mountain slopes. Landscapes of steep slopes formed by lava flows make up about 43% of the island's area. The ancient volcanoes cover about 17% of the area. There is a great number of streams: the slopes and bottoms of streams make up more than 20% of the overall area. There are hardly any lakes. Their total area is about 2 km^2. The anthropogenically disturbed territories account for 5.5%, but with a tendency to increase due to the development of the gold deposit in the south part of the island (Ganzey, 2010). The complex indented coastline and rugged terrain of the island limit the possibility of conducting field surveys.

According to the geobotanical division, Urup Island belongs to the southern Kuril province with dominant vegetation consisting of the stone-birch with bamboo on ocher-podzolic soils (Vorobiev, 1963; Ganzey, 2010). Some authors distinguish a separate floristic Urup Region (Barkalov, 2002). Urup is the northernmost island of the Kuril archipelago, where forests of stone birch *Betula ermanii* Cham. are conserved. The forests are located in the central and northern parts of the island. Stone birch forests account for up to 60% of the island's area, but the height of trees does not usually exceed 10 m (Urusov & Chipizubova, 2000). Forests are fragmented. The historically recent degradation of the taiga, which once completely covered Urup in one of the preceding interglacial periods, caused sparseness of the forest (Krivolutskaya, 1973). In addition, active Late Pleistocene and Holocene volcanism greatly affects forest vegetation. The last large coniferous trees had disappeared there by the beginning of the 20th century (Urusov & Chipizubova, 2000). The Ainu inhabited the southern part of the island, and permanent Russian settlements have existed here since the end of the 18th century, people practiced agriculture and animal husbandry (Sergeev, 1947). This is one of the reasons of gradual disappearance of the forest on the southern part of the island. Now the landscape of the south of the island is a plain overgrown with various grassland communities.

The forest structure also includes *Duschekia maximowiczii* (Call. ex C.K. Schneid.) Pouzar and *Sorbus commixta* Hedl. often together with a continuous undergrowth of bamboo *Sasa kurilensis* (Rupr.) Makino et Shibata. The bamboo on the island is a key species in the vegetation of Urup Island. Therefore, the height of the bamboo corresponds to the thickness of the snow cover. *Ilex rugosa* Fr. Schmidt, *Skimmia repens* Nakai, *Toxicodendron orientale* Greene, *Taxus cuspidata* Siebold et Zucc., *Sorbus sambucifolia* Cham. et Schlecht., *Linnaea borealis* L., *Vaccinium vitis-idaea* L., *V. uliginosum* L., *V. praestans* Lamb., *Euonymus alata* (Thunb. ex Murray) Siebold, *E. macroptera* Rupr., *E. sachalinensis* (Fr. Schmidt) Maxim., *Lonicera caerulea* L., *L. chamissoi* Bunge ex P. Kir. grow under the forest canopy. In the floodplains of rivers, the vegetation is formed by treelike and shrub willows (*Salix caprea* L., *S. ketoiensis* Kimura). The river floodplains are characterized by the presence of dense tall grasses (up to 3 m): *Reynoutria sachalinensis* (Fr. Schmidt) Nakai, *Cirsium kamtschaticum* Ledeb. ex DC., *Filipendula camtschatica* (Pall.) Maxim., *Cacalia kamtschatica* (Maxim.) Kudo, *Petasites japonicus* (Siebold et Zucc.) Maxim., *Heracleum lanatum* Michx., and thickets of *Rosa rugosa* Thunb. shrubs that are more common along the sea coast (Urusov & Chipizubova, 2000; Barkalov, 2009).

On the slopes of the hills, where forest is absent, there are usually extensive thickets of the Siberian dwarf pine *Pinus pumila* (Pall.) Regel often with bamboo. The upper boundary of the dwarf pine runs at the altitude of 600 to 800 m asl (Korsunskaya, 1958). The highlands do not have a continuous vegetation cover and are represented by bare stones and rubble.

The coastal zone is heterogeneous: narrow sandy and rocky beaches within indistinct bays are combined with steep and highly fissured rocks. This creates conditions for the formation of marine littoral communities with a high diversity of animals and plants. In the group of algae, the most common and abundant species are from the genera *Fucus*, *Halosaccion*, *Porphyra*, *Heterochordaria*, *Rhodymenia*, *Rhodoglossum*, *Monostroma*, *Acrosiphonia*, *Ulva*, *Clathromorphum*, *Alaria*, etc. Among mollusks, the dominants of marine communities are *Littorula*, *Nucella*, *Lacuna*, *Falsicingula*, *Collisella*, *Mytilus*, etc. Common and widespread species of crustaceans in the coastal waters of Urup Island are *Anisogammarus*, *Idotea*, *Ischyrocerus*, *Pagurus*, *Parallorchestes*, *Synidotea*, *Allorchestes*, *Najna*, *Archaeomysis*, *Balanids*, *Chthamlita*, *Tetraclita*, etc. There is a great biomass of pycnogonids (*Achelia*), polychete (*Nereis*), oligochaetes, turbellarians and sea urchins (Kussakin *et al*., 1974). Many of the above groups of invertebrates can be the food for terrestrial animals in the littoral zone after a low tide and in the form of organic waste after regularly occurring storms.

There are several fish species in the rivers and streams of Urup Island, which are a potential food resource for foxes. Salmonids (*Oncorhynchus gorbuscha* Walbaum, 1792; *O. keta* Walbaum, 1792; *O. kisutch* Walbaum, 1792; *Salvelinus leucomaenis* Pallas, 1814; *S. malma krascheninnikovi* Taranetz, 1933; *S. curilus* Pallas, 1814 massively migrate to inland waters in autumn for spawning, and juveniles of these fish develop throughout the year here. Other freshwater inhabitants are small-sized fish species *Gasterosteus aculeatus* Linnaeus, 1758 and *Pungitius sinensis* Guichenot, 1869. However, the overall fish productivity in the fresh waters of the island is insignificant (Shedko, 2002; Zhivoglyadov *et al*., 2011).

The growing season is short. On the central Kuril Islands, the marine climate features are most pronounced. It is a cloudy and foggy region in both winter and summer. There is a lot of precipitation (1015–1230 mm in average annually). Large masses of snow accumulate in the floodplains. There are no low temperatures. The average annual air temperature is +2.2–2.7°C. The average temperature in the winter is –6.3–6.6°C. The maximum depth of snow cover is 76 cm. The number of days with strong winds in open areas is 100–150 days a year, they are especially strong in the autumn-winter (up to 40 m/s) (Ganzey, 2010), so foxes dig a large number of permanent and temporary burrows.

We have used the scat analysis for investigating the diet of foxes. This method is considered traditional while researching the feeding and nutrition of wild canids (e.g. Zharkov *et al*., 1932; Borodina, 1940; Teplova, 1947; Chirkova, 1948; Nasimovich, 1948; Murie, 1959; Petrov, 1967; Gavrin & Krapivny, 1965; Reynolds & Aebischer, 1991; Klare *et al*., 2011; Reshamwala *et al*., 2018; O'Connor *et al*., 2020). In Hokkaido Island, the red fox does not make long migrations, and most of the individuals in the population move within a range of several kilometers (Tsukada, 1997; Uraguchi, 2018). Therefore, we have assumed that the red foxes of the northern and southern parts of Urup Island, living at a distance of about 100 km from each other, may well represent different population groups. We collected fresh fox scats from August 31 to September 12, 2019. The potential diversity of food items in this period is maximum for assessing the food selection by a fox. Scat samples were kept in 70% ethanol. All samples were collected in the western (Okhotsk Sea) part of the island. Samples ($n = 27$) from the northern (forested) part of the island were collected within a radius of 15 km near the camp (N 45.2097°, E 150.3186°). Samples ($n = 27$) from the southern (grassland ecosystems) part of the island were collected within a radius of 15 km from another camp (N 45.6128°, E 149.4622°), including the area of Van der Linde Cape. Most of the scat samples were found near the coasts. Scats in the interior of the island were collected along footpaths, roads and along river banks.

In the laboratory, the scats were soaked in water for 24 hours, being stirred occasionally. Subsequently, the samples were thoroughly washed through a set of 7 sieves (diameter 5, 3, 2, 1, 0.5, 0.25, and 0.025 mm). The sediment after sieving and the contents of the fractions from each sieve were dried in a thermostat at a temperature of 90°C. Each fraction was weighed and its composition was identified. The identification of items in the sediment after sieving was not carried out.

The proportion of biomass of each sieve fraction and the biomass of certain components within the fraction of the total dry weight of the scat sample was determined. The discrete mean (dMean) of particle size was calculated according to the standard method for each scat sample (Fritz *et al*., 2012). The occurrence of food categories in each sample was assessed by percent of frequency of occurrence (FO) — number of scats containing specific food item/total number of scats ×100 and by the percent of biomass (PB) — biomass of specific food item in total for all sieves/total biomass of all food categories ×100. The statistical analysis was performed by Statistica 12.0 software. We used the t-test to assess the significance of differences among samples with a normal distribution. When carrying out the correlation analysis, non-parametric methods were used. The geometric analysis of the results was performed by the right-angled mixture triangle (Raubenheimer, 2011) using three dimensions: the ratio of food constituents represented by vertebrates, invertebrates, and a group of plants with algae. The position of each sample in this graphical field is commensurately represented by its calculated proportions of these three components, which together should be 100%.

Results

We have found an appreciable frequency of occurrence for most food categories (Tab. 1). This suggests that the red fox uses all available forages whenever possible. The remains of various marine crustaceans, insects, birds, algae and berries are often found in the fox scats (Tab. 1). Fragments of the skeleton of fishes, mollusks, and sea urchins were detected in only a few samples. The hair and bones of mammals are on average only in every fifth sample of the scats. In terms of biomass, crustaceans and insects also form the basis of the diet of the red fox — about 65% (Tab. 1). The second most important category is the plant forages consisting mainly of berries and nuts. The total fraction of the undigested vertebrate remains is only about 6% (Tab. 1). There is a high occurrence of non-food objects (stones) (Tab. 1), which accidentally get in the digestive tract as a result of constant consumption of the impure foods in the tidal zone. We found differences in the frequency of occurrence of some food items in the fox scats from the northern and southern parts of the island. In the northern part of the island, the bird fragments are most often represented in the scats (Tab. 1). This is due to the forest and shrub cover in this area that supports a large diversity of avifauna. In the northern part of the island, there was higher occurrence of algae and sea urchins in the scats that confirms the constant use of the coastal habitats by this predator. In the southern part of the island, on the contrary, the remains of rats are often found in the scats (Tab. 1), that is most likely directly related to the significant rodent population near the weather station and human camps in the area of mining.

Most of the samples of the fox scats that we have analyzed contain predominantly invertebrates, which is not observed in other parts of the species range of this predator (Fig. 1). This allows us to take a closer look at the unique trophic strategy of the red fox on Urup Island.

The muscles of vertebrates are more digestible forage than different parts of plants and invertebrates with a hard chitinous exocuticle. Therefore, mechanical and chemical breaking and crushing of this hard feed play a pivotal role in improving the efficiency of digestion.

The largest fraction of particles makes up a significant part of the biomass of the scat sample (Fig. 2). The discrete mean of the particle size (dMean) from fox scats for the samples from the northern part of the island is 2.09 ± 0.13 mm, for the southern part of the island it is 2.85 ± 0.17 mm. The differences in the dMean between foxes from different island locations are significant at $p < 0.05$ ($t = –3.489$, $df = 52$, $p = 0.000997$). The average dMean for the scats on Urup Island is 2.47 ± 0.12 mm. According to the results of Spearman's rank correlation (Tab. 2), a strong positive correlation is revealed between dMean and the mass of the largest fraction of faecal particles. The reliable negative correlation is between dMean and the mass of the smallest-size fraction of particles. Thus, the value of dMean is determined by the proportion of the largest fraction of food items in the scats (Fig. 4). The qualitative composition of the fox diet in most cases does not affect the particle size value, with one exception. The proportion of insects in the total biomass positively correlates with the fraction of the smallest faecal particles (Tab. 2) that indicates a thorough mechanical and chemical destruction of these food items in the processes of chewing and digestion. Therefore, the proportion of insects also reliably negatively correlates with the dMean.

In the northern part of the island, the proportion of crustacean biomass in the fox scats is higher than that in the southern part. On the contrary, foxes from the southern site of the island have a higher proportion of vertebrates and plants in the scats, the fragments of which are difficult to digest; therefore, for these samples, the percentage of the fraction of large faecal particles is higher (Fig. 2). The red fox prefers vertebrate foods, but the lack of this forage forces it to use a significant amount of different plants as an alternative. A negative reliable correlation exists between the proportion of crustaceans and insects and between the proportion of crustaceans and plants in the scats (Tab. 2).

Discussion

The red fox is considered an omnivorous mesopredator and an opportunistic trophic generalist (Reynolds & Aebischer, 1991; Diaz-Ruiz *et al*., 2013; Fleming *et al*., 2017). First of all, this carnivorous mammal consumes foods that are easier for foraging, often in proportion to its occurrence, abundance and availability in an ecosystem (Yoneda, 1979; Doncaster *et al*., 1990; Tsukada & Nonaka, 1996). The distribution of samples presented in the right-angled nutrition triangle (Fig. 1) in terms of the ratio of different food components in the scats has a strong bias to the upper left corner (predominance of invertebrates in the diet), which is in sharp contrast to the literature data obtained for other regions of Eurasia. Only some samples of the fox scats from Urup Island have similarities to the diets typical for other locations of the species distribution. The populations of red foxes from the nearby island of Hokkaido (Misawa, 1979; Tsukada & Nonaka, 1996), the desert plains of Central Asia (Petrov, 1967) and in some areas of the Mediterranean (Bakaloudis *et al*., 2015) survive consuming significant amounts of invertebrates and plants. A similar trophic

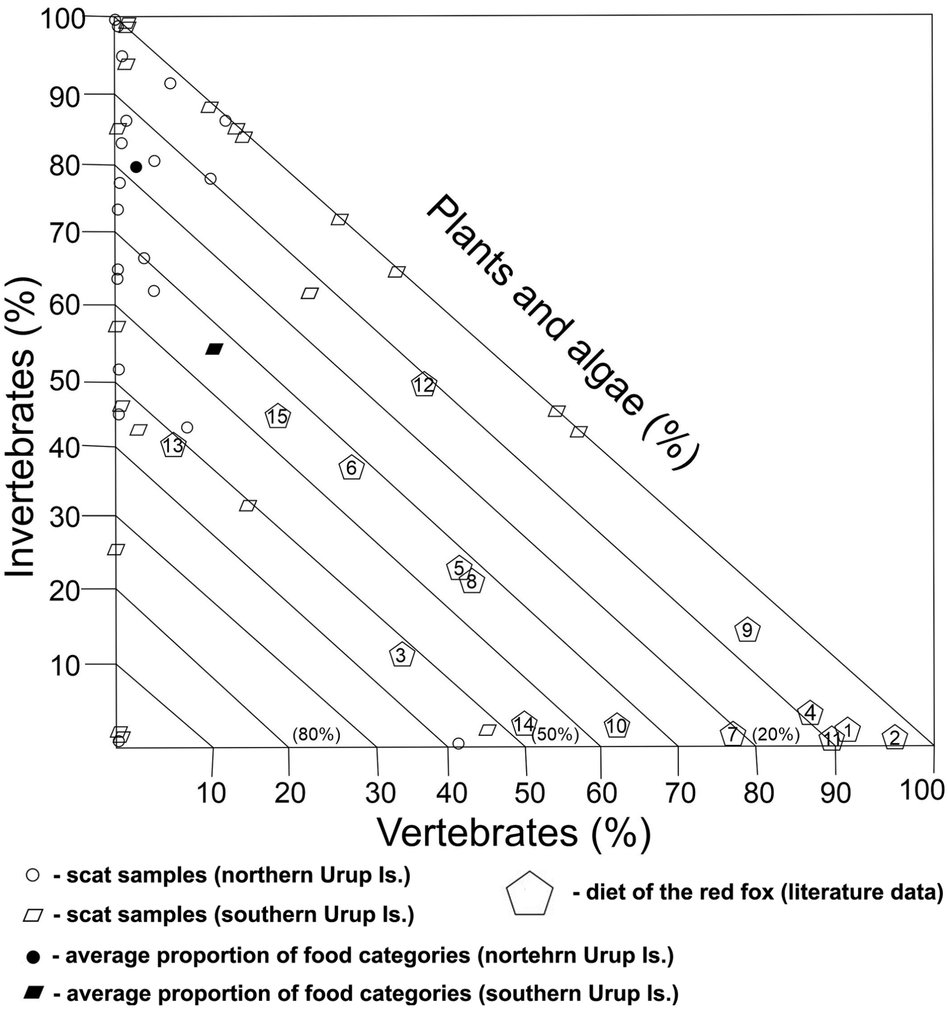

Fig. 1. The proportions of food categories in the red fox *Vulpes vulpes* graphically represented by the right-angled mixture triangle: own data from the northern and southern parts of Urup Island and published data on diets of the red fox. Literature data: 1 — September–October 1971–1973, Hokkaido Is., Japan (Abe, 1975); 2 — June–August 1988–1990, Poland (Borkowski, 1994); 3 — autumn 1989–1991, northern Italy (Brangi, 1995); 4 — winter 1999, Spain (Carvalho & Gomes, 2001); 5 — autumn 1989–1991, northern Italy (Cavallini & Volpi, 1995); 6 — 2003–2005, Greece (Bakaloudis *et al.*, 2015); 7 — 2006–2009, western Poland (Jankowiaki & Tryjanowski, 2013); 8 — summer–autumn 1998–2008, Czech Republic (Hartova-Nentvichova *et al.*, 2010); 9 — 1993–1994, southern Spain (Fedriani, 1996); 10 — summer 1997–2000, Hungary (Lanszki *et al.*, 2007); 11 — summer 1997–2009, Ukraine (Mikheyev, 2011); 12 — summer 1975–1976, Hokkaido Is., Japan (Misawa, 1979); 13 — 1961–1963, Uzbekistan (Petrov, 1967); 14 — 1999, Germany (Russell & Storch, 2004); 15 — 1993–1994, Hokkaido Is., Japan (Tsukada & Nonaka, 1996).

strategy is revealed for red foxes from Urup Island. Most other studies have shown a clear predominance of small mammals in the diet of the red fox in wild (Fig. 1). This is observed even on some neighboring islands. On the main islands in Japan, the fox diet is well studied. Its main food consists of small mammals, insects, and fruits (Uraguchi, 2009). The same trophic trend of this mesocarnivore has been recorded on Sakhalin Island. When analyzing many scat samples and the gut contents, it has been found that mammals are the basis of the diet of the red fox throughout the year, but in the summer other forages, including plants, are often consumed (Berzan, 1990) (Tab. 3). The occurrence of mammals in the fox diet on the surveyed Kuril Islands is lower (Tab. 3). It is associated with a smaller diversity of micromammals and probably with their lower density population. However, on the southern Kuril Islands (Kunashir, Iturup), the features of feeding of the red fox is similar to that of the mainland: rodents (mainly voles) make up about 70% of the diet (Kostenko *et al.*, 2004).

There are no small mammals on Urup Island, with the exception of the brown rat *Rattus norvegicus caraco* Pallas, 1878, and in recent years the house mouse *Mus musculus* L., 1758, has been discovered in a few residential buildings in the south of the island (Kostenko *et al.*, 2004). Studies of the biology of foxes on Urup

Table 1. Frequency of occurrence (FO) and percentage of biomass (PB) of food items in fox scats from the northern and southern parts of Urup Island.

Food items	Northern part of Urup Island, August–September, 2019 $n = 27$		Southern part of Urup Island, August–September, 2019 $n = 27$		On average for Urup Island, $n = 54$	
	FO, %	PB, %*	FO, %	PB, %*	FO, %	PB, %*
Bird feathers and bones	48.10	2.09	25.90	1.92	37.00	2.01
Hairs and bones of mammals	7.40	0.89	29.60	7.58	18.50	4.02
Fish bones	0	0	7.40	0.91	3.70	0.43
Beetles	22.20	1.10	14.80	0.79	18.50	0.96
Other insects	48.10	15.28	51.90	15.25	50.00	15.26
Crustaceans	66.70	58.78	70.40	38.97	68.50	49.52
Mollusk shells	11.10	0.07	11.10	0.24	11.10	0.15
Seaweed	51.90	9.30	14.80	1.71	33.30	5.75
Remains of the shell of sea urchins	11.10	5.01	0	0	5.60	2.67
Nuts of *Pinus pumila*	7.40	1.91	11.10	15.68	9.30	8.34
Berries	22.20	2.26	25.90	14.32	24.10	7.90
Seeds and plant remains	7.40	3.31	7.40	2.63	7.40	2.99
Non-forage objects: stones	44.4	–	48,1	–	46,3	–

Note: * the assessment of non-forage items was not taken into account.

Table 2. Results of Spearman rank correlations: the discrete mean (dMean) of faecal particle size and indicators of the fractional composition of fox scats ($n = 54$). Statistically significant values ($p < 0.05$) are in bold.

	dMEAN	The mass of the largest particle fraction	The mass of the smallest particle fraction	Proportion of insects in the diet	Proportion of crusta-ceans in the diet	Proportion of verte-brates in the diet	Propor-tion of plants in the diet
dMEAN	1.0						
The mass of the largest particle fraction	**0.96**	1.0					
The mass of the smallest particle fraction	**–0.79**	**–0.66**	1.0				
Proportion of insects in the diet	**–0.31**	**–0.28**	**0.31**	1.0			
Proportion of crustaceans in the diet	–0.20	–0.24	0.002	**–0.29**	1.0		
Proportion of vertebrates in the diet	–0.12	–0.10	0.20	–0.08	–0.23	1.0	
Proportion of plants in the diet	0.17	0.20	–0.06	**–0.34**	**–0.57**	0.02	1.0

Island that were carried out 70 years ago showed a high proportion of rats in the diet of this predator (Kuznetsov, 1949; Shmeleva, 1958, 1963). During those years, the rat population peak was noted (Voronov, 1974). Rats multiplied rapidly on the island after the appearance of sea mammal hunters in the 18th century (Voronov, 1974). Subsequently, rats formed a self-reproducing population in the natural conditions of the Kuril Islands with a mild climate, a wide littoral zone, with the presence of permanent freshwater sources. These rodents usually inhabit sites of excessive moisture and along river valleys (Kostenko, 2000). In the absence of other small mammals, the brown rat occupied the niche of both a predator and an omnivorous mammal on many islands (Kostenko, 2000). On Urup, Iturup, Kunashir and Shikotan, the rat resides in natural ecosystems all year round (Voronov, 1974). The high rat population on Urup Island in the last century was largely supported by the constant presence of people and their economic activities (Voronov, 1974). Eventually, two land mammals of Urup Island — the red fox and the brown rat — are leveraging wide food diversity, quickly changing their trophic trajectories in the omnivory-predation system depending on the current availability of foods. The divergence in the specific ecological niches of these mammals occurs due to using

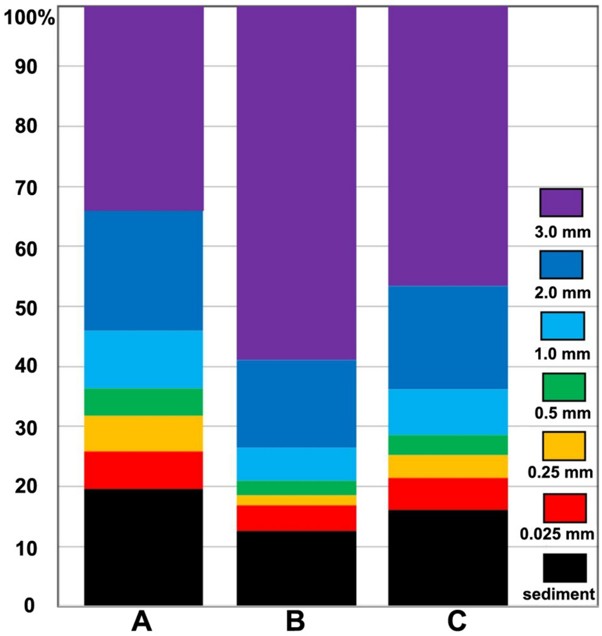

Fig. 2. Proportion of different fractions of faecal particles from fox scat samples. A — the northern part of Urup Island; B — the southern part of Urup Island; C — for all samples from Urup Island.

food items of different-size classes and, probably, due to different circadian foraging behaviors.

Currently Urup Island is practically uninhabited. The rat population density on the island is low at present. We could not catch rodents in traps. Therefore, the current population density of foxes is noticeably lower than it was earlier in the years of a peak rat population (Voronov, 1974). During the fieldwork, the density of foxes at the northern part of Urup Island was 3.3 ind/km^2, in the southern part it varied in different sites from 3.7 to 6.0 ind/km^2.

In our study, the occurrence of rats in the diet of foxes is less than 20%. In terms of biomass, the proportion of the rat recalcitrant (indigestible) substances in the scats is even less (Tab. 1). If compared to voles, rats are not optimal foods for mesocanids. It is rather difficult to catch them as they are crepuscular animals and often burrow in impenetrable bamboo thickets. In addition, rats are less digested by foxes than other small rodents (Yudin, 1986). Therefore, the trophic fox behavior is often aimed at searching for other forage sources. The deep waters surrounding Urup Island harbor many cetacean species. The carcasses of these marine mammals are often thrown ashore. This contributes to the concentration of red foxes so that in the face of stiff competition they dig up a large number of burrows in such plots (Fig. 3). It was

Fig. 3. The color morphs of the Urup fox *Vulpes vulpes*. A — the red fox under canopy of the high-grassy community; B — the silver fox on the stream bank; C — the cross fox within the coast vegetation; D — the burrows of foxes under carcass of the sperm whale *Physeter macrocephalus*.

Table 3. Frequency of occurrence of food items in fox scats on islands of the Sakhalin Region. Data sources:* — Shmeleva, 1958; ** — Shmeleva, 1963; *** — Berzan, 1990.

Food items	Frequency of occurrence, %					
	Sakhalin Island, *n* = 6, the gut analysis, December 1959–February 1960 **	Iturup Island, *n* = 8, the gut analysis, December 1959–February 1960 **	Urup Island, *n* = 24, the stomach analysis, August, 1955 *, **	Sakhalin Island *n* = 374, the scats and gut analysis (average annual data for 1987–1989) ***	Iturup Island *n* = 98, the scats and gut analysis (average annual data for 1987–1989) ***	Paramushir Island, *n* = 54, the scats and gut analysis (average annual data for 1987–1989) ***
Mammals	50.0	37.5	75.5	94.4	61.2	53.7
Voles	50.0	37.5	0	84.2	57.1	44.4
Rats	33.3	0	75.0			
Birds	0	37.5	88.8	14.7	50.0	51.9
Reptilia	0	0	0	0.5	0	0
Amphibia	0	0	0	1.9	0	0
Fish	16.7	37.5	65.0	5.1	10.2	0
Carrion	33.3	12.5	18.2	5.6	4.1	25.9
Insects	0	0	0	5.1	5.1	1.9
Crustaceans	0	12.5	72.0	1.3	26.5	5.6
Mollusks	0	0	0	8.0	2.0	5.6
Seaweed	16.7	0	0	0	0	0
Plant forages	83.4	87.5	83.0	21.1	36.7	16.7
Berries	0	12.5	0	8.8	24.0	6.8
Parts of *Sasa kurilensis*	0	87.5	83.0	0	4.1	0
Vegetative parts of grasses and forbs	83.4	12.5	0	16.8	11.2	5.6

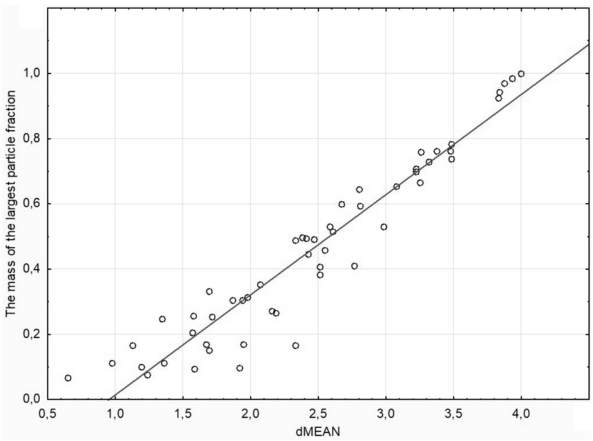

Fig. 4. The relationship between the dMean and the mass of the largest particle fraction (LPF) in fox scats. Linear regression equations: LPF = –0.2929+0.307 × dMean; mean = 1.0812+2.9843 × LPF.

previously indicated that red foxes can gather in and around whale carcasses in groups of up to 20 individuals (Voronov, 1974). Arctic foxes on the Commander Islands also have much greater aggregation around the remains of whales — up to 80 individuals (Ilina, 1950). The winter survival success of many populations of the red foxes on the Kuril Islands depends on the number of marine mammal carcasses. The state of the red fox population in Japan is largely determined by the presence of carrion (Abe, 1975; Yoneda, 1982). The situation is similar on the mainland. The red fox often starves in the taiga in the winter (Gavrin & Krapivny, 1965). Therefore, the more severe climatic conditions and the lower population density of small mammals are, the stronger the survival rate of red foxes depends on the presence of carrion and the ability of these predators to find some forage. This was noted both in the latitudinal gradient (an increase in the value of animal carcasses as food source for foxes near the northern taiga border) (Nasimovich, 1948), and in an altitudinal gradient (an increase in the role of carrion food for fox populations with an increase in altitude above sea level in the mountains) (Fedosenko, 1974).

Pinnipeds cannot be considered as one of the main food sources. There is information from archaeological sites about the consumption of various marine mammals by red foxes. The ancient microsculpture of a fox pulling a seal pup out of the water was found on Shikotan Island (Vasilevsky & Potapova, 2017). Zoologists have also observed such cases of attacks by a group of foxes on seal pups (Voronov, 1974). The spotted seal *Phoca largha* Pallas, 1811 and Steller sea lion *Eumetopias* *jubatus* Schreber, 1776 inhabit Urup Island but they dwell on isolated small rocks far from the main island, which does not allow foxes to migrate there. Therefore, the described cases of a fox hunting pups of pinnipeds are often accidental.

The birds occur more frequent in the red fox's diet on the Kuril Islands (Tab. 3), than on the mainland. However, we have detected only an insignificant proportion of the bird`s remains in the scats. This is largely due to the fact that the nesting time for most species is already over and the diversity of ground-nesting birds is insignificant. Most likely, the strong pressure by predators (foxes and rats) severely undermined the populations of ground-nesting representatives of the avifauna long ago. The rock ptarmigan *Lagopus muta* Montin, 1776, noted for some islands of the Kuril archipelago, does not inhabit Urup Island. The red foxes exert a strong trophic pressure on ptarmigan previously described for Yakutia, Kamchatka, and the Aleutian Islands (Murie, 1959; Vershinin & Lazarev, 1974; Revin, 1976; Bailey & Kaiser, 1993). The occurrence of waders is low on Urup Island, despite the presence of suitable habitats. In our samples, the fragments of feathers in the fox scats belong to passerines. The most abundant birds on Urup Island, potentially available for foxes, are *Emberiza variabilis* Temminck, 1835; *Troglodytes troglodytes* Linnaeus, 1758; *Locustella ochotensis* Middendorff, 1853; *Luscinia calliope* Pallas, 1776; *Turdus chrysolaus* Temminck, 1831, etc. However, it is rather difficult to assess the role of foxes in the mortality of certain birds without special studies. However, it is often indicated that the impact of predators on the avifauna in island ecosystems remains underestimated (Coonan *et al*., 2010).

High occurrence of fish in the stomach contents of red foxes on Urup Island was mentioned earlier (Shmeleva, 1958, 1963). The significant role of fish in the fox diet was also confirmed for Japan (Abe, 1975; Tsukada, 1997). We found the fish bones in the scats only in some individuals as the samples were collected at the very beginning of the autumn salmon migration, when the dead fish were not yet massively found along the river banks. Visual observations of the behavior of foxes allow us to conclude that carnivores are not able to catch live salmon that rise to spawn, but they use only the carcasses of dead fish. Other authors have also emphasized this fact (Yudin, 1986). Therefore, it is most likely that salmonids are important foods for only a short spawning period. The small fish inhabits some island streams year-round, but they are food resources mainly for the introduced American mink *Neovison vison* Schreber, 1777 and the river otter which is now extinct. Historically, the river otter *Lutra lutra* L., 1758 existed in large rivers of Urup Island, but its population was very low, and it quickly disappeared after the foundation of stationary human hunting settlements (Sergeev, 1947).

The littoral zone has become the main forage territory for the red fox on Urup Island. This mesopredator is concentrated along the coastal line. On the Kuril Islands, the daily activity of foxes is shifted to the time of low tide that contributes to searching for foods within the drying littoral zone (Kostenko *et al*., 2004). Another reason for the concentration of foxes along the coast is the high depth of snow cover inland of the island which prevents the carnivore from moving and feeding there (Averin, 1948). It has long been noted that with high snow cover, which is often observed in this geographic region, red foxes cannot forage and are forced to starve for a long time (Inukai, 1943).

The red foxes most often occur on the western (the Sea of Okhotsk) side of Urup Island, since there are fewer areas with a wide littoral zone on the Pacific side. There is a very strong impact of the surf on the eastern side of the island, therefore, in many parts of the coast, large algae and most of the littoral crustaceans are partially or completely absent (Kussakin *et al*., 1974). We have indicated a significant role of crustaceans in the fox's diet (Tab. 1). Many gammarid amphipods are abundant on beaches and littoral sites after low tide. For example, the biomass of *Anisogammarus* in the coastal zone reaches 90 g/m^2 (Kussakin *et al*., 1974). For some central Kuril Islands, the ubiquitous occurrence of crustaceans has been noted for large samples of fox scats (Kuznetsov, 1949; Kostenko *et al*., 2004). The great importance of gammarids in the diet of red foxes has also been recorded in the coastal zone of other regions of the Sea of Okhotsk (Yudin, 1986), and in red foxes and Arctic foxes on the Aleutian Islands (Murie, 1959; West, 1987).

Invertebrates play an important role in the diet of large carnivorous mammals, even if the proportion of this category is insignificant. This is primarily important for maintaining energy metabolism as a source of protein and essential amino acids (Fujiwara *et al*., 2013; Mattson, 2001; Yamazaki *et al*., 2012). In addition, crustacean tissues contain a large amount of free amino acids — glycine, glutamine, alanine, arginine and taurine (Li *et al*., 2021). Surprisingly, it is precisely these amino acids that have the highest concentration in the blood plasma in canids (for example, dogs) (Chan *et al*., 2009), and it indicates their importance in maintaining a normal physiological state of a mammal. Contrary, a lack of arginine leads to hyperammonemia, and a deficiency of taurine is the cause of medicated dilated cardiomyopathy in dogs (Oberbauer & Larsen, 2021) Therefore, it is likely that the consumption of crustaceans and other invertebrates can sufficiently satisfy the nutritional needs of the mammalian mesopredators.

Mollusks are much less common in the fox's diet. *Littorina*, *Falsicingula*, *Nucella* and others, which are massively distributed here, but do not represent food value for mammals. The fox scats of the northern part of the island often contain the shell of sea urchins (*Strongylocentrotus*). A high occurrence of sea urchins in the diet has also been noted for Arctic foxes *Vulpes lagopus* on the Commander and Aleutian Islands (Ilina, 1950; West, 1987). Algae are much more often included in the fox's diet especially in the northern part of the island. This is possibly due to the large concentrations of marine organic debris after storms. For example, only the biomass of *Fucus* algae alone in marine communities reaches 16 kg/m^2 (Kussakin *et al*., 1974).

There is an assumption that the appearance of melanistic coloration in island foxes may be associated with the peculiarities of their diet, which includes a variety of marine organisms (Macfadyen, 1963). The hypothesis is based on the assertion that melanins of the integumentary derivates are synthesized with the participation of the amino acids (cysteine and phenylalanine cysteine), which are abundant in fish meat, bird eggs and marine invertebrates (Prota, 1992; Barboza *et al*., 2009; Bender, 2012; Watson *et al*., 2018), being one of the main food sources of canids on the islands of the North Pacific. Malnutrition can cause visible lightening of hair color (Ito & Wakamatsu, 2011). The deficiencies of some micronutrients can also affect the coloration of the hair (Morris, 2002). The recent experiments have shown that a diet with high-dose tyrosine and phenylalanine increases the intensity of black hair in predators (Anderson *et al*., 2002; Watson *et al*., 2015, 2017, 2018). The distribution of color variants of foxes on different Kuril Islands is not the same (Ishino, 1925; Klumov, 1960; Voronov, 1974). Some authors have repeatedly specified that the red foxes have different color morphs (red, silver, and cross) on Urup Island (Polonsky, 1871; Kuznetsov, 1949; Voronov, 1974). At the beginning of the last century, up to 2000 red foxes lived on Urup, of which 10–20% were silver ones (Tikhenko, 1914). Now, of all the accounting foxes, 25–30% of individuals are represented by a silver morph (Fig. 3). Historical records show the presence of melanistic foxes on the Kuril archipelago — from Rasshua Island and further to the south. Contrary, no silver foxes were recorded on the northern Kuril Islands (Bolkhovitinov, 2005).

The insects have accounted for a significant proportion in the analyzed scat samples (Tab. 1). The most common taxonomic group is beetles. We have accurately identified fragments of a few beetles: *Carabus arvensi*s Herbst, 1784, *C. opaculus* Putzeys, 1875, and *C. kolbei* Roeschke, 1897. These beetles are unevenly represented on the island: the most numerous and widespread species in the southern part of the island is *C. opaculus*, the rarest is *C. kolbei* (Klitin, 2007). The presence of the imago fragments of corpse-eating insects (*Necrodes littoralis* (Silphidae), and *Creophilus maxillosus* (Staphylinidae)) in the scats on Urup Island allows us to conclude that foxes feed on carrion (the decomposed remains of seabirds, large invertebrates and locally marine mammals are common on the coast). The presence of fragments of these beetles in the fox scats was described earlier (Shmeleva, 1958). The scats often contain many puparia particles of flies from the family Coelopidae. These flies are abundant among rotten algae on the coast of Urup Island (Krivolutskaya, 1973).

There is an opinion that insects are poorly digestible food in red foxes due to the lower digestibility of insect chitin (Reshamwala *et al*., 2018), although the biomass of indigestible chitin in insects usually does not exceed 10% (Bosch *et al*., 2016). Therefore, the conversion factor used for estimating the fresh insect ingested is 2–3 times less than for vertebrate-source foods (Reynolds & Aebischer, 1991). Nevertheless, insects are represented by fragments with a high degree of destruction by digestion, therefore the mass of the smallest fraction of particles in the scats correlates with the proportion of insects in the diet (Tab. 2). Possibly, the nutritional value of different taxonomic groups of insects for foxes is underestimated. The chemical profiles of insects can vary appreciably. Nevertheless, in general, the protein concentration in insects is quite comparable to its content in vertebrate meats and the amount of fat in some groups of insects is very high (Bukens, 2005). For example, there are very high digestibility coefficients for insect larvae in the European badger *Meles meles* L., 1758 (Rosalino *et al*., 2003). The nutritional value of insects for carnivorous mammals digesting chitin extremely poorly strongly depends on the taxonomic insect group (Bosch *et al*., 2016; Jonas-Levi & Martinez, 2017), and there has not been any research carried out for foxes on the Kuril Islands. However, it is known that there is chitinase activity in gastric mucosa that allows the red fox to use insects as food (Stevens & Hume, 1995).

Insects are common in the fox diet even in the territory where rodents are the main food. The red foxes feed on many beetles in Japan (Yoneda, 1982; Koike *et al*., 2012). In the boreal zone of Eurasia, the occurrence of insects in the fox diet varies from 10 to 60%, and the most often eaten beetles are species from Scarabaeoidea and Carabidae (Zharkov *et al*., 1932; Grigoriev & Teplov, 1939; Borodina, 1940; Teplova, 1947; Chirkova, 1948; Gavrin & Krapivny, 1965; Petrov, 1967; Pandolfi *et al*., 1991). The red fox consumes invertebrates in large quantities chiefly in semi-desert and desert territories (Formozov & Osmolovskaya, 1963; Palvaniyazov, 1974; Nurgeldyev *et al*., 1988; Dell'Arte & Leonardi, 2005). Therefore, we cannot agree with the conclusion made by some researchers (Yudin, 1986) that invertebrates (crustaceans, insects, and mollusks) do not affect the state of the fox population. On the Kuril Islands, when most of the coastal zone is accessible to foxes throughout the year, marine organisms create the only permanent source of food. With a lack of this forage, foxes become severely depleted and often die, which has already been noted for the Kuril Islands (Voronov, 1974).

The consumption of invertebrates is most often associated not with the preference of this forage, but with its abundance in the environment. This applies to both specialized insect consumers — myrmecophages (Redford, 1987), and large omnivorous predators (bears) switching to the eating of mass invertebrate species during the season of their abundance and outbreaks (Fujiwara *et al*., 2013).

Berries are the main plant forages on Urup Island in the late summer–early autumn, but there is some evidence that the fox eats bamboo shoots (Voronov, 1974). Various plants mainly associated with forest communities can be sources of berries: trees — *Sorbus commixta* Hedl. and *Padus maximowiczii* (Rupr.) Sokolov, shrubs and subshrubs — *Sorbus sambucifolia* Cham. et Schlecht., *Rosa acicularis* Lindl., *R. rugosa* Thunb., *Vaccinium ovalifolium* Smith., *V. vitis-idaea* L., *V. uliginosum* L., *V. praestans* Lamb., *Arctous alpina* (L.) Niedenzu., *Oxycoccus palustris* Pers. and *O. microcarpus* Turcz ex Rupr. and grass — *Rubus chamaemorus* L. (Tatewaki, 1933; Barkalov, 2002, 2009). The Siberian dwarf pine (*Pinus pumila*) seeds are one of the most common and a high-calorie forage. However, we have found these seeds in the scats in few individuals wandering near the island highlands. It has been reported that in the autumn the nuts of *Pinus pumila* become foods for red foxes in the mountain landscapes of the Kuril Islands, Kamchatka and Chukotka (Kuznetsov, 1949; Vershinin & Lazarev, 1974; Novikov, 1982). In the tundra zone of the Siberian mainland, *Pinus pumila* nuts are found with a frequency of up to 30% in the scats (Yudin, 1986). The red fox on the mainland territories also actively eats the seeds of *Pinus pumila* and the berries of *Rosa, Sorbus, Vaccinium, Rubus*, etc. (Borodina, 1940; Teplova, 1947; Nasimovich, 1948; Petrov, 1967; Yudin, 1986). Overall, in red foxes and Arctic foxes the occurrence of plant food reaches 60% in the summer–autumn on the islands (Abe, 1975; West, 1987) and up to 80% on the mainland (Grigoriev & Teplov, 1939; Nasimovich, 1948).

On Urup Island, on average, plant residues account for a fifth of the biomass of fox scats. In the southern part of the island, the occurrence of berries is higher, since there is a significant area of the abundantly fruiting low-sized form of *Sorbus sambucifolia* in herbaceous communities. The presence of vegetable parts in the scats correlates negatively with the proportion of crustaceans (Tab. 2). That is, with the lack of crustaceans in the diet, red foxes consume plant foods more frequently. Plants are poorly digestible food (Ferreras & Fernandez-de-Simon, 2019), so they form the basis of the coarse fractions in the scats. The consumption of plants by carnivorous mammals is often necessary because many fruits contain readily digestible carbohydrates and plant foods improve digestion processes, for example, by reducing the concentration of putrefactive fermentation products (De Cuyper *et al*., 2017).

It is known that the ratio of fine and coarse particles in scats is a reflection of the dietary structure in carnivorous mammals (De Cuyper *et al*., 2018). Mechanic processing of the forage by teeth is the first step that determines the effectiveness of feeding and digestion (Sanson, 2016). In contrast to herbivores, the participation of the dental system of carnivorous mammals in the process of effective chewing of forage is not so significant, and the size of ingested food particles depends more on its quality and the speed of passage through the digestive tract.

In predators that eat predominantly meat, the digestion is most efficient and the assimilation of food constituents is great. Usually only recalcitrant substances (the remains of bones, hair, feathers, and shells) are preserved indigestible, although their ratio in the scats often does not reflect the real consumption of the ingested food items. The digestion of the hard components of the forage may depend on the chewing effectiveness. Especially when carnivores switch to the strategy of being omnivorous. The consuming of non-vertebrate-source foods is largely determined by the intensity of chewing, since the plants, skeletons and shells of marine animals are practically not digested in the stomach and are excreted as whole objects.

The variability of the size of faecal particles in samples from different populations may be the indicator of tense trophic conditions: the lean times at shortage of food resources. The use of the dMean value allows one to compare certain populations and the time intervals with different states of the available food supply in a local habitat. The higher this value is, the higher the proportion of recalcitrant substances in the scats is. It can indirectly indicate the usage of the trophic strategy by a fox population aimed at the transition towards the consumption of less nutritious non-meat-source foods.

The red fox on Urup Island uses abundantly forage resources from invertebrates, which are rather well processed by the digestive system of this predator. This is indirectly confirmed by the fact that a large mass of faecal particles is represented by fine fractions, consisting of this category of the feed. It was found that when the predators chew insects more thoroughly, the enzymatic activity in their gut is higher and there is the higher output and assimilation of nitrogen-containing food compounds — amino acids (Moore & Sanson, 1995). The higher dMean value of the scats found in the fox population in the southern part of the island gives grounds to speak of the use of forages that are poorly digested in the gut and are poorly broken down during mastification. The high dMean value is primarily determined by the largest fraction of particles in the scats due to the consumption of berries, nuts and bones, which are often excreted unbroken. We have found a negative correlation between the proportion of crustaceans and insects, as well as the proportion of crustaceans and different parts of plants. This suggests that the red fox uses the feed selectively — most often, the carnivore directs the priority of choice to the resource that is most available and abundant at a given time. Therefore, it can be assumed that an increase of the dMean value is accompanied by the consumption by the red fox of a less digestible, less nutritious food with a lack of essential nutrients, which, as a result, should affect the body and the state of carnivore population. Nevertheless different-sized digesta fractions, including indigestible plant fibers, also play a positive role: they are likely to influence gastric emptying time, passage rate, nutrient absorption and satiety in an animal (De Cuyper *et al*., 2017).

Significantly higher consumption of insects, crustaceans and plants compensates the lack of meat forage for the red fox. The trophic pre-adaptation of the red fox to the use of secondary foods, in the absence of basic forage (rodents), is confirmed by studies in different parts of the vast species range (Palvaniyazov, 1974). Many mesocanids are able to survive successfully by maintaining a wide range of basal metabolism, depending on the used foods (McNab, 1989). Thus, the frequent occurrence and high consumption of these secondary food sources, along with various edible sea waste and marine organisms from the littoral zone, contribute to the long-term existence of the fox population on Urup Island.

Conclusion

Small mammals are absent on Urup Island, with the exception of introduced brown rats. Crustaceans and insects are the basis of protein nutrition of the red fox under conditions of a lack of meat forages. Invertebrates can be considered as an alternative food source for some omnivorous mammalian species (Diaz-Ruiz *et al*., 2013). This category of forage is efficiently digested by the red fox, that is reflected in a significant proportion of exoskeleton fragments in the smallest faecal fractions. The conversion of crustaceans into the small-sized fraction of faecal particles presupposes a high degree of digestibility of this forage (especially if the protein concentration and amino acid profile are the same as in vertebrates), which provides good prerequisites for the formation of a new trophic strategy of the carnivore in the absence of small mammals. It can be concluded that the trophic adaptation of the red fox on Urup Island has a convergent ecological similarity with the trophic strategies of other carnivorous mammals (sea otter, walrus, extinct sea mink) of the North Pacific, which represent the different ecotypes of the durophages (Vermeij, 2018).

The lack of typical forages on the island limits the distribution and greatly narrows the trophic niche of terrestrial carnivorous mammals. The red fox is the only species of terrestrial carnivores that has formed a large population on Urup island. The habitation of red foxes has become possible due to its high dietary plasticity, which is reflected in the rapid switch from vertebrate-source foods to feeding on invertebrates and plants. The red fox has the possibility to go to alternative forage sources due to the island's vast coastal zone and the availability of marine organisms at low tide. This is a pivotal adaptive feature of mesocanids on oceanic islands. It allows them to become apex predators that can reach high population densities increasing the intensity of top-down regulation in the ecosystems substantially (Ilina, 1950; Murie, 1959; Kostenko *et al*., 2004; Roemer *et al*., 2009; O'Connor *et al*., 2020).

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