ISSN 1062-3590, Biology Bulletin, 2010, Vol. 37, No. 9, pp. 964–980. © Pleiades Publishing, Inc., 2010.
Original Russian Text © M.E. Gol'tsman, O.G. Nanova, S.N. Sergeev, A.N. Shienok, 2010, published in Zoologicheskii Zhurnal, 2010, No. 10, pp. 1246–1263.

The Food Habits of Arctic Fox (*Alopex lagopus semenovi*)
4 Reproductive Families on Mednyi Island (Commander Islands)

M. E. Gol'tsman[a], O. G. Nanova[b], S. N. Sergeev[a], and A. N. Shienok[a]

[a] *Moscow State University, Moscow, 119992 Russia*

[b] *Zoological Museum, Moscow State University, Moscow, 125009 Russia;*
e-mail: migolts@gmail.com, nanova@mail.ru

Received August 4, 2009
Accepted for publication February 20, 2010

Abstract—In total, 1406 samples of scat of 19 arctic fox families and 1755 prey remains collected near the dens of 32 families during the cub rearing period were analyzed. This is the first attempt to evaluate the food use in the population according to averaged data for a large number of families. After the population had passed through the bottleneck, the arctic fox diet changed considerably. Colonies of petrels—the northern fulmar *Fulmarus glacialis rodgersii* and the storm-petrels *Oceanodroma furcata* and *O. leucorhoa*—became the main food source, whereas the use of alternative resources (alcids, cormorants, marine invertebrates, and otarid rookery products) decreased considerably. The following factors are assumed to determine the arctic fox foraging strategy, i.e., the selectivity in food acquisition: (1) passing of the population through the bottleneck; (2) termination of anthropogenic influence due to the liquidation of human settlements on the island; (3) decrease in both the bird populations and abundance of marine invertebrates (sea urchins and mussels); and (4) stable low density of the current arctic fox population. A hypothetical scenario for formation of the foraging specialization in the island population is discussed.

Keywords: arctic fox, *Alopex lagopus*, foraging strategy, foraging specialization, Commander Islands

DOI: 10.1134/S1062359010090104

It is traditionally considered that the foraging strategy of the arctic fox is opportunistic; i.e., this strategy is reduced to consumption of any food sources available at the moment. The diet of the arctic fox, studied in many works, comprises a wide range of food objects (for a review, see, for example, Geptner and Naumov, 1967). In various regions of the circumpolar area, the arctic fox encounters different ecological situations
1 with various spatiotemporal distributions of food resources. On the long-term scale, this distribution can be fluctuating (for example, depending on rodent population cycles) or stable (predictable in time and space, such as the distribution of bird colonies). The former situation is common for the inner regions of the continental tundra, and the latter, for marine
2 3 coasts (Tannerfeldt and Angerbjorn, 1996, 1998; Goltsman et al., 2005a). Since the arctic fox is very mobile, there are no isolated populations on the major part of the area (except for several Pacific islands); correspondingly, it is not reasonable to expect any strict specialization in the use of certain food resources.

The conditions determining specialized foraging strategies can be met on islands, where the populations are isolated, the arctic fox mobility is limited, and the distribution of resources is stable and predictable. From this standpoint, it is interesting to analyze the arctic fox foraging strategy on Mednyi Island (Pacific 4
Ocean). This population has been isolated for several tens of thousands of years (Dzhikiya, 2008), and the spatiotemporal distribution pattern of food resources 1
has not changed for at least many generations of arctic foxes (Goltsman et al., 2005a).

The ecological conditions of Mednyi Island drasti- 4
cally differ from the arctic fox habitats on the continent, because (1) the small closed available space limits the animal mobility; (2) the population density is several tenfold higher as compared with the population densities on the continent; and (3) the food resources are stable and abundant, and their distribution is highly predictable in space and time. Since the island lacks rodents, the food sources for arctic foxes are ocean wrecks cast ashore (corpses of marine animals), invertebrates of the tidal zone, and products of otarid rookeries and sea bird colonies. These specific ecological features had drastically changed the behavior and population structure of the island arctic foxes. The continental arctic foxes can migrate over large distances, and the colonization and migration distances vary in a very wide range. On the contrary, the arctic foxes of Mednyi Island are very conservative: 4
females produce families at the natal sites, while males disperse within several kilometers. During reproduction periods, the island arctic foxes inhabit the same

dens and territories and, most likely, use the same food sources. As for the continent, the arctic fox families are mainly formed of reproductive pairs using large family territories and rearing large litters (Gol'tsman et al., 2003; Goltsman et al., 2005, 2005a). On the contrary, the arctic foxes on the island form large families on small territories inherited maternally; these families comprise several reproducing adults and helpers, which fiercely defend the territory from outsiders and jointly nurse a small litter (Kruchenkova et al., 2009). The food sources are spread along the coast as 1 spots. The high predictability of their spatiotemporal distribution in combination with a conserved population structure possible elevates the likelihood of specialization of the arctic fox foraging strategies.

On the other hand, the trend for pantophagy and wide use of various feeds can be also maintained in the island arctic fox population. The arctic foxes scavenging on marine wrecks, with the most utilized part of their territory confined to a narrow tidal band along the shore, had to become able to use all the seafood cast ashore. In addition, migration to neighboring sites under conditions of a spot distribution of heterogeneous resources can considerably change the range of available food and, correspondingly, the arctic fox diet.

Thus, two opposite trends can potentially determine the foraging strategy of the island arctic foxes, namely, (1) foraging specialization as a consequence of spatial conservation of their territories and high predictability of clustered food sources and (2) foraging opportunism as a consequence of rather unpredictable and manifold sea wrecks and differences in food availability on the neighboring territories.

Study of the foraging strategies of the arctic foxes 4 inhabiting Mednyi Island is of special interest, since this population endured a rare and drastic collapse. In 5 the 1970s–1980s, a sudden epizootic of ear mange among cubs led to almost complete disappearance of arctic foxes (Goltsman et al., 1996). The island population, which amounted to 500–700 individuals and even up to 1000 and more in some years (Il'ina, 1950) decreased to several individuals. The population began to recover in the late 1980s; since 1993, the population has a stable low size of 60–90 individuals (Goltsman et al., 1996; Gol'tsman and Kruchenkova, 2001; Goltsman et al., 2005a). Having passed through the bottle- 4 neck, the Mednyi Island population preserved its specific social organization characteristic of islands (Gol'tsman et al., 2003; 2005, 2005a; Kruchenkova et al., 2009); however, the foraging ecology of these arctic foxes has changed. Zagrebel'nyi (2000) compared the 4 summer diet of the Mednyi Island arctic foxes during 1990–1998 and that described for the 1950s and noticed changes in several directions, namely, the fraction of seabirds, especially the northern fulmar (*Fulmarus glacialis rodgersii* Cass.), increased and the fraction of marine invertebrates and mammals decreased. This is a very important inference, because the changes in diet took place after the arctic fox population passed through the bottleneck and actually a new population appeared on the island. However, these changes are rather difficult to quantify. All researchers used an *ad libitum* sampling for their studies without taking into account whether the scat samples were of the same animals or same sites. For example, if a considerable part of the specimens are sampled near only one den located in the vicinity of a salmon spawning ground, this cannot representatively reflect the entire population area. Taking into account that the sampling volumes were rather small, this specific feature of the method used interferes with an adequate quantification of the changes in the diet.

To form a more reliable background for further studies into foraging ecology of the Mednyi Island arc- 4 tic fox population, we described the summer diets of different reproductive arctic fox families, estimated variations in the diets of individual families and their correlations with the distribution of the resource, and, based on these data, attempted to determine the opportunistic pattern in selection of food sources. In addition, comparing our data and the data obtained by several researchers who studied the arctic fox feeding on the island over the 20th century, we tried to analyze the main factors that had determined the changes in the arctic fox foraging ecology.

STUDIED AREA, MATERIALS, AND METHODS

The studies were performed on the south half of Mednyi Island (Commander Islands). The island is 4 located in the westernmost part of the Aleutian island arc in an ice-free part of the North Pacific at a distance of 175 km from the eastern coast of Kamchatka. Its area is about 187 km^2 with a length of about 55 km and a width of 0.3 to 7.5 km.

Mednyi Island is the top of a submarine ridge rising 4 to an altitude of 30–700 m above sea level surrounded by a narrow intertidal coast. Tundra occupies the main part of the island, and the hillsides are covered with shore meadows. The arctic fox is the only representative of terrestrial mammals inhabiting the island; however, marine mammals are abundant in the water area. Harbor seals (*Phoca vitulina kurilensis*) and sea otters (*Enhydra lutris*) are encountered throughout the year; the sea lion (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) rookeries are on the shore.

The most numerous avian species are colony-forming seabirds; the most abundant of them is the fulmar with the extended colonies reaching several tens of dozens of individuals (Kartashev, 1961; Artyukhin, 1991). The first fulmars come there at the end of March, and the colonies eventually form at the end of May. Egg laying commences in June and continues throughout July; younglings appear in August. Fulmars select steep seashores for nesting. The main part of the birds chooses grassed sites in the upper part

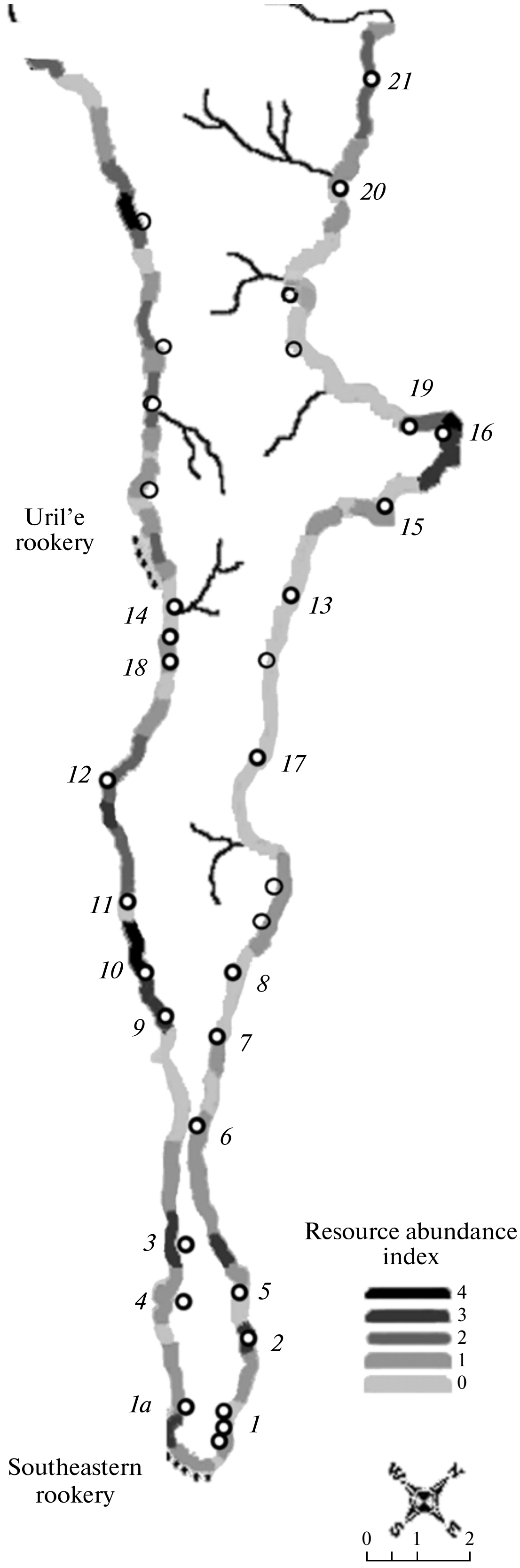

Fig. 1. Distribution of 500-m regions with different fulmar abundance indices along the coast of the southeastern part of Mednyi Island: 0, no colonies; 1, small colonies less 4 than 100 nests; 2, colonies of 100–400 nests; 3, colonies of 400–1000 nests; and 4, over 1000 nests. Chains of dots denote the rookeries of marine mammals. The brooks entered by humpback salmon for spawning are shown. Circles denote the locations of arctic fox litter dens: (*1*) Southeastern dens; (*2*) den near the Drovyanye Stolby Cape; (*3*) den 3; (*4*) den 4; (*5*) den on the Ivanovskii Cape; (*6*) den on the Isthmus; (*7*) den near the Aleutian trap; (*8*) den in front of the Pestryakov Cape; (*9*) den in front of the Dlinnyi Cape; (*10*) den near the Dlinnyi Cape; (*11*) den on the Kalamak Cape; (*12*) den on the Palata Cape; (*13*) den near the Venedikt Upal Cape; (*14*) dens on Uril'e; (*15*) den in the Kukhninskaya Bay; (*16*) den on the Chernyi Cape; (*17*) den in the Glinka Bay; (*18*) den in the Sobach'ya Dyra Bay; (*19*) den in the Khlebnaya Bay; (*20*) den in the Vodopad Bay; and (*21*) den in the Orlovaya Bay.

of coastal cliffs, where they make nests among tufts of cereals. Fulmars leave the island by the end of October.

The colonies of guillemots (*Uria lomvia* and *U. aalge*) and black- and red-legged kittiwakes (*Rissa tridactyla* and *R. brevirostris*) contain several tens of thousands to several thousand individuals (Chernyi Cape) (Artyukhin, 1991); however, their colonies are less numerous than those of the fulmar.

The colonies of cormorants (*Phalacrocorax pelagicus* and *Ph. urile*), horned (*Fratercula corniculata*) and tufted puffins (*Lunda cirrhata*), pigeon guillemots (*Cepphus columba*), and whiskered auklets (*Aethia pygmaea*) are considerably smaller in size and evenly spread along the coast (Sergeev, 1999[1]).

The colonies of fork-tailed (*Oceanodroma furcata*) and Leach's (*O. leucorhoa*) storm-petrels are widespread on the island. The Leach's storm-petrels are less abundant than the fork-tailed storm-petrels, which are numerous near the fulmar and puffin nesting sites (Kartashev, 1961; Artyukhin, 1991). Both storm-petrel species nest in dens with a length of 0.5 to 1 m or in rock crevices (Dement'ev and Gladkov, 1991) and form colonies with a density of 6 dens per 10 m^2. The storm-petrels appear on the island in mid-April and leave it by the end of September (Artyukhin, 1991).

We explored the southern part of the island from its southeastern end to the Vodopadskii Cape along the western coast and from the Korabel'nyi Cape along the eastern coast (Fig. 1). The area of the examined territory was about 26.2 km^2. Two large otarid rookeries were located on this territory: the Southeastern, a mixed rookery of fur seals and sea lions, and the Uril'e rookery of northern fur seals. Seabird colonies were located along the coastline.

[1] Sergeev, S.N., Nutrition and Spatial Structure of the Mednyi 4 Island Arctic Fox (*Alopex lagopus semenovi*) Population, *Diploma Paper*, Moscow: MGU, 1999.).

The humpback salmon (*Oncorhynchus gorbusha*) enters part of the brooks; its main spawning areas are located in the northern part (Glinka, Staraya Odinochka, and Vodopad bays and Gorelyi and Uril'e capes). The humpback salmon enters only the outflow of the majority of them (except for Vodopad Bay) and not every year. Nonetheless, the diet of the arctic fox families living near such brooks can drastically change during this period: arctic foxes switch to fish eating, sometimes bringing it from a distance of 1 km and more.

Sampling

The sampling was organized so that it was possible to differentially estimate the summer diets of individual families. We have analyzed the scat samples collected in 1997, 2002, 2003, and 2005 from the animals of 19 families and described the prey remains of 32 families with litters in the southern part of the island in 1997, 2002, 2003, 2005, 2006, and 2008. Scat and prey remains were collected from the end of May (in some years, end of June) to the end of August (Table 1).

Scat samples were collected around the dens with arctic fox litters (litter dens). The coordinates of sampling sites and the distance from the sampling sites to the nearest den were determined using GPS (eTrex Garmin) with an accuracy of 5 m. The scat samples collected within a radius of 200 m from a litter den were regarded as belonging to this family, because the
4 Mednyi Island arctic foxes during the reproduction period are strictly territorial, with the hosts continuously defending the space around the litter den driving away outsiders (Naumov et al., 1981; Kruchenkova and Gol'tsman, 1994; Gol'tsman et al., 2003; Goltsman et al., 2005a; Kruchenkova et al., 2009). When collecting scat, the samples were sorted into summer and winter groups and those belonging to adult animals and cubs. The separation into summer and winter samples was based on scat color, degree of dryness, consistency, and odor. The winter scat samples are whitish, fragile, and odorless even at a fracture. We have analyzed only summer scat. For the majority of families, the scat samples were collected during the entire summer season with intervals of several days to 2–3 weeks. In the remaining cases, scat was collected over several days from late June to mid-August.

Since arctic foxes during summer do not exchange their dens and the same family lives in a particular den for the entire season, we pooled for analysis all the collected scat belonging to an individual den in a single sample and assumed that this sample characterized the feeding of the family that used this den during the season. Description of the diet common for an entire family is justified by the fact that the members of the family use the resources of the same habitat and, although they are unlikely to interact directly during hunting, they share the prey with one another. During the entire summer season, adult arctic foxes bring the food to their den to feed lactating females and cubs. Although individual diets of the family members can differ (our unpublished data), they are undoubtedly interdependent and controlled by the same external factors.

The area within a radius of 10–20 m from the litter den contains uneaten prey remains, sometimes forming large heaps. When sorting prey remains, we counted the number of left and right wings for each avian species to estimate the number of caught birds and determine the minimum possible number of birds (for example, when finding four left and five right wings, we considered that five birds were carried to the den).

In total, 1406 summer scat samples of 19 families were collected within a 200-m area around the litter dens and analyzed, as were 1755 prey remains of 32 families. Thus, the conclusions about the summer diet of one family were, on average, based on analysis of 74 scat samples ($N = 19$) and 55 prey remains ($N = 32$).

Analysis of Scat

Each specimen was dried, weighed, washed in a fine sieve, dried again, and sorted into fractions according to species composition. Each fraction was weighed, and its percent volume relative to the total scat volume was visually assessed (Sokolov, 1949; Zagrebel'nyi, 2000a).

The birds were identified to the species level according to feather coloration and macrostructure comparing them with the specimens of ourown collection (S.N. Sergeev and O.G. Nanova) as well as using the collection of the Chair of Vertebrate Zoology (Moscow State University). Cormorants, kittiwakes, and guillemots were identified to the genus level. When only bird bones were present in scat or feathers were considerably damaged, the remains were regarded as undetermined.

Of bird younglings, only grownup fulmar younglings were determined to the species level. In the remaining cases, the younglings were not ascribed to species but rather pooled into a separate group common for all species. We could not precisely identify the species according to the egg shells and envelope fragments but assumed that in the majority of cases they belonged to fulmars. This was justified by the fact that (1) the color and external characteristics of shell fragments were similar to the fulmar egg shell; (2) we frequently found broken fulmar eggs near dens; and (3) we frequently met arctic foxes carrying fulmar eggs in their teeth.

Mammalian species were identified according to their fur comparing it with the specimens of our (S.N. Sergeev and O.G. Nanova) collection.

The scat lacking identifiable remains was regarded as the result of eating meat. Such scat found in the

Table 1. Sampling dates and the volume and type of specimens collected near arctic fox dens

No. in Fig. 1	Name of den	Year	Sampling dates (day–day, month)	Number of scat samples	Number of prey remains
1	Southeastern Cape	1997	29.06; 2–27.07; 2–4, 8, 20–21.08	58	12
		1997	22.08		71
		2003	27–30.06; 1–15.07; 2–17.08	89	
		2005	25–28.05; 1–17, 20–28.06; 8–16, 26.07; 2–19.08	105	45
		2006	7.06–1.08		82
2	Drovyanye Stolby Cape	1997	19.08		27
		2005	29.05–17.06	156	108
			18.06–14.07		45
			5–19.08		79
		2006	16.06		80
			22.07		51
		2008	10.07		86
			15.08		103
3	Den 3	2002	3–4.07; 5–8.08	60	
		2003	8–14, 28.07	141	72
		2008	7, 12, 18, 19.07; 14.08		51
4	Den 4	2002	4.07	28	
5	Ivanovskii Cape	2003	4–9, 21.07; 5.08	84	29
		2005	7–30.06; 5–16.07; 10–18.08	174	91
6	Isthmus	2003	5–8, 24–30.07; 4–6.08	53	23
		2005	27.07		8
7	Aleutian trap	2003	14.07; 5, 6, 12.08	62	
8	Pestryakov Cape	1997	20–29.07	28	9
		2003	14.07; 5, 6, 12.08	32	
		2005	27.07	47	97
9	Den in front of Dlinnyi Cape	1997	29.07		11
		2005	30.07		65
10	Dlinnyi Cape	1997	29.07		45
11	Kalamak Cape	1997	14.08		6
12	Palata Cape	2005	6.07		17
13	Venedikt Upal Cape	2003	11–16.06; 11.07	127	26
		2005	27–29.07	44	
		2008	21, 27.06		26
14	Uril'e	1997	9, 17.07; 10, 11, 18.08	42	17
		2006	24.07; 5.08		18
15	Kukhninskaya Bay	2003	17–23.07	20	40
16	Chernyi Cape	2003	17.23.07	56	64
17	Glinka Bay	2008	23.07–6.08		39
			11.08		38
18	Sobach'ya Dyra Bay	2008	20, 25.07; 1, 2.08		69
19	Khlebnaya Bay	2008	12.08		33
20	Vodopad Bay	2008	7, 8.08		41
21	Orlovaya Bay	2008	10.08		29

vicinity of seal rookeries was regarded as those containing seal meat. Scat also contained fish vertebrae. The fish remains found in the vicinity of a seal rookery was most likely a seal's spews, although arctic foxes are accustomed to scavenge sea wrecks for fish. The seal's spews consist of fish, and we repeatedly saw (observations of S.N. Sergeev) that both adult arctic foxes and cubs ate it.

The scats also contained shells of freshwater shrimps (Amphipoda), beetles (Carabidae, Coleoptera), flies (Muscomorpha, Diptera) and their pupae (puparia), tunics of sea squirts (Ascidiae), and squid beaks. Squids are main feeding object of fulmars (Dement'ev and Gladkov, 1954) and are likely to enter the arctic fox digestive tract from fulmar stomachs. We repeatedly found fulmar stomachs in arctic fox scat; these stomachs passed as a whole filled with squid beaks through the arctic fox gastrointestinal tract. All eight fulmar stomachs found near dens contained squid beaks. Sometimes many squids beach themselves onto the intertidal coastline, and arctic foxes can, presumably, eat them. Beached squids were identified (by O.G. Nanova at the Chair of Invertebrate Zoology, Moscow State University) as *Gonatopsis octopedatus* Sasaki 1920.

The nonfood objects (stones, chips, etc.) were discarded when analyzing specimens.

The scat composition was assessed according to the following characteristics:

(1) The frequency of a particular fraction in sorted specimens, $F(\%)$:

$F = (n/N) \times 100\%$,

where n is the number of scat samples where the fraction was found and N is total number of scat specimens.

(2) The relative frequency of a fraction, $F_{\rm rel}$ (%), among all fractions.

When calculating the relative frequency, the number of scat samples containing a fraction was divided by the total number of instances of finding all fractions:

$$F_{\rm rel} = (n/M) \times 100\%,$$

where n is the number of scat specimens where the fraction was found and M is the total number of instances of finding all fractions.

Thus, the sum of all relative frequencies for all fractions is 100%.

(3) The relative volume of a component, $V_{\rm rel}$ (%), calculated similarly to the relative frequency:

$$V_{\rm OTH} = \frac{\sum V_{\rm Individual component}}{\sum V_{\rm all components}} \times 100\%$$

The sum of the relative volumes of all fractions is 100%.

Data Collection on Distributions of Arctic Fox Litter Dens and Fulmar Colonies

All the dens with litters that appeared during the observation period were recorded and mapped with indication of their coordinates. The majority of dens and shelters in stones were repeatedly used although not every year. The arctic fox habitats on the island are located along the coastline, where the food resources are localized. This makes it possible to assess the food capacity of a habitat according to the abundance of a food resource along the coastline. The entire coast of the studied part of the island was arbitrarily divided into 500-m regions with the help of GPS and markers placed at each kilometer of the coastline (S.N. Sergeev). The litter dens (the shelters where an arctic fox litter lived at least for one season over the observation period) were mapped with respect to these 500-m regions (Fig. 1).

The fulmar nesting density was assessed in 1997–1998. The nests were counted in all 500-m segments of the coastline with a total length of 70.5 km to ascribe the following scores for each segment: 0, no colonies; 1, less than 50 nests; 2, colonies of 100–400 nests; 3, colonies of 400–1000 nests; and 4, over 1000 nests (Goltsman et al., 2005). We based this on the assumption that, if the absolute size of a bird colony changed over the observation period, the relative size was on average preserved and the possible changes did not provide for a significant error in our calculations.

The resource abundance indices are shown in Fig. 1.

Statistical Processing of Data

The data on locations of collected scat relative to the dens were processed using the OziExplorer v. 3.90.3a software. The Statistica 6.0 (StatSoft Inc.) software package was used for statistical computations.

In total, the diets of 19 arctic fox families were described by analyzing scat (Tables 2–4). The families that lived on the same territory in different years were regarded as individual families; i.e., the description of family diet (more precisely, a family per year) is averaged data on the nutrition of one family during one summer season. When comparing the degree of consumption of the prey belonging to different species (for example, birds, mammals, and invertebrates; Fig. 2) by arctic foxes, the sample of families was reduced. To avoid the influence of spatial pseudoreplication (for example, see Hulbert, 1984), we formed the sample so that each spatial region was represented in it only once. In particular, when scat from a region was collected for 3 years over the observation period (i.e., the scat of three families), these data were averaged for analysis. Consequently, the number of families/year used in our analysis was reduced from 19 to 12. Note that this change had almost no effect on the results.

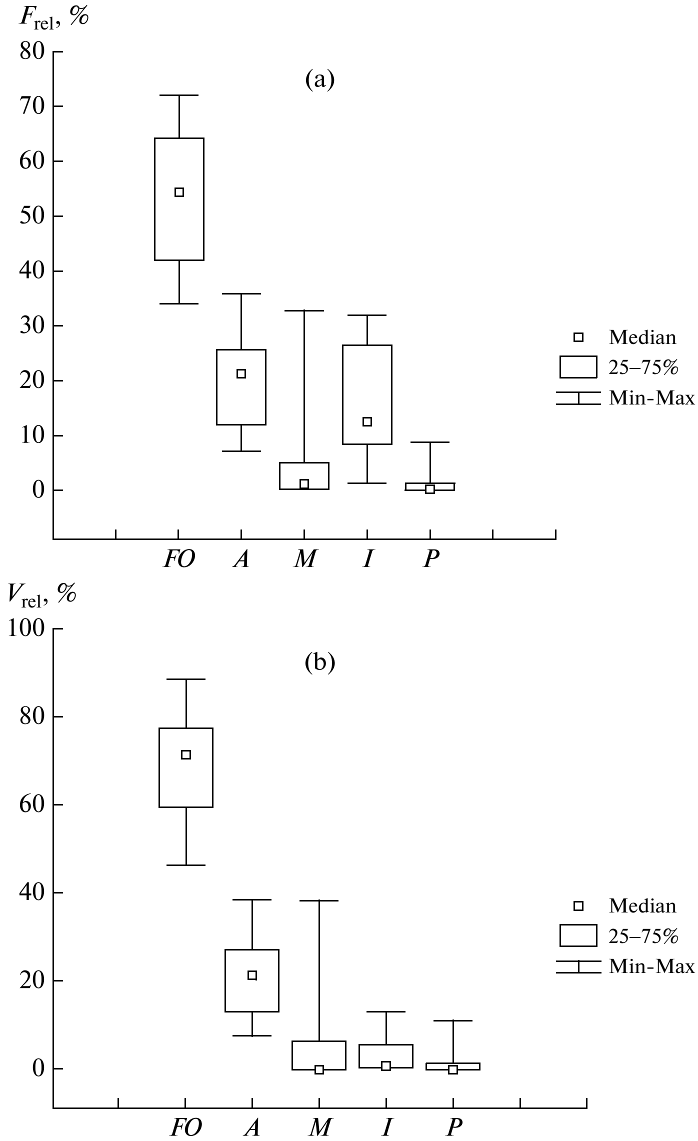

Fig. 2. The ratio of food objects in the diets of arctic fox families living in different habitats: (a) relative frequency of components (F_{rel}) and (b) relative volume of components (V_{rel}); *FO*, petrels (fulmar, fork-tailed, and Leach's storm-petrels); *A*, other birds except for petrels; *M*, mammals (northern fur seal and sea otter); *I*, invertebrates; and *P*, fish.

RESULTS

The Main Strategy in Using Food Resources

The main food resource for all the studied arctic fox families was seabirds (Figs. 2a, 2b).

The fractions of mammals, invertebrates, and fish in their diet were considerably smaller.

Only the arctic fox families whose dens were within a radius of 1 km from rookeries regularly ate pinnipeds.[2] Such families represent a relatively small part of the reproductive families. In particular, 150 arctic fox families with litters were recorded on the island in summer seasons of 1994–2005, and only 18 of them lived within 1 km from a rookery. The territories of the remaining 88% of the families were at a considerable distance from rookeries, and the members of these families even if they sometimes visited a rookery,[3] could not use it as a regular food source.

Study of the diet of four families living in the vicinity of a rookery demonstrated that they used its food resource considerably less intensively as compared

[2] This distance approximately corresponds to the size of arctic fox
4 individual territories on Mednyi Island: the territories are stretched along the coastline; the average length of a territory along the coastline in 1994–1999 was 2 km (1.1 to 5 km, *SD* = 1.1; Goltsman et al., 2005a).

[3] Sometimes, the family members not involved in reproduction left the family territory for one or several days. During this period, some of them were recorded in rookeries.

Table 2. Diets of 19 families assessed according to the frequency F (%)

Food objects	Den no.																			*M*	*SD*
	1a	1		2	3		4	5		6	7	8			13		14	15	16		
	Sampling year; *N* is parenthesized																				
	1997 (58)	2003 (89)	2005 (105)	2005 (156)	2002 (60)	2003 (141)	2002 (28)	2003 (84)	2005 (174)	2003 (53)	2003 (62)	1997 (28)	2003 (32)	2005 (47)	2003 (127)	2005 (44)	1997 (42)	2003 (20)	2003 (56)		
Birds	82.8	79.8	84.8	98.3	100.0	96.5	100.0	96.6	94.3	98.1	95.2	92.9	100.0	95.7	98.4	93.2	64.3	100.0	98.2	93.1	9.2
Fulmarus glacialis	44.8	33.7	8.9	38.8	85.5	55.3	60.7	48.9	69.3	83.0	46.8	60.7	93.8	68.1	33.9	43.2	28.6	15.0	10.7	48.9	24.6
Oceanodroma sp.	8.6	18.0	38.4	35.1	12.7	12.1	32.1	10.2	13.1	5.7	14.5	3.6	0.0	27.7	36.2	50.0	9.5	65.0	57.1	23.7	19.0
Alcidae, Phalacrocoracidae	15.5	1.1	12.5	7.7	5.5	0.7	3.6	10.2	6.3	0.0	0.0	7.1	6.3	4.3	1.6	0.0	4.8	0.0	19.6	5.6	5.6
Rissa sp.	1.7	3.4	0.0	0.1	0.0	1.4	0.0	10.2	0.0	0.0	6.5	7.1	3.1	0.0	0.8	0.0	9.5	5.0	1.8	2.7	3.4
Unidentified species	13.8	28.1	32.1	22.7	5.5	28.4	7.1	26.1	10.2	9.4	27.4	14.3	3.1	23.4	27.6	6.8	11.9	30.0	14.3	18.0	9.7
Bird eggs	6.9	9.0	1.8	3.9	10.9	12.8	10.7	14.8	9.1	7.5	8.0	0.0	6.3	21.3	7.9	0.0	0.0	5.0	5.4	7.4	5.4
Mammals	44.8	24.7	3.6	1.2	0.0	0.0	3.6	1.1	0.0	0.0	1.0	0.0	0.0	0.0	0.0	4.5	28.6	0.0	3.6	6.1	12.4
Callorhinus ursinus	44.8	24.7	3.6	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	28.6	0.0	0.0	5.5	12.6
Enhydra lutris	0.0	0.0	0.0	0.6	0.0	0.0	3.6	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	1.8	0.5	1.0
Invertebrates	1.7	20.2	2.7	19.3	7.3	12.8	10.7	11.4	27.8	34.0	40.3	46.4	34.4	53.2	52.0	59.1	31.0	15.0	5.4	25.5	18.3
Amphipoda	1.7	4.5	0.0	8.3	3.6	0.7	0.0	0.0	21.6	9.4	20.2	35.7	21.9	31.9	38.6	56.8	23.8	5.0	3.6	15.1	16.4
Insecta	0.0	1.1	1.8	1.7	0.0	2.1	0.0	0.0	0.0	11.3	8.1	25.0	0.0	29.8	11.8	0.0	4.8	5.0	0.0	5.4	8.7
Teuthida	0.0	1.1	0.9	9.9	3.6	0.7	10.7	10.2	5.7	15.1	8.1	3.6	15.6	8.5	0.0	2.3	0.0	0.0	1.0	5.1	5.3
Fish	0.0	3.3	0.0	1.1	0.0	0.0	0.0	2.3	0.0	1.9	0.0	7.1	0.0	2.1	0.8	0.0	42.9	0.0	0.0	3.2	9.8

Note: $F = (n/N) \times 100\%$, where n is the number of scat samples containing a particular fraction and N is the total number of scat samples. Locations of dens are shown in Fig. 1; M is the mean value, and SD, the standard deviation.

Table 3. Diets of 19 families assessed according to the relative frequency F_{rel} (%)

Food objects	Den no.																		
	1a	1		2	3		4	5		6	7	8			13		14	15	16
	Sampling year; *N* is parenthesized																		
	1997 (58)	2003 (89)	2005 (105)	2005 (156)	2002 (60)	2003 (141)	2002 (28)	2003 (84)	2005 (174)	2003 (53)	2003 (62)	1997 (28)	2003 (32)	2005 (47)	2003 (127)	2005 (44)	1997 (42)	2003 (20)	2003 (56)
Birds	60.8	57.7	92.2	77.5	83.3	78.6	80.0	78.3	75.0	69.3	55.7	63.4	71.1	55.6	61.9	59.4	38.6	83.3	87.3
Fulmarus glacialis	32.5	25.9	9.9	31.7	66.2	47.9	47.2	39.5	52.8	62.8	26.1	37.0	69.7	31.1	21.3	26.4	17.1	11.5	9.0
Oceanodroma sp.	6.3	13.8	36.0	21.1	9.1	10.4	25.0	8.6	11.6	4.3	8.1	2.2	0.0	12.6	22.8	30.6	5.7	50.0	47.8
Alcidae, Phalacrocoracidae	11.4	0.9	13.5	1.2	3.9	0.6	2.8	8.6	4.3	0.0	0.0	4.3	4.7	1.9	1.0	0.0	2.8	0.0	16.5
Rissa sp.	1.3	2.6	0.0	0.4	0.0	1.2	0.0	8.7	0.0	0.0	3.6	4.3	2.3	0.0	0.5	0.0	5.7	3.8	1.5
Unidentified species	10.0	21.6	33.3	24.3	5.2	24.5	5.6	22.2	6.9	7.1	16.2	8.7	2.3	5.8	16.3	4.2	7.1	19.2	12.0
Bird eggs	5.0	6.9	0.9	2.6	7.8	11.0	8.3	11.5	7.7	5.7	9.9	0.0	4.7	9.7	5.0	0.0	0.0	3.8	4.5
Mammals	32.9	17.9	3.9	1.0	0.0	0.0	2.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	2.9	17.1	0.0	3.2
Callorhinus ursinus	32.5	17.9	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	17.1	0.0	0.0
Enhydra lutris	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	1.4	0.0	0.0	1.5
Invertebrates	1.3	14.6	2.0	17.0	8.3	10.4	8.6	9.4	15.5	24.0	32.1	31.7	24.4	30.9	32.7	37.7	18.6	12.5	4.8
Amphipoda	1.3	3.4	0.0	6.2	3.9	0.6	0.0	0.0	9.9	7.1	24.3	22.5	16.3	14.6	24.3	34.7	14.3	3.8	3.0
Insecta	0.0	0.9	0.9	1.8	0.0	1.8	0.0	0.0	0.0	8.6	2.7	15.2	0.0	13.6	7.4	0.0	2.8	3.8	0.0
Teuthida	0.0	0.9	0.9	7.5	3.9	0.6	8.3	0.0	4.7	1.4	4.5	2.2	0.0	3.9	0.0	1.4	0.0	0.0	1.5
Fish	0.0	2.6	0.0	1.3	0.0	0.0	0.0	1.0	0.0	1.4	0.0	4.3	0.0	1.0	0.5	0.0	25.7	0.0	0.0

Designations as in Table 2.

Table 4. Diets of 19 families, V_{rel} (%)

Food objects	Den no.																		
	1a	1		2	3		4	5		6	7	8			13		14	15	16
	Sampling year; *N* is parenthesized																		
	1997 (58)	2003 (89)	2005 (105)	2005 (156)	2002 (60)	2003 (141)	2002 (28)	2003 (84)	2005 (174)	2003 (53)	2003 (62)	1997 (28)	2003 (32)	2005 (47)	2003 (27)	2005 (44)	1997 (42)	2003 (20)	2003 (56)
Birds	61.6	74.0	95.4	98.9	98.4	99.1	99.4	99.7	97.0	94.4	85.0	74.5	99.2	96.9	91.5	91.7	33.0	99.6	94.7
Fulmarus glacialis	40.8	31.3	9.1	45.0	79.7	56.5	60.0	47.5	69.7	81.4	45.9	51.3	92.8	63.4	33.4	38.9	19.3	13.9	9.2
Oceanodroma sp.	7.4	13.8	38.2	30.3	9.7	12.4	28.7	9.1	12.8	5.4	13.7	3.8	0.0	17.3	34.7	46.1	5.2	59.7	55
Alcidae, Phalacrocoracidae	5.7	1.1	12.6	2.1	2.3	0.7	3.6	6.4	5.3	0.0	0.0	6.8	0.3	2.4	1.6	0.0	5.0	0.0	17.8
Rissa sp.	0.0	3.3	0.0	0.9	0.0	0.8	0.0	10.2	0.0	0.0	5.3	0.0	3.1	0.0	0.8	0.0	0.0	1.0	1.8
Unidentified species	7.7	24.5	35.5	20.6	6.7	28.7	7.1	26.5	9.2	7.6	20.1	12.5	3.0	12.8	20.9	6.7	3.5	24.8	10.9
Bird eggs	0.0	0.1	0.0	0.1	0.3	0.2	0.3	0.2	0.8	0.1	0.3	0.0	0.2	0.8	0.2	0.0	0.0	0.1	1.8
Mammals	38.2	23.7	3.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	2.5	26.7	0.0	2.6
Callorhinus ursinus	38.2	23.7	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	26.7	0.0	0.0
Enhydra lutris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.2	0.0	0.0	1.8
Invertebrates	0.2	0.4	0.0	0.8	1.2	0.6	0.3	0.2	2.1	3.8	13.1	21.3	0.6	2.3	8.2	5.8	7.0	0.4	0.8
Amphipoda	0.0	0.1	0.0	0.1	1.0	0.0	0.0	0.0	1.7	1.1	11.7	12.0	0.3	0.9	6.7	5.8	4.4	0.3	0.8
Insecta	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	1.1	8.2	0.0	1.0	1.3	0.0	2.5	0.1	0.0
Teuthida	0.0	0.1	0.0	0.7	0.2	0.5	0.3	0.2	0.3	0.4	0.1	1.1	0.2	0.4	0.2	0.0	0.0	0.1	0.0
Fish	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	4.2	0.0	0.0	0.0	0.0	33.3	0.0	0.0

Designations as in Table 2.

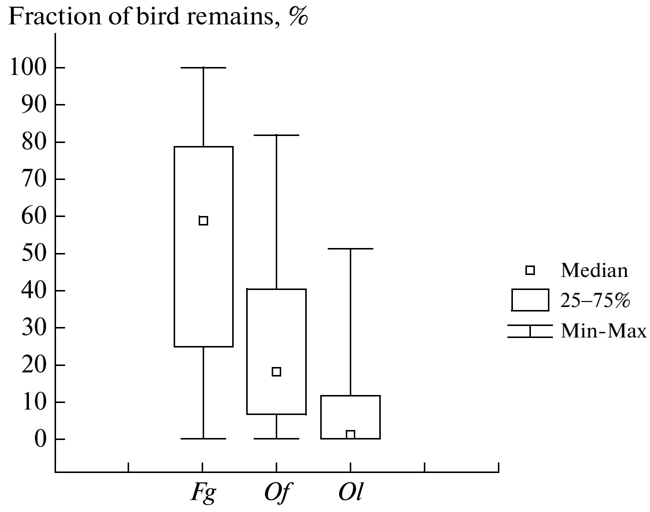

Fig. 3. The fraction of petrels among the bird remains (N = 1675) near arctic fox dens (according to analysis of 1755 prey remains of 32 families): *Fg*, fulmar; *Of*, fork-tailed storm-petrel; and *Ol*, Leach's storm-petrels.

with bird colonies ($F_{\text{rel mammals}} = 17.9 \pm 11.8\%$; $F_{\text{rel birds}} = 62.3 \pm 22.2\%$; $n = 4$).

On the other hand, the corpses of marine mammals (usually, northern fur seals, sea lions, harbor seals, sea otters, and sometimes whales) beached on family territories not only attracted arctic foxes, but made them bring their litters to shelters located close to the corpses. We repeatedly recorded in different years and at different sites that a beached corpse drastically changed the activity of the entire family and the corpse was used for a long period. However, such cases had almost no effect on the quantitative diet estimates for the families studied in this work.

The invertebrates, which arctic fox families picked up on the tidal coastline, supplemented the diets of all families although to different degrees (Tables 2, 3). Amphipods were most frequently found in scat. However, the total fraction of invertebrates in the diet was considerably smaller as compared with that of birds (Fig. 2); moreover, the relative frequency was 15.8 ± 10.5% ($M \pm SD$ with a median of 12.5), whereas the consumed volume was only 3.1 ± 4.2% (median, 0.9).

In the second half of August on the territories with brooks where humpback salmon go to spawn, the arctic fox families can completely switch to fishing. Among the studied families, this was observed for only three families, as the remaining family territories either lacked brooks or the humpback salmon did not enter the brooks.

Birds as a Food Resource for Arctic Foxes

When hunting on coastal cliffs, arctic foxes catch birds open-nesting on rocks and carry still struggling birds down to disjoint them. The arctic fox either eats the prey immediately under the rock or carries it to the den, sometimes decapitating it first. The arctic fox spends much energy for distant transportation of large birds, such as the fulmar (with a weight of about 900 g); in the cases when we directly observed such transportation, the animal stopped several times for rest, sat down, and put the prey nearby.

As for hunting storm-petrels, it is unknown whether arctic foxes dig out their nests or catch them flying out. We did not succeed in observing this ourselves and failed to find any description in the literature. However, we repeatedly observed arctic foxes bringing two storm-petrels at once to the den. As for younglings of the snow bunting (*Plectrophenax nivalis*) and gray-crowned rosy finch (*Leucosticte tephrocotis maxima*), the arctic fox sometimes bring entire litter of them to its den (observations of O.G. Nanova).

We have found remains of at least 15 avian species in arctic fox scat. However, the main food objects were petrels (fulmars, fork-tailed, and Leach's storm-petrels; Fig. 2), and fulmars were the main type of these three (Fig. 3). Some families also frequently caught large alcid birds (guillemots, tufted, and horned puffins; Tables 2–4, for example, families 1 and 1a). Cormorants, seagulls, small passerines, and rock ptarmigans (*Lagopus mutus*) were secondary or accidental food objects for arctic foxes. Their fraction in the family diets never exceeded 5%, usually accounting for 0.2%.

Correlation between Spatial Distributions of Arctic Fox Families and Fulmar Colonies

The fulmar colonies are unevenly located along the coast in a spotty way (Fig. 1). Large stable food sources are present only on 11% of the coast (colony abundance index of 3 and 4) and are absent on the main length of the coast (64.5%, abundance index of 0 or 1).

About 30% of the family territories of the arctic foxes with litters (N = 37) were located near large bird colonies (abundance index, 3 or 4) and about 43%, at a large distance from them in the regions where the fulmar nests were absent or few.

On the coast regions where an arctic fox family with its litter lived for at least one season (reproductive areas), the number of nests was significantly higher as compared with the regions without litters (Fig. 4).

In the reproductive areas, the frequency of litters positively correlated with the bird abundance index (Spearman $R = 0.55$, $t(N-2) = 3.594$, and $p = 0.001$; Fig. 5).

Seabirds constitute the main part of diets even of those families inhabiting the territories without or with few bird colonies, i.e., on the territories with bird abundance indices of 0 and 1, although the fraction of birds in the diets on such territories is significantly lower (Mann–Whitney U test: U = 9, Z = 2.89, $N1$ = 8, $N2$ = 11, and $p = 0.0038$) as compared with the ter-

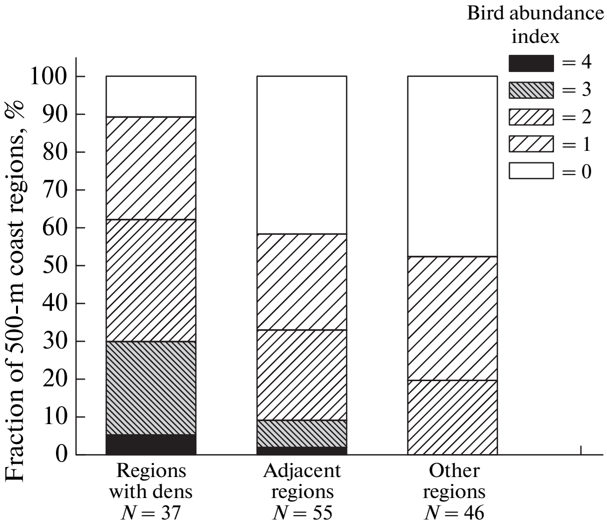

Fig. 4. Fractions of the 500-m coast regions with different fulmar nest abundance indices where arctic fox litters have been found at least once over the observation period.

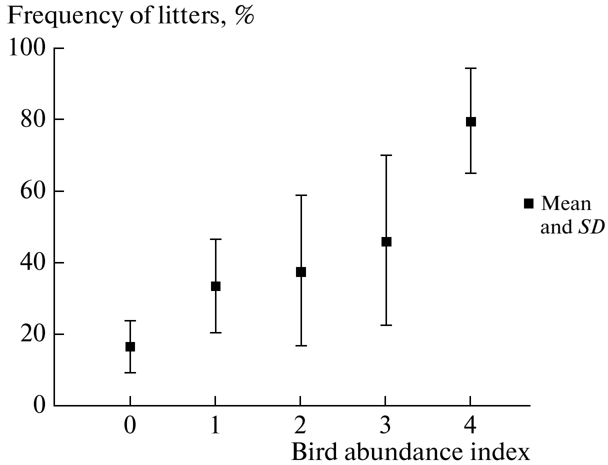

Fig. 5. Relative frequency of arctic fox litters in the regions with different fulmar abundance indices. Only reproductive regions are taken into account, i.e., the regions where a family with a litter was recorded at least once over the observation period. The percent ratio of the total number of litters over the observation period to the number of years in which this region was observed (some regions were not examined every year) was calculated for each region.

ritories containing colonies (indices of 2 to 4; Fig. 6). On the other hand, consumption of invertebrates is significantly higher (Mann–Whitney U test: U = 0, Z = 3.63, $N1 = 8$, $N2 = 11$, and $p = 0.0003$) on the territories poor in seabirds (Fig. 7). Presumably, insufficiency of birds leads to increased consumption of marine invertebrates.

Use of Pinniped Rookeries

The rookeries were supplementary rather than the main food source even for the arctic fox families living near rookeries, whereas seabird colonies were the main source. We analyzed in detail the diets of four families that used rookeries as a food source, namely one family that lived near the Uril'e rookery in 1997 and three families that lived near the Southeastern rookery in 1997, 2003, and 2005.

Birds were predominant in the diets of these four families ($F_{\text{rel birds}} = 62.3 \pm 22.2\%$ and $V_{\text{rel birds}} = 66.0 \pm 26.0\%$ versus $F_{\text{rel mammals}} = 17.9 \pm 11.8\%$ and $V_{\text{rel mammals}} = 23.0 \pm 14.4\%$). Moreover, the families living near the same rookery used this resource to different degrees. For example, 24 seal remains (33.8% of prey remains) were found near the den near the Southeastern rookery in 1997 with $F_{\text{rel mammals}} = 32.9\%$. In 2003, $F_{\text{rel mammals}} = 17.9\%$ for the family living near this place and in 2005, $F_{\text{rel mammals}} = 3.6\%$ (4.4% among 45 prey remains). In 2006, among 82 prey remains of the arctic fox family living on the same territory, the seal remains accounted for 2.4%.

The family living near the Uril'e rookery (1997), where the nearest bird colonies were rather small and hard to reach, preyed on birds to a lesser degree than the families living in the vicinity of the Southeastern rookery (Tables 2–4, family 14). Nonetheless, birds there were also the main food, although the adult arctic foxes took their the cubs in August to the very border of the rookery and, concurrently, to the brook where humpback salmon came to spawn. The number of prey remains ($n = 17$) near this den was considerably smaller as compared with the dens near the Southeastern rookery, and 17.6% of them were seal remains.

DISCUSSION

Changes in the Foraging Strategy

The arctic fox families on the southeastern half of
Mednyi Island use a wide range of food objects when 4
rearing their cubs; however, our data demonstrate that the components of this range are unequal. Petrel colonies are the main food source and the alternative resources, namely, sea wrecks, invertebrates, fish, products of pinniped rookeries, and even colonies of other seabirds, are now supplementary. In our opinion, a pronounced asymmetry in the current use of food resources by arctic foxes is an interesting phenomenon, which can be analyzed due to the well-known history of this arctic fox population.

The feeding of arctic foxes on Mednyi Island has 4
been studied repeatedly in the 20th century (Chersky, 1920; Freiberg, 1929; Barabash-Nikiforov, 1939; Il'ina, 1950; Marakov, 1964; Zagrebel'nyi, 2000, 2000a). These studies were performed at different time; however, all these works except for those by Zagrebel'nyi, were performed when the arctic fox population exceeded manifold the current size and the

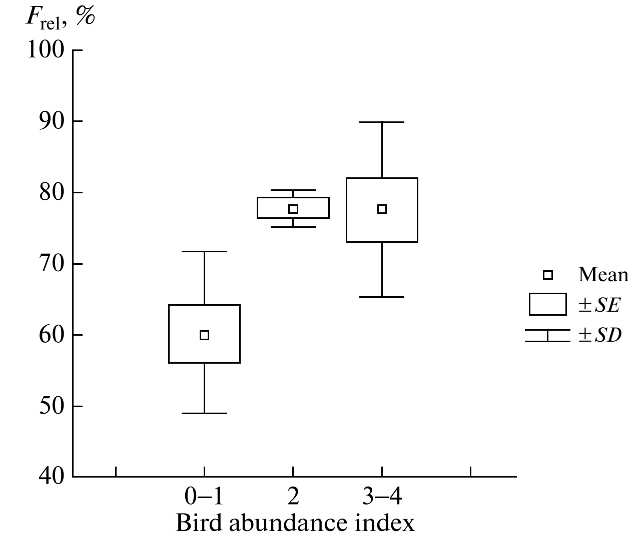

Fig. 6. The fraction of birds in the arctic fox family diet depending on bird abundance on the coast territory with a litter den. Horizontal axis shows the reproductive areas with different fulmar abundance indices (see the text): 0–1 low (no colonies; $n = 8$); 2, medium ($n = 3$); and 3–4, high (large colonies; $n = 8$); the vertical axis shows the relative abundance of bird remains in scat sample.

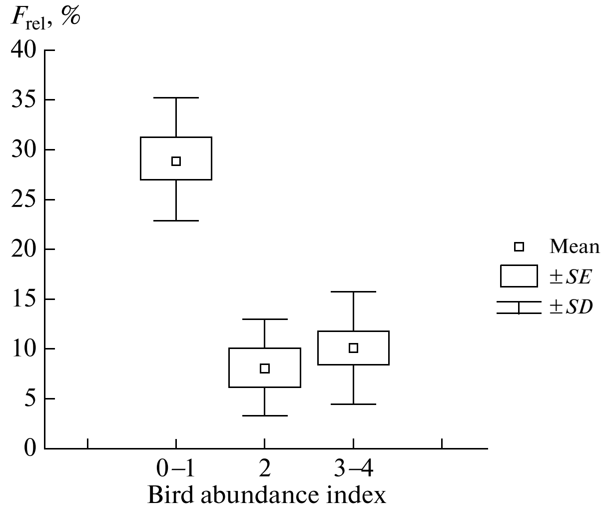

Fig. 7. The fraction of invertebrates in the arctic fox family diet depending on bird abundance on the territory. Horizontal axis shows the reproductive areas with different fulmar abundance indices (see text): 0–1 low (no colonies, $n = 8$); 2, medium ($n = 3$); and 3–4, high (large colonies; $n = 8$); the vertical axis shows the relative abundance of invertebrate remains in scat samples.

goals were confined to a total description of the diet. Unfortunately, it is rather difficult to quantitatively compare our data and the published lists of food objects due to methodical reasons. In addition, the samples (mainly, stomach contents) were collected during the winter period (hunting season) and sampling sites were not indicated. Nonetheless, these studies covering the period from the 1920s to 1990s make it possible to trace the main trends of the changes in the arctic fox diet that took place after the arctic fox population passed through the bottleneck and to clarify the factors that have determined these changes.

Increase in the dependence on seabird colonies. All the studies staring from the earliest ones noted that the arctic foxes in summer depended on the seabird colonies (for example, see the review by Il'ina, 1950). This trend by now has become even more pronounced. According to the data of Barabash-Nikiforov (Il'ina, 1950, p. 93), in April–August birds were found in 30–50% of the arctic fox stomachs and scat; invertebrates, in 70–72%; and fish, in 28–40%. According to our data, the rate of birds increased to 93.1 ± 9.2% (median, 96.5%; lower quartile, 92.9%; and upper quartile, 98.4%); the rate of invertebrates decreased to 25.5 ± 18.3% (median, 20.2%; lower quartile, 10.7%; and upper quartile, 40.3%); and the rate of fish decreased to 3.2 ± 9.8% (median, 0; lower quartile, 0; and upper quartile, 2.1%).

Thus, our study confirms the conclusions of Zagrebel'nyi (2000) about an increase in the fraction of seabirds and a decrease in the use of alternative sources in the arctic fox diet. Of special interest is the fact that actually only the fraction of petrels has increased, whereas the fractions of other species including seabirds not only failed to increase but even decreased considerably.

A differential estimation of the diets of individual families demonstrates that petrels have become the dominating food objects for almost all families and fulmars, for the majority of families. A considerable contribution of the main alternative food objects (alcid birds, invertebrates, and products of seal rookeries) was found for only a small number of families. These families lived on the territories lacking petrel colonies and containing abundant alternative sources.

Decrease in the use of sea wrecks and invertebrates. Sea wrecks and invertebrates of the coastline are still an important supplement to the arctic fox diet. In winter after the birds flew away, this food source is likely to become the main one (Zagrebel'nyi, 2000, 2000a; our data) and the contribution of beached corpses of marine mammals increases (Il'ina, 1950; Marakov, 1964; our data). It is likely that the amount and composition of the sea wrecks has gradually changed over the 20th century, reflecting the state of the ocean. The rate of the sea urchins (genus *Strongylocentrotus*)[4] in

[4] Barabash-Nikiforov (1939) found the green sea urchin (*S. droebachiensis*) in the arctic fox stomachs ($N = 89$) and Zagrebel'nyi (2000) found the sea urchin *S. polyacanthus*. We still cannot say whether this is a mistake in species identification or the result of changes in the sea wreck composition. The sea urchin *S. polyacanthus* is the most abundant species in Mednyi Island 4
(Zh.G. Antipushina, personal communication).

the winter diet was earlier about 30%, and the rate of mussels (genus *Mytilus*), about 11% (Barabash-Nikiforov, 1939). Now both organisms have almost disappeared from the arctic fox diet both in summer and in winter (Sergeev, 1999[5]; Zagrebel'nyi, 2000, 2000a; Nanova, 2006[6]. This is evidently associated with a drastic decrease in these resources; one of the reasons for this decrease is in the growth in the sea otter population in the water area around the island from several tens of individuals in the 1920s to 2500–3000 in the 1960s (Barabash-Nikiforov et al., 1968).

However, the changes in the consumption of invertebrates by arctic foxes are presumably connected not only with the changes in their abundance. The consumption of amphipods also decreased due to some reasons. Barabash-Nikiforov (Il'ina, 1959) reported that the arctic fox scat contained 39% of crustaceans (presumably, amphipods) in April–May and up to 70% in July–August versus our data that the average fraction of amphipods for 19 arctic fox families was 15.1 ± 16.4% (median, 8.3; lower quartile, 1.7; and upper quartile, 23.8), although this is hardly explainable by a decrease in accessibility of this resource.

Decrease in the use of rookery products. The fur seal
4 rookeries on Mednyi Island are located only on the southern part; there they can potentially serve as an abundant food source for the arctic fox. This resource does not yield to seabird colonies in its accessibility and predictability in time and space. During the reproductive season, numerous seal cubs appear in the rookeries and placentas accumulate on the delivery sites. The number of northern fur seal cubs in the
4 Southeastern rookery of Mednyi Island amounts to approximately 17000–20000 (Chelnokov, 1970; Stus and Nesterov, 2002; Stus, 2004). The number of cubs in the same rookery of sea lions is about 200 (Mamaev and Burkanov, 2006). Dozens of arctic fox families concentrated around the rookeries in the 1960s–1970s (Chelnokov, 1970). Now the concentration of arctic fox families near the rookeries is absent and no more than one or two arctic fox family use the rookery products and only as a supplementary source. The reasons for this situation (see Kruchenkova, Shienok, et al., in press) are outside the focus of this work; however, we would like to underline that the main change in the arctic fox foraging ecology is a decrease in the use of the food resources alternative to seabird colonies.

Formation of specialization in preying on petrels. The fulmar colonies are numerous on the island but distributed over the island as distinct spots. Therefore, the family territories of arctic foxes considerably differ in the abundance of this resource. Nonetheless, all the arctic fox family territories independently of the abundance of bird colonies and distance to them specialize in preying on seabirds, in the overwhelming majority of cases on fulmars and storm-petrels. Three facts suggest this inference: first, the highest rate of remains of these birds in arctic fox scat and prey remains around their dens; second, localization of the litter dens near fulmar colonies; and third, a significant positive correlation between the number of litters that appeared on the studied area over the observation period and the fulmar abundance index. In addition, the presence of marine invertebrates in the diet of a family displays a significant negative correlation with the abundance of fulmars on the territory and decreases on the territories with accessible seabird colonies.

According to the data of Barabash-Nikiforov (1939) and Il'ina (1950), the consumption of fulmars by arctic foxes in the first half of the 20th century did not exceed the consumption of cormorants, guillemots, and even ducks; in the 1960s (Marakov, 1964), the role of fulmars in the arctic fox diet was high, although Marakov did not differentiate the other birds in his work. We did not find any published data about arctic fox preying on storm-petrels before the paper by Zagrebel'nyi (2000a), although Marakov (1972) reported a very high density of the storm-petrel population on Mednyi Island. 4

Thus, comparison of our data and published data demonstrates that the arctic fox diet was considerably more diverse in the early 20th century, when the arctic fox population on the island was seven- to tenfold higher than now (see, for example, Gol'tsman et al., 2003). Currently, seabirds are predominant in the summer arctic fox diet, whereas the use of all alternative prey types has drastically decreased. Moreover, the range of the preyed seabird species has narrowed, the petrels in colonies becoming the main prey.

A decrease in the number of the used food objects is unexplainable only by a change in their accessibility, although this could have been one of the main initial reasons followed by a cascade of consequences. The currently observed predominant use of petrels is evidently beyond the opportunistic foraging strategy and suggests a foraging specialization.

The Main Factors in Development of Foraging Specialization

We postulate the following four factors that have played the major role in development of the current arctic fox foraging specialization.

(1) *Origin of the current arctic fox population from several individuals that survived after the population collapse.* Only several reproductive families survived on the island in the 1980s during the period of minimal population size and gave rise to the current small population. The outbreak of ear mange for several years led to practically the complete elimination of cubs (Gol'tsman and Kruchenkova, 2001; Goltsman et al., 1996). Litters died out; for example, of seven litters in

---
[5] See Footnote 1.
[6] Nanova, O.G., The Use of Food Resources by the Arctic Fox
4 (*Alopex lagopus semenovi* Ognev 1931) on Mednyi Island (Commander Islands), *Diploma Paper*, Moscow: MGU, 2006.)

1978 all cubs of the six litters died during August (Ovsyannikov, 1981). Thus, the population was restored from a few surviving founder families.

(2) *Liquidation of human settlements on the island.* Various anthropogenic impacts commenced in the mid-18th century and continued to the late 1960s; then the human population was evacuated from the island. The most important consequences for arctic foxes were (i) removal of the hunting pressure, which systematically killed about half the population and destroyed its spatial, demographic, and social structures and (ii) cessation of directed and random artificial supplementary feeding, which profoundly changed the foraging strategy of the arctic fox population. Elimination of these two factors could enhance the rapid formation of a foraging habit.

(3) *Changes in distribution of food sources.* When the population passed through the bottleneck, many changes significant for the arctic fox both associated and unconnected with direct anthropogenic impacts took place in the island ecosystem. For example, the composition of sea wrecks and invertebrates in the tidal zone changed, as did the seabird population, and the sizes of their colonies decreased. The fulmar colonies are the most abundant on the island as well as the most extended and large. The total decrease in the bird population has led to the disappearance of small colonies, mainly of cormorants, auks, and fulmars (E.P. Kruchenkova and M.E. Gol'tsman, unpublished data) and, possibly, to a considerable decrease in very large fulmar colonies. Moreover, complete disappearance of small food resources could have a more pronounced influence on the prey accessibility for arctic foxes and food capacity of their territories than a considerable decrease in large bird colonies.

(4) *Decrease in the arctic fox population density.* One of the most evident and pronounced changes in the
4 arctic fox ecology on Mednyi Island after it had passed
through the bottleneck is the change in its population
4 density. The Mednyi Island population density was extremely high over its entire known history. Many traits in the behavioral ecology demonstrate that this specific feature had been preserved over a period of an evolutionary scale (Goltsman et al., 2005a). Stable retention of a low density should undoubtedly influence the spatial distribution of arctic fox families as well as the load on concentrated food sources.

Proposed Scenario for Development of Foraging Specialization

5 Several families that survived the epizootic actually
founded the new population on the island. This population has formed without any anthropogenic effects damaging its structure and under conditions enhancing transmission of foraging habits. There are grounds to assume that the families with surviving litters during the period when the population passed through the bottleneck were living at the sites with large fulmar colonies. In particular, in 1976 the only completely surviving litter in the southeastern part of the island lived near the Palata Cape (region no. 17 on the map), and in 1978, such an arctic fox family lived near den 3 (region no. 3; M.E. Gol'tsman and E.P. Kruchenkova, unpublished data). Presumably, the accessibility of petrel colonies on the territories of the families that founded the restoring population guided the development of this foraging specialization. This agrees with the observations that the use of pinniped rookery products drastically decreased in this particular period (Kruchenkova and Gol'tsman, 1999).

A decrease in the seabird population sizes (E.P. Kruchenkova and M.E. Gol'tsman, unpublished data), which took place during the same period, made the fulmar colonies the most abundant and highly predictable food source. In addition, the accessibility, constant use, and high quality of these prey species could have formed stable foraging preferences of arctic foxes. We cannot confirm this by quantitative data; however, according to our experience, the lure of fulmar remains is much more attractive for arctic foxes as compared with those of seagull, black-legged kittiwake, or fur seal remains.

In our opinion, the situation when the most abundant food resource becomes the most preferable is quite logical. The specialization of arctic foxes in hunting the most abundant and numerous prey has also been reported for continental populations. For example, a study performed in Swedish Lapland in the 1980s–1990s (Elmhagen et al., 2000) demonstrated that the arctic fox specialized in summer in hunting the Norway lemming (*Lemmus lemmus*) even when the lemming population was low. In summer, the frequency of lemming remains in scat reached 85%. The reproductive success of arctic foxes depended on this particular fluctuating resource. On the other hand, the alternative prey—birds, ungulate carrion, and voles—were used opportunistically. Depending on the local accessibility, they supplemented the arctic fox diet. A study of the arctic fox diet on Saint Lawrence Island (Fay and Stephenson, 1989), inhabited by the collared lemming (*Dicrostonyx exsul*), tundra vole (*Microtus oeconomus*), red-backed vole (*Clethrionomys rutilus*), and arctic ground squirrel (*Spermophilus parryii*), suggested the same conclusions. Arctic foxes actively hunted tundra voles (frequency of 52%), whereas the red-backed vole was found in only one of the 1218 examined arctic fox stomachs and lemming remains were found only twice. Thus, the foraging specialization of arctic foxes in preying on the most abundant food develops even when the accessibility of this food is subject to pronounced periodical fluctuations.

On Mednyi Island, the predictability of the most 4
abundant food sources for the arctic fox is combined with conserved spatial and social relationships of this species (i.e., typical are small habitats preserved for the entire life and used by many generations, stable fami-

lies, and short distances of migration from the natal den), which favors a foraging specialization.

The specialization in preying on seabirds is likely to have ancient roots and continues the foraging strategies of the population before anthropogenic intervention. These traditional habits enhanced the preservation of territories with accessible and stable spots of specific food resources for the offspring.

ACKNOWLEDGMENTS

The authors are grateful to N.N. Pavlov, S.V. Zagrebel'nyi, and A.M. Mironova (Commander Islands Nature Reserve) for their support at all stages of the expeditions. At the initial stage of this work, the scat samples were sorted under the guidance and with the assistance of S.V. Zagrebel'nyi. N.A. Bocharova, L.O. Doronina, A.A. Raspopova, and A.A. Chagaeva (students of the Biological Faculty, Moscow State University) considerably contributed to collection and primary processing of specimens. We are grateful to E.P. Kruchenkova for her assistance in field studies, determination of bird colony sizes, and valuable advice while preparing the manuscript. The criticism of A.V. Chabovskii and N.A. Formozov, who comprehensively analyzed the manuscript, was most helpful for preparing the final version.

4 The expidition to Mednyi Island and organization of the field works could not have been performed without the assistance of V.N. Burkanov and A.M. Burdin. We are very grateful to E.G. Mamaev and his team,
4 who every year worked on Mednyi Island and helped us in every possible way in both sampling and expedition life.

This work was supported by the Russian Foundation for Basic Research (project nos. 96-04-49703, 01-04-48433, 04-04-49303, and 07-04-00745).

REFERENCES

Artyukhin, Yu.B., The Nesting Avifauna of the Commander Islands: Current State, Dynamics, Conservation and Prospects for Use, *Cand. Sci. (Biol.) Dissertation*, Moscow: Moscow State Univ., 1991.

4 Barabash-Nikiforov, I.I., Materials on Feeding of the Mednyi Island Arctic Fox, *Alopex beringensis semenovi* Ogn., *Byul. Mosk. O–va Ispyt. Prir., Otd. Biol.*, 1939, vol. 48, pp. 74–80.

Barabash-Nikiforov, I.I., Marakov, S.V., and Nikolaev, A.M., *Kalan (Morskaya vydra)* (The Sea Otter), Leningrad: Nauka, 1968.

Chelnokov, F.G., On Relationships of Arctic Foxes and Northern Fur Seal Pups, in *Voprosy geografii Kamchatki* (Problems in the Geography of Kamchatka), Petropavlovsk-Kamchatskii, 1970, vol. 6, pp. 151–158.

Cherskii, A.I., The Arctic Fox on the Commander Islands, *Materialy po izucheniyu rybolovstva i pushnogo promysla na Dal'Nem Vostoke* (Materials to Studies on Fishery and Fur Hunting in the Far East), Tokyo, 1920, vol. 1, pp. 60–107.

Dement'ev, G.P. and Gladkov, N.A, *Ptitsy Sovetskogo Soyuza* (Birds of the Soviet Union), Moscow: Sovetskaya Nauka, 1954, vol. 2, pp. 310–337.

Dzhikiya, E.L., Genetic Polymiorphism of Arctic Fox (*Alopex lagopus semenovi* Ognev, 1931) Populations on the Commander Islands, *Cand, Sci. (Biol.) Dissertation*, Moscow: Moscow State Univ., 2008.

Elmhagen, B., Tannerfeldt, M., Verucci, P., and Angerb- 2 3
jorn, A., The Arctic Fox (*Alopex lagopus*): An Opportunistic Specialist, *J. Zool.*, 2000, vol. 251, no. 2, pp. 705–714.

Fay, F.H. and Stephenson, R.O., Annual, Seasonal, and Habitat-Related Variation in Feeding Habits of the Arctic Fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea, *Can. J. Zool.,* 1989, vol. 67, no. 8, pp. 1986–1994.

Freiberg, E.N., The Blue Arctic Fox on the Commander Islands, *Okhotnik*, 1929, no. 9.

Geptner, V.G. and Naumov, N.P., The Arctic Fox *Alopex lagopus* Linnaeus, 1758, in *Mlekopitayushchie SSSR* (Mammals of the Soviet Union), Moscow: Vysshaya Shkola, 1967, vol. 2, part 1, pp. 194–208.

Goltsman, M.E. and Kruchenkova, E.P., The Blue Arctic
Fox, *Alopex lagopus semenovi* Ognev, 1931, from Mednyi 4
Island, in *Krasnaya Kniga Rossiiskoi Federatsii (zhivotnye)* (The Red Data Book of the Russian Federation: Animals), Moscow: Astrel', 2001, pp. 621–629.

Goltsman, M.E., Kruchenkova, E.P., and Macdonald,
D.W., The Mednyi Arctic Foxes: Treating a Population 4
Imperilled by Disease, *Oryx*, 1996, vol. 30, no. 4, pp. 251–258.

Goltsman, M.E., Kruchenkova, E.P., Sergeev, S.N., and
Volodin, I.A., The Mednyi Island Arctic Fox (*Alopex lago-* 4
pus semenovi): Specific Features of Insular Population, *Zool. Zh.*, 2003, vol. 82, no. 4, pp. 514–524.

Goltsman, M.E., Kruchenkova, E.P., Sergeev, S.N., Johnson, P.J., and Macdonald, D.W., Effects of Food Availability on Dispersal and Cub Sex Ratios in the Mednyi Arc- 4
tic Fox, *Alopex lagopus* Semenovi, *Behav. Ecol. Sociobiol.*, 2005a, vol. 59, pp. 198–206.

Goltsman, M.E., Kruchenkova, E.P., Sergeev, S.N., Volodin, I.A., and Macdonald, D.W., "Island Syndrom" in a
Population of Arctic Fox (*Alopex lagopus*) from Mednyi 4
Island, *J. Zool.*, 2005b, vol. 267, pp. 1–14.

Hurlbert, S.H., Pseudoreplication and the Design of Ecological Field Experiments, *Ecol. Monogr.*, 1984, vol. 54, pp. 187–211.

Il'ina, E.D., *Ostrovnoe zverovodstvo* (Fir Farming on Islands), Moscow: Mezhdunarodnaya Kniga, 1950.

Kartashev, N.N., Birds of the Commander Islands and Some Proposals for Their Rational Management, *Zool. Zh.*, 1961, vol. 10, no. 9, pp. 1395–1409.

Kruchenkova, E.P. and Goltsman, M.E., Parental Behavior
of Arctic Foxes (*Alopex lagopus semenovi*) on Mednyi 4
Island: Factors Determining the Connection between Adults and Cubs, *Zool. Zh.*, 1994, vol. 73, no. 5, pp. 88-103.

Kruchenkova, E.P. and Goltsman, M.E., "Cultural" Traditions of Foraging in the Insular Arctic Fox Population, *Tezisy dokl. 6-go Teriol. s"ezda RAN 13-16 aprelya 1999* (Abstr. 6th Theriol. Conf. Russ. Acad. Sci., April 13–16, 1999), Moscow: Ross. Akad. Nauk, 1999, p. 139.

Kruchenkova, E.P., Goltsman, M.E., Sergeev, S.H., and
Macdonald, D.W., Is Alloparenting Helpful for Mednyi 4

Island Arctic Foxes, *Alopex lagopus semenovi?, Naturwissenschaften*, 2009, vol. 96, no. 4, pp. 457–466.

Mamaev, E.G. and Burkanov, V.N., The State of the Reproductive Group of Steller Sea Lions (*Eumetopias jubatus*) in
4 the Southeastern Rookery on Mednyi Island in 2005, in *Morskie mlekopitayushchie Golarktiki. Sbornik nauch. trudov* (Holarctric Marine Mammals: Collected Scientific Works), St. Petersburg: ROO Sovet po Morskim Mlekopitayushchim, 2006, pp. 342–347.

Marakov, S.V., *Priroda i zhivotnyi mir Komandor* (The Nature and Fauna of the Commander Islands), Moscow: Nauka, 1972.

Marakov, S.V., Mammals and Birds of the Commander Islands, *Cand, Sci. (Biol.) Dissertation*, Kirov: All-Union Res. Inst. of Animal Raw Materials and Furs, 1964.

Naumov, N.P., Goltsman, M.E., Kruchenkova, E.P., Ovsyanikov, N.G., Popov, S.V., and Smirin, V.M., Social Behav-
4 ior of Arctic Foxes on Mednyi Island: Factors Determining
1 the Spatiotemporal Pattern of activity, in *Ekologiya, struktura populyatsii i vnutrividovye kommunikativnye protsessy u mlekopitayushchikh* (Ecology, Population Structure, and Intraspecific Communicative Processes in Mammals), Moscow: Nauka, 1981, pp. 31–75.

4 Ovsyanikov, N.G., The Arctic Fox of Mednyi Island Is at Risk of Extinction, *Priroda* (Moscow), 1981, no. 9, pp. 59–61.

Sokolov, E.A., Diets and Feeding of Commercial Mammals and Birds, *Okhotnich'i Zhivotnye*, 1949, no. 1, p. 155.

Stus, A.I., The Northern Fur Seal (*Callorhinus ursinus*) on the Commander Islands: Current State and Rational Management of Stocks, in *Morskie mlekopitayushchie Golarktiki: Sbornik nauchnykh trudov* (Holarctric Marine Mammals: Collected Scientific Works), Moscow: KMK, 2004.

Stus, A.I. and Nesterov, G.A., Current State of the Northern Fur Seal (*Callorhinus ursinus*) Population on the Commander Islands and Prospects for Its Rational Management, *Morskie mlekopitayushchie Golarktiki. Tezisy dokl. konf* (Abstr. Conf. on Holarctric Marine Mammals), Moscow: ROO Sovet po Morskim Mlekopitayushchim, 2006, pp. 246–248.

Tannerfeldt, M. and Angerbjorn, A., Life History Strategies 3
in a Fluctuating Environment: Establishment and Reproductive Success in the Arctic Fox, *Ecography*, 1996, vol. 19, pp. 209–220.

Tannerfeldt, M. and Angerbjorn, A., Resource Fluctuations 3
and the Evolution of Litter Size in the Arctic Fox, *Oikos*, 1998, vol. 83, pp. 545–559.

Zagrebel'nyi, S.V., Feeding Ecology of Two Arctic Fox Subspecies (Carnivora, Canidae) on the Commander Islands: *Alopex lagopus beringensis* Merriam, 1902 on Bering Island
and *A. l. semenovi* Ognev, 1931 on Mednyi Island, *Zool. Zh.*, 4
2000, no. 5, pp. 595–697, 2000a.

SPELL: 1. spatiotemporal, 2. Tannerfeldt, 3. Angerbjorn, 4. Mednyi, 5. epizootic