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Structure of Arctic Fox (*Alopex lagopus beringensis*) Colonies in the Northern Extremity of Bering Island

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Abstract—Data on the spatial structure of an Arctic fox (*Alopex lagopus beringensis*) colony were obtained in July–August 1995, using walk counts and observations near living dens around the Northern rookery of the northern fur seals located on Bering Island (Commander Islands). The home ranges of 31 Arctic fox families (61 adults and 145 pups inhabiting 66 dens) were found over 27 km of the coastline. Sixty individuals (3 adults and 57 pups) were marked by color ear-tags. Among adult foxes, 24 (39.3%) were recognized as females and 12 (19.7%) as males; the sex of 25 (41.0%) foxes was not recognized. Among 57 marked cubs, 26 (45.6%) were females and 31 (54.4%) were males. The best studied families (13) had 3–11 pups (6.7 ± 0.7, on average). The survival of cubs at an age younger than 2.0–2.5 months was 82.5%; 30.8% of the families consisted of more than two adults. The distribution of the Arctic fox dens and home ranges along the coastline has been studied; specific features of the location of dens have been described. In the studied area, Arctic foxes have been foraging on birds (67.6% of dens with food remains), northern fur seals (40.5), other marine mammals (13.5), Pacific salmon (29.7), and reindeer (2.7%), as well as on amphipods and voles. Rich constant food sources (rookeries, marine bird colonies, and spawning places of the blueback salmon) were found in 7 home ranges of the Arctic fox; 6 home ranges included temporary food sources (spawning streams of the humpback salmon); and 18 home ranges were poor in food resources. Arctic foxes whose home ranges lie within 6–7 km around a "food patch" used the concentrated food resources together. Food resources are supposed to become important only after the raised pups turn to self-feeding. Differences in the use of space, foraging and breeding of the two Arctic fox subspecies (*A. l. beringensis* and *A. l. semenovi*), and arrangement of colonies around the northern fur seal rookeries are discussed.

Keywords: breeding season, family plot, location of dens, structure of families, demographic composition, concentrated sources of food

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INTRODUCTION

Commander Islands are home to the most ancient isolated Arctic fox (*Alopex lagopus beringensis* and *A. l. semenovi*) populations. The habitat conditions of island subspecies differ sharply from the continental ones. The sizes of populations are small, but these populations have survived since the Pleistocene. There are no other native land predators on the islands, the climatic conditions are quite mild, and the sources of food resources are stable and highly productive (sea mammal rookeries, bird colonies, and spawning grounds of salmons) (Il'ina, 1950; Marakov, 1972; Naumov et al., 1981; Zagrebel'nyi, 2000; Goltsman et al., 2003, 2005a, 2005b, 2010).

The high density, absence of migrations, abundance of food, and high degree of attachment of animals to their plots, which developed in such conditions, make the endemic island Arctic fox populations in the Commander Islands important objects of comparative behavioral ecology. The greater part of research is performed on the subspecies *A. l. semenovi* from the Mednyi Island (Naumov et al., 1981; Kruchenkova and Goltsman, 1994; Goltsman et al., 2005a, 2005b; Kruchenkova et al., 2009). The social behavior and spatial relationships in the Bering subspecies *A. l. beringensis* have been studied much less and the majority of the data was obtained in the first half of the 20th century (Barabash-Nikiforov, 1937; Il'ina, 1950). Some data on the demography of this population appeared only recently (Zagrebel'nyi, 2000; Ryazanov, 2002). The study undertaken by us should fill in the existing gap to a certain degree.

The aim of our work is to study the spatial structure and behavior of the Arctic fox during the breeding season in the environs of the Northern rookery of northern fur seals. The main tasks included the following: (1) revealing the spatial distribution and territorial relationships of Arctic fox families, (2) describing the

structure of the family plots and their use, (3) determining the structure of families and demographic composition of the population, and (4) establishing the main food objects and their use depending on the distance from the concentrated food sources.

EXPERIMENTAL

Area of Studies

The studies were performed on Bering Island, which is the largest in the group of Commander Islands. It is 90 km long, 5–40 km wide, and 1667 km^2 in area. The northern part of the island consists of lowlands, with distinct low, mildly sloping hills. It descends toward the sea forming several terraces. A laida (pebbly, sandy, or rocky shore strip partially flooded with water during the high tide) adjoins the water directly. The first terrace rises over the laida by 0.5–2 m; its width varies from several meters to half a kilometer. In many places, the first terrace is not pronounced. The second terrace rises above the laida by approximately 10–30 m and often passes into a steep precipice toward the sea. It stretches deep into the island to the line of low hills, which form a third terrace (Ponomareva and Isachenkova, 1991).

Plain areas of the northern part of Bering Island are covered with various tundra plant communities. There are many tundra lakes in this place, among which the largest lake of the island is Lake Sarannoe with an area of around 31 km^2, which is connected to the sea by a river of the same name. Dense grass vegetation is found only near the sea and along the banks of small rivers and streams that cut through the tundra with deep (up to 10 m deep) river valleys. Tundra with bare hills and a weathered broken rock surface predominated on the highlands of the third terrace (Ponomareva and Yanitskaya, 1991).

The climate of the island is typical of northern Pacific islands: cold summer with the maximum average day temperature of +11°C in August and relatively mild winter with the minimum temperature of –4°C in January–March. Very high average annual humidity and constant winds that often change direction are also characteristic of the island. In winter, strong wind causes blizzards. Storms are typical for the nonfreezing sea, and they are especially strong in the fall and spring. Clear days are rare, and in summer, the island is often shrouded in mist, which is accompanied by a drizzling rain called *bus*.

Among the animal population of the island, colonial sea birds, which nest on rocky cliffs, are especially numerous: fulmars (*Fulmaris glacialis*), cormorants (*Phalacrocorax pelagicus, Ph. urile*), gulls (*Larus glaucescens*), kittiwakes (*Rissa tridactyla*), red-legged kittiwakes (*R. brevirostris*), guillemots (*Uria lomvia* and *U. aalge*), pigeon guillemot (*Cepphus columba*), horned piffin (*Fratercula corniculata*), and tufted piffin (*Lunda cirrhata*) (Artyukhin, 1991). In the northern part of the island, bird colonies were located only in two places: in the Pasenyuk Bay and on cliffs over the Northwest rookery of northern fur seals.

In terms of sea mammals, the most numerous is the northern fur seal (*Callorhinus ursinus*), which occupies two rookeries from early spring to late fall. Two large rookeries on Bering Island (the Northern and Northwestern ones) are located at the northern extremity of the island. Throughout the entire year, Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina kurilensis*), and sea otters (*Enhydra lutris*) also stay close to the island.

The only native land mammal of the island is the Arctic fox—the remaining species were introduced by man. The following species are found outside inhabited areas: reindeer (*Rangifer tarandus*) that became wild, the American mink (*Mustela vison*), and the northern red-backed vole (*Clethrionomys rutilus*), whose numbers are very high in the northern lowland part of the island (Marakov, 1972).

In May, the run of the blueback salmon (*Oncorhynchus nerka*) starts. It enters several of the largest rivers and Lake Sarannoe and stays in them until winter. In August–September, the humpback salmon (*Oncorhynchus gorbusha*) rises up the majority of rivers and streams. In addition, dolly varden trout (*Salvelinus malma*) and coho salmon (*Oncorhynchus kisutsch*) are found (Savvaitova and Maksimov, 1987).

The area of study selected by us in the northern extremity of the Bering Island is one of the places where Arctic foxes concentrate, both in the breeding season and in winter (Zagrebel'nyi, 2000; M.V. Zhalgaubaev, personal message).

History of the Studied Population

The hides of the island blue Arctic fox were valued highly until the first half of the 20th century, so from the discovery of the Commander Islands in 1741, the populations of both islands were subjected to intense exploitation. In the middle of the 18th century, in the course of the winter period, one vessel procured approximately 2000 Arctic foxes (Suvorov, 1912). By the end of the 19th century, owing to intense uncontrolled hunting, the numbers of Arctic foxes significantly decreased: in some years, the number of animals killed reached 1000 (Krupnik, 1987). From 1932 to the mid-1950s, so-called island animal breeding existed on the Commander Islands. During this period, intensive regulated hunting with the use of a well-organized system of food traps was conducted. The best individuals were left for breeding, while the rest were rejected and slaughtered. Owing to abundant extra feeding, the number of Arctic foxes considerably increased and reached 3000 individuals (Il'ina, 1950). In the 1950s, an animal farm was created on Bering Island to breed the local blue Arctic fox, which was replaced with the American mink in the 1960s. Measures on extra feeding were stopped, but hunting of the

Composition of families, fraction of cubs that survived to the age of 2.5 months, and feeding value of Arctic fox plots in the area of the Northern rookery of northern fur seals on Bering Island

Family plot	Number of used dens	Number of adult animals (females/males/unknown)	Number of cubs	Fraction of surviving cubs	Feeding value of the plot	Marked Arctic foxes (adults/cubs)
1c	4	2 (1/0/1)	5	1.0	3	1 (0/1)
2c	1	1 (1/0/0)	9	0	1	8 (0/8)
3c	2	2 (1/0/1)	None	–	1	0
4c	1	3 (1/0/2)	5	0.6	1	3 (0/3)
5c	2	2 (1/1/0)	5	1.0	2	2 (1/1)
6c	3	3 (1/1/1)	9	0.78	2	7 (0/7)
7c	2	3 (2/1/0)	7	1.0	2	1 (0/1)
8c	4	2 (1/1/0)	3	1.0	1	1 (1/0)
1h	2	2 (1/1/0)	11	1.0	3	10 (0/10)
2h	2	2 (1/1/0)	6	1.0	3	4 (0/4)
3h	1	2 (1/1/0)	4	0.75	1	2 (0/2)
4h	2	1 (1/0/0)	7	1.0	1	6 (0/6)
5h	5	3 (2/1/0)	9	1.0	1	6 (1/5)
Total	31	28	80			51 (3/48)

The feeding value of the plot: (1) plots with scant food resources, (2) plots with temporary food sources, and (3) plots with steady rich food sources.

Arctic fox continued. However, owing to a decrease in the demand for the long-hair fur, Arctic fox hunting significantly decreased and became irregular.

From the beginning of the 1970s onward, the number of Arctic fox of the Mednovskii subspecies (*Alopex lagopus semenovi*) decreased catastrophically more than tenfold due to an epizooty of ear mange and currently constitutes 100–120 animals (Goltsman et al., 1996). At the same time, the numbers of the Arctic fox population of the Bering Island decreased 2–2.5 times and for the last 20 years has remained at a stable level of 800–1000 animals during the period of appearance of the young out of the dens (Danilina, 1987; Ryazanov, 2002). Until 1997, hunting was conducted in winter time; however, owing to the insignificant numbers of animals obtained it did not influence significantly the population structure of the Arctic fox (Zagrebel'nyi, 2000).

Methods of Material Collection

The material was collected in the northern part of Bering Island from July 8 to August 13, 1995. Twenty-seven km of the shoreline were examined, from the Northwestern Cape to the mouth of the Sarannaya River, 1.5–3 km deep into the island, to the beginning of the bare table land of the third terrace. The walk counts were performed in the daytime from 10 a.m. to 11 p.m. along the shoreline to the southwest and southeast from the Northern rookery of northern fur seals. Altogether, 36 walk counts were performed in the direction of the Northwestern Cape and 43 walk counts were performed in the direction of the Sarannaya River. The dens in a radius of 3–5 km from the Northern rookery were visited every day; more distant counts were made approximately once every 4–5 days. The whole length of the shore from the Northwestern Cape to the mouth of the Sarannaya River was examined completely twice.

At the first stage, the entire shoreline was studied 1.5–3 km deep into the land to discover dens, paths, and other signs of activity of Arctic foxes. Special attention was paid to the most likely places where dens could be located: the laida, the shore cliff, and the beds of numerous streams that run along the surface of the second terrace. Afterward, the majority of routes passed through the already discovered dens, since during the period when the young keep close to the dens, the adults also spend most of their time near the dens (Kruchenkova and Goltsman, 1994; Kruchenkova et al., 2009).

During the walk counts, all findings of Arctic foxes, their age, sex, and behavior were registered. On the whole, 1007 animals were registered over 610 findings of dens. The location of all discovered dens was plotted on a map. For the dens discovered for the first time, food remains were described, subsequent description was performed only if fresh residues appeared. Some dens were observed for 2–4 h per day. One of the families (a couple with 11 cubs, living in the Northern rookery) was observed daily from August 1 to 13 (4–16 h a day, 131 h of observations in all).

The gender of adult Arctic foxes was determined visually by the external sexual characters from a short

distance. To identify the animals individually and to determine the number of pups and their movements around the family plot, the Arctic foxes were captured, weighed, and marked with colored plastic ear tags. The animals were captured with net live traps with a falling door (40 × 40 × 90 cm) provided with bait (meat of the northern fur seal, parts of bird carcasses, and bits of fish) or directly from den holes using a tightening loop or just by hand on the laida and in the tundra. Altogether, 57 pups and 3 adult Arctic foxes were marked.

We considered adult Arctic foxes to belong to a certain family group if they manifested territorial behavior (characteristic barking sounds, accompanying the observer with barks and/attacking them) near breeding dens (Naumov et al., 1981; Goltsman et al., 2003; Kruchenkova et al., 2009); marked signal hillocks accumulated near the dens and along the paths with excrements and urine (Naumov et al., 1981; Goltsman et al., 2003, 2005a); or used characteristic observation points to observe the dens or entered the dens with the cubs. Since in most cases we could not identify adult Arctic foxes individually, the number of adult animals in a family was determined by the maximum number of simultaneously counted animals. If the Arctic foxes did not manifest territorial behavior and did not keep close to specific dens, it was considered that these animals are not associated with the family group that inhabited that territory. The number of cubs in a brood was determined by adding up the number of marked and maximum number of simultaneously counted unmarked cubs.

The animals (adults and cubs) that jointly used one or several dens were united into one family group (family). Regular findings of the same animals at certain places of the shore, and the presence of dens and paths used by Arctic foxes in these areas, as well as the characteristic behavior related to their protection and usage, allowed us to distinguish family plots of various groups. An examination of the plots was conducted periodically during the entire season of studies; we examined 13 of the best studied plots from 8 to 31 times.

RESULTS

Structure and Spatial Distribution of Family Plots and Dens Used

General Structure of the Family Plot

Altogether, the plots of 31 families of Arctic foxes were determined from the Northwestern Cape to the mouth of the Sarannaya River (Fig. 1). Most family plots included a section of the laida and a tundra part; only in four cases (12.9%) was the plot located far from the sea and did not include a strip of the shore. The center of the plot consisted of dens with pups near which the activity of all family members was concentrated. The dens used for many years have, as a rule, many entrance holes often concealed in dense grass. The space at the entrance is trampled down and littered with food remains and excrement, and a characteristic smell emanates from the den itself. Rookeries of adult animals used by them as observation points are situated not far from the dens. Signal hillocks rising above the place marked by Arctic foxes with their urine and feces are scattered along the paths and especially next to the dens. Apart from the dens, temporary refuges are found on the plot: shallow hollows in the ground, sometimes at the base of signal points. The dens, signal hillocks, and observation points are joined together by a system of paths, forming a network of well-pronounced visual and smell landmarks.

Use of Dens

On 12 out of 13 of the best studied plots, broods were registered (table). On four of these plots, we observed at least once a division of the brood between two dens, and on one plot, a division between three dens was observed. In another three families, at least once during the time of observations, the entire brood moved into another den. Thus, on 8 plots out of 12, we observed a complete or partial movement of the brood between the dens.

The dens of Arctic foxes near which pups and/or adults were registered at least once or the dens in which no Arctic foxes were observed but fresh food remains were found were considered as used. From the Northwestern Cape to the mouth of the Sarannaya River, 66 used dens were found on 31 family plots. For 13 of the best studied family plots, the average number of dens used constituted 2.4 per plot. Apart from the dens used, uninhabited abandoned dens were also found. In some cases, such dens were subsequently dug out again and occupied by Arctic foxes grown broods, and thus put to use.

Location of Dens

The majority of Arctic fox dens are situated in places strategically convenient for observation. The dens located immediately in the tundra and on the upper edges of river valleys are often positioned on small hillocks presiding over the area. Such a position of the den makes it convenient to observe the environs from it, and it is almost impossible to approach the den unnoticed across the open tundra space. The dens in the shore cliff are also positioned the most conveniently for observation: both the laida and a significant part of the second terrace can be observed simultaneously from them. The highest position is occupied by the dens on the bare flatlands: several kilometers of tundra of the second terrace can be seen from them. Often, the neighboring dens can also be seen, so, generalizing slightly, the dens can be represented as a network of observation points that preside over the locality.

The dens used by the Arctic foxes on the laida were located in large rock and log obstructions (7 dens, 10.6%). A third of the used dens was located at the

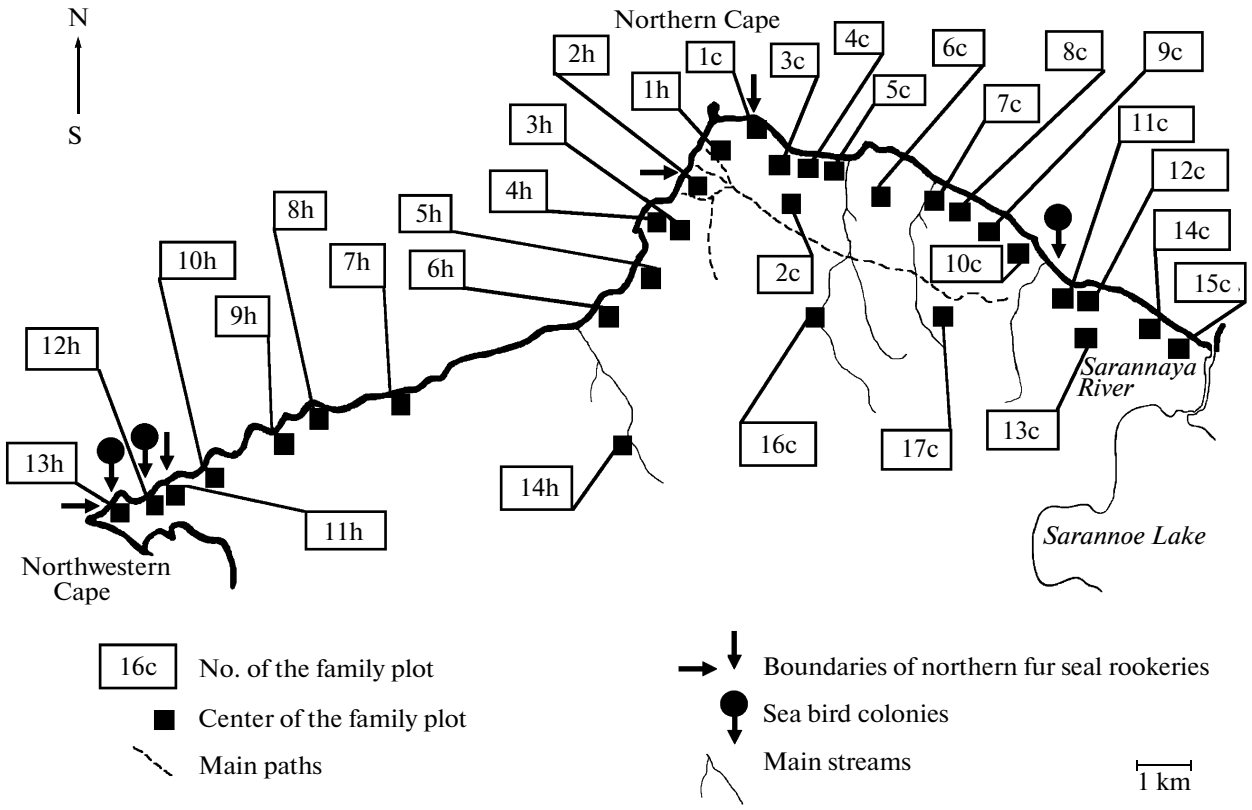

Fig. 1. Spatial distribution of family plots of the Arctic fox at the northern extremity of Bering Island. Plots 5h–8c were visited the most frequently.

edge of the shore cliff of the second terrace or was removed from it by no more than several dozen meters (24 dens, 36.4%). The dens located in the tundra were not, for the most part, removed from the coast by more than 500 m (32 dens, 48.5%). We found only three dens, at the edge of the bare flatland, (4.5%) removed by more than 1 km from the sea (Fig. 1).

On the whole, the greater the distance from the sea, the less often traces of life activity of Arctic foxes (dens, paths, and signal hillocks) are found. At a distance of 1–1.5 km from the shore, the possibility of finding an Arctic fox or traces of its activity is very small. Thus, the Arctic fox colony at the northern extremity of the island stretches in a narrow ribbon along the shoreline (Fig. 2).

Distance between the Dens

To calculate the distance between the dens, we measured the distances between all dens of family plots or the closest dens of neighboring plots, sorting them into distance classes with a step of 250 m. The dens of the three family plots located more than 1 km from the shore were not included.

The mean distance between the dens of one family was 0.5 ± 0.03 km ($n = 64$), and only in one case did it reach 1250 m. The mean distance between the closest dens of neighboring plots constituted 0.8 ± 0.09 km ($n = 31$), usually, 250–1000 m. Only in one case was the distance lower than 250 m, and in five cases the dens were removed from each other by more than 1 km, 2.5 km at maximum.

Distribution of the Used Dens along the Coastline

Figure 3 shows the relative number of used dens at the northern extremity of the island from the Northwestern rookery of northern fur seals to Lake Sarannoye. To plot a chart, we divided the shore hypothetically into strips 3 km long and 1 km wide. By moving the next strip 500 m relative to the previous one, we calculated the number of used dens within each strip. The dens of three family plots more than 1 km from the sea were not counted.

At increasing distance from the places of food concentration (rookeries, spawning grounds, and bird colonies), the density of dens decreased, which was especially noticeable in the gap between the rookeries of northern fur seals (Fig. 3). The highest density of the used dens near the Northern rookery was observed at a distance of approximately 2.5 km to the southwest and 1.5 km to the east. Immediately in the area of the Northern rookery, the density of the used dens was lowered, which is associated, in our opinion, with a

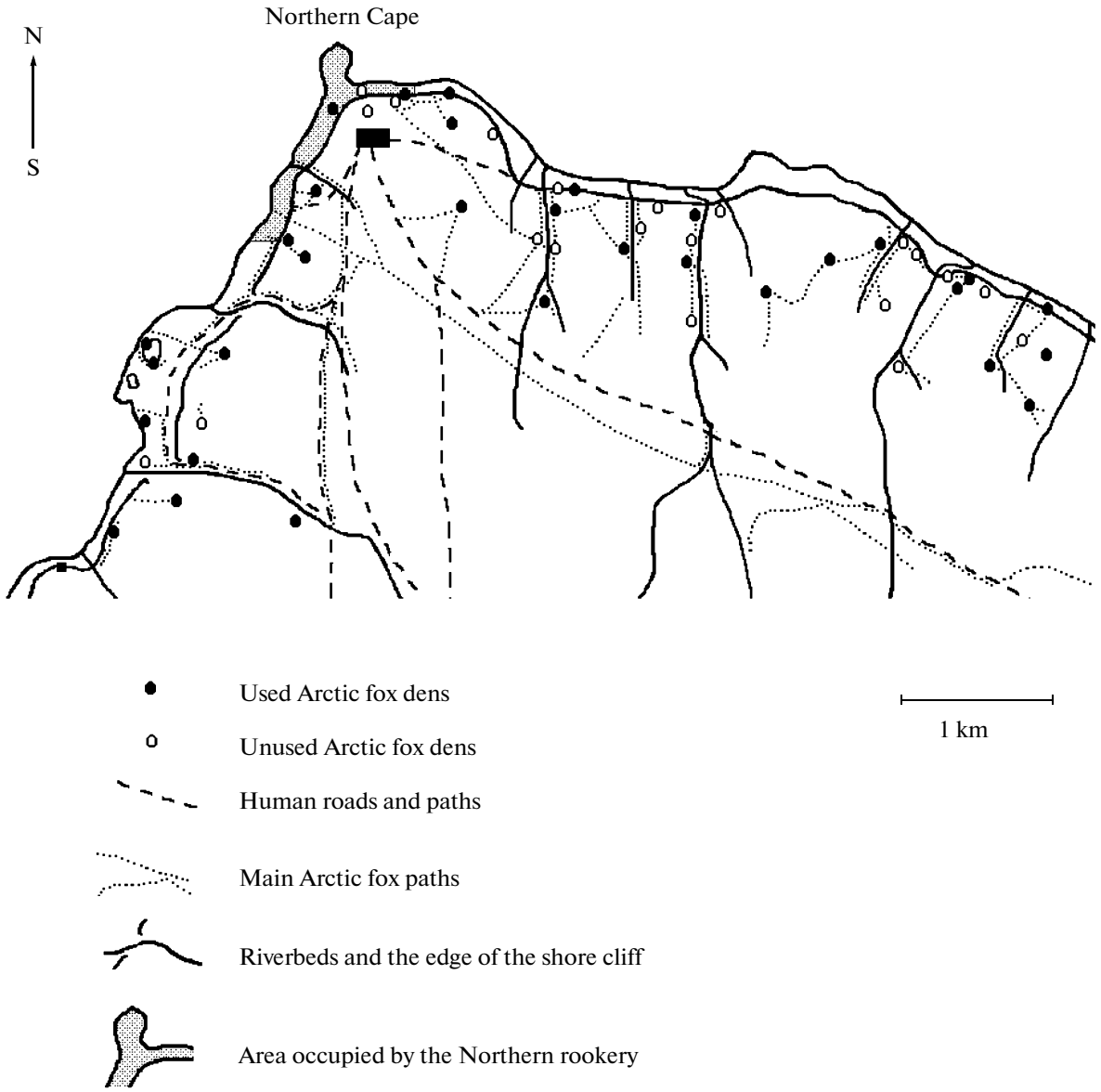

Fig. 2. Location of Arctic fox dens and main paths in the area of the Northern rookery of northern fur seals.

leash-free husky at a small human settlement situated near the rookery. A reliable negative correlation was found between the number of used dens along a three-kilometer stretch of the coast and the distance of the center of this plot from the closest concentrated food source (Spearman correlation, $r = -0.61$ and $p < 0.001$).

Demographic Structure of the Colony

Ratio of Sexes

Sixty-one adult Arctic foxes were registered on 31 family plots from the Northwestern rookery to Lake Sarannoe that demonstrated elements of territorial behavior. Among them, 24 (39.3%) were determined as females and 12 (19.7%) were determined as males; the sex of 25 Arctic foxes (41.0%) was not determined. Of the 57 marked cubs, 26 (45.6%) were females and 31 (54.4%) were males.

Composition of Families

Broods were found on 28 family plots of Arctic foxes. In eight cases, the Arctic foxes attached to the territory did not breed: plots 3c and 6h were occupied by couples consisting of a female and young Arctic fox of an undetermined sex, apparently, born in the previous year, while plot 13c was occupied by one adult Arctic fox, presumably a female (Fig. 1). The table gives a description of the composition of 13 of the most studied families whose plots were located in direct proximity of the Northern rookery. Seven families

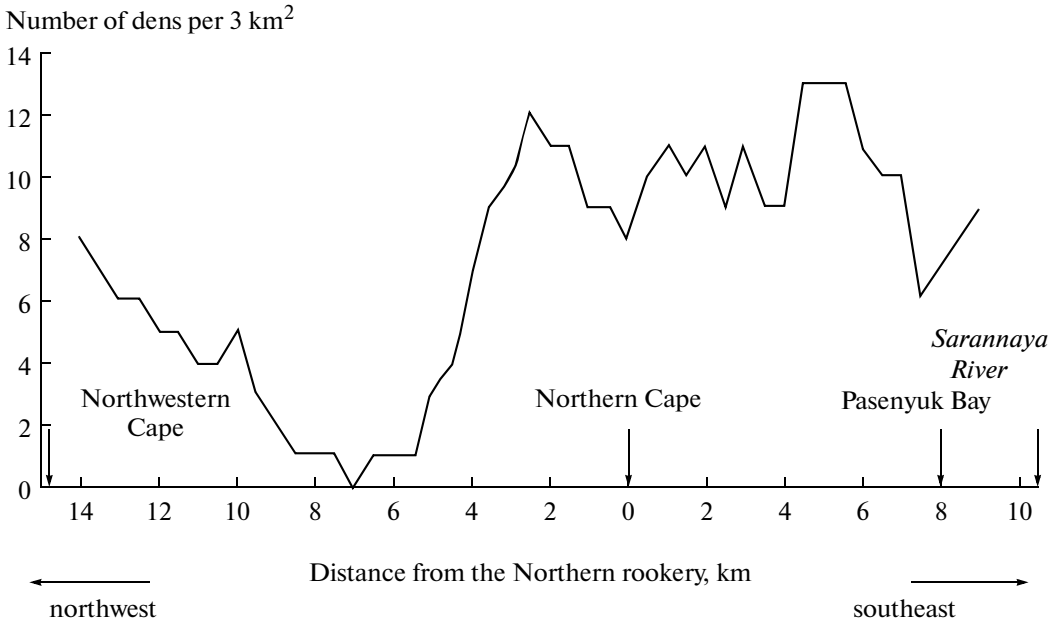

Fig. 3. Relative number of used dens in the northern extremity of Bering Island from the Northwestern Cape to the mouth of the Sarannaya River. The arrows indicate the position of concentrated food sources.

(53.8%) contained two adult animals, and four families (30.8%) had more than two couples. In two of these families (5h and 6c), both females had reproduced since the cubs in the broods differed noticeably in age. The brood of family 1h also consisted of cubs of two age groups; however, during the period of long observations of this family for 13 days, we noted only two adult Arctic foxes: a female and male.

In two families (15.4%), the females raised their broods single-handedly. We did not observe any other adult animals apart from the female mother on the plot of family 2c. On the territory of family 4h, apart from the female, we also observed a male from the neighboring family 4h. At our approach, the male ran away to plot 4h, which was repeated three times. In addition, three times we found him resting on the laida near the observation point of family 4h. If the female was also at the observation point, she did not pay any attention to the male. Thus, although the male from family 3h has never been seen immediately at the dens of plot 4h, it is possible that families 3h and 4h are one complex family consisting of a male with two females and broods in different dens.

Size of the Brood and Death Rates of Cubs

The number of cubs in the broods of 13 families varied from 3 to 11, being on average 6.7 ± 0.7 (±*SE*) pups per family (table). The average number of cubs per feeding female amounted to 5.3 ± 0.5. In three families, the broods were distinctly mixed (the cubs varied noticeably in age).

Over the time of our observations, mortality of cubs in all families, with the exception of one (2c), was not high. Two cubs from families 6c and 4c died. It is likely that one cub from family 3h also died: it fell greatly behind in growth from its siblings and in the last week of work, we no longer saw it at the den. In addition, the corpse of another marked pup from family 4c was found near the den of the neighboring plot of family 2c.

Family 2c consisted of a female and 9 cubs. The den with the cubs was situated on the bank of a small stream 800 m from the sea coast. At the beginning of July, eight cubs were marked and weighed. The female remained almost constantly in the den and fiercely protected the brood at the appearance of observers. Compared with other inhabited dens, there were very little food residue near the den. In a month after marking, the three cubs were captured and weighed again. The pups had not put on weight, and their appearance also indicated their bad condition. During the last visit to the den in the middle of August, only two emaciated and ill pups remained. Thus, the brood died out almost completely. After the end of breastfeeding, the female spent most of the time in the den and, probably, provided the cubs with very little food. There was no male in the family. The den was situated too far from the sea, and the cubs could not descend to the laida on their own and start feeding on sea wastes and amphipods. Loss of pups due to starvation started in the brood, accompanied by cannibalism (only tags and bits of hide remained from the cubs that died). The pup from the neighboring plot was probably killed by the female and brought to the den as prey.

Summarily, from mid-July to mid-August, 12 cubs died out of 80 and another two probably died soon after. The fraction of the cubs that died during this

period from the total number of counted cubs amounted to 17.5%.

Food Objects and Distribution of Food Sources

Food Sources of the Arctic Fox

The animals used by Arctic foxes for food were determined by the residue collected around 37 dens. On 29 used dens, no food remains were found.

Most frequently (25 dens with food remains, 67.6%), bird remnants were found, mainly colonial sea species: cormorants, gulls, kittiwakes, guillemots, and others, as well as remains of the Lapland longspur (*Calcarius lapponicus*) and calidrids (*Calidris* sp.).

Remains of sea mammals, first of all, the northern fur seal, accounted for a significant part of residue (17 dens, 45.9%). Usually, we found parts of skeleton, hides, bits of flippers, and skulls of young northern fur seals (15 dens, 40.5%), but sometimes remains of adult animals were also found (6 dens, 16.2%). Remains of sea otters were observed at five dens (13.5%).

Fish remains were found near 11 dens (29.7%).

They belonged mainly to humpback salmon at dens located in the vicinity of larger streams and to sockeye salmon at dens around Lake Sarannoe. There often were several partly eaten fish near a den.

The bones of reindeer, including the lower jaw, were found near one den (2.7%), and gnawed skeletons of these animals were near two more dens. Thus, it is quite probable that Arctic foxes scavenge on killed or dead reindeer, should an opportunity arise. Moreover, we repeatedly observed Arctic foxes consuming large amounts of gammarids on the laida. Their feces found on the laida and near dens often contained the remains of these crustaceans. Arctic foxes also preyed on voles. On three occasions, we noted them bringing voles to their offspring (den 1h in the rookery), and once observed an adult Arctic fox engaged in mouse hunting.

Feeding Value of the Plots

The greater part of the northern extremity of the coastline of Bering Island is not rich in food, though in some places abundant food resources are concentrated. Depending on the presence and accessibility of food resources, we divided the family plots of Arctic foxes into three groups:

(3) Plots with rich and constant (in the summer period) sources of food: rookeries of northern fur seals, bird colonies, and the Sarannaya River, up which the blueback salmon rises during the entire summer. The area of the Northwestern Rookery and the bird colonies nearby was inhabited by three Arctic fox families; the plots of three other families were situated on the territory of the North Rookery; and another family lived in the mouth of the Sarannaya River. A colony of cormorants in Pasenyuk Bay was located in the space between Arctic fox plots (Fig. 1). Thus, rich constant food sources were found only on 7 plots out of 31 (22.6%).

(2) Plots with temporary but sufficiently abundant food sources, namely, streams, up which the humpback salmon rises for spawning. The rise of the humpback salmon starts at the beginning of August, when the grown pups pass completely on to feeding on solid food. In many cases, the humpback salmon becomes the main, if not the only, food for cubs in this period. In the northern extremity of Bering Island, the bed of humpback salmon spawning streams passed through 6 (19.4%) plots of Arctic foxes: 5c, 6c, 7c, 10c, 16c, and 17c (Fig. 1).

(1) Plots with scant food resources without "food patches" were occupied by 18 (58.1%) families.

The table gives data on the ratio of some demographic parameters and the feeding value of the plots. Correlations between the feeding value of the plot, on one hand, and the number of adults animals, total number, and fraction of the surviving cubs, on the other, were not high in all three cases and did not reach the threshold of reliability (Spearman correlation, $r = 0.11$ and $p = 0.73$; $r = 0.21$ and $p = 0.50$; $r = 0.47$ and $p = 0.12$, respectively).

Use of Concentrated Food Sources

Concentrated food sources are, first of all, rookeries of northern fur seals. Remains of northern fur seals (mainly, skulls of cubs) were found both on the dens next to the Northern rookery and at a significant distance from it. Such residues were found on all plots from 10c to the East to 6h to the West from the rookery, and on plot 16c 3 km away from the rookery into the island (Fig. 4). Thus, parts of dead northern fur seal cubs are spread by Arctic foxes to a distance of 6–7 km from the rookery.

Apart from the rookeries, bird colonies also represent an abundant source of food. On the coast to the east of the Northern rookery, a single cormorant colony was located in Pasenyuk Bay (Fig. 4). Cormorant residues were present to a greater or lesser degree near the dens located at a distance of up to 4 km from the colony (on plots from 6c to 13c, inclusive). Apart from this colony, cormorants, tufted puffins, kittiwakes, and other colonial birds nested on the cliffs of the Northwestern rookery. The remains of birds from these colonies were found on all plots in the environs of the Northwest rookery and those 5 km away along the coastline (until plot 7h inclusive).

Another food resource is Lake Sarannoe and the river that flows from it. During the entire summer, they are a constant source of red fish—the blueback salmon—for Arctic foxes. According to our observations, at the end of the first ten-day period of August, the dens of Arctic foxes around the lake are literally covered in fish. The blueback salmon is present in the food residue on plot 14c and 15c located on the coastline near the Sarannaya River (Fig. 4).

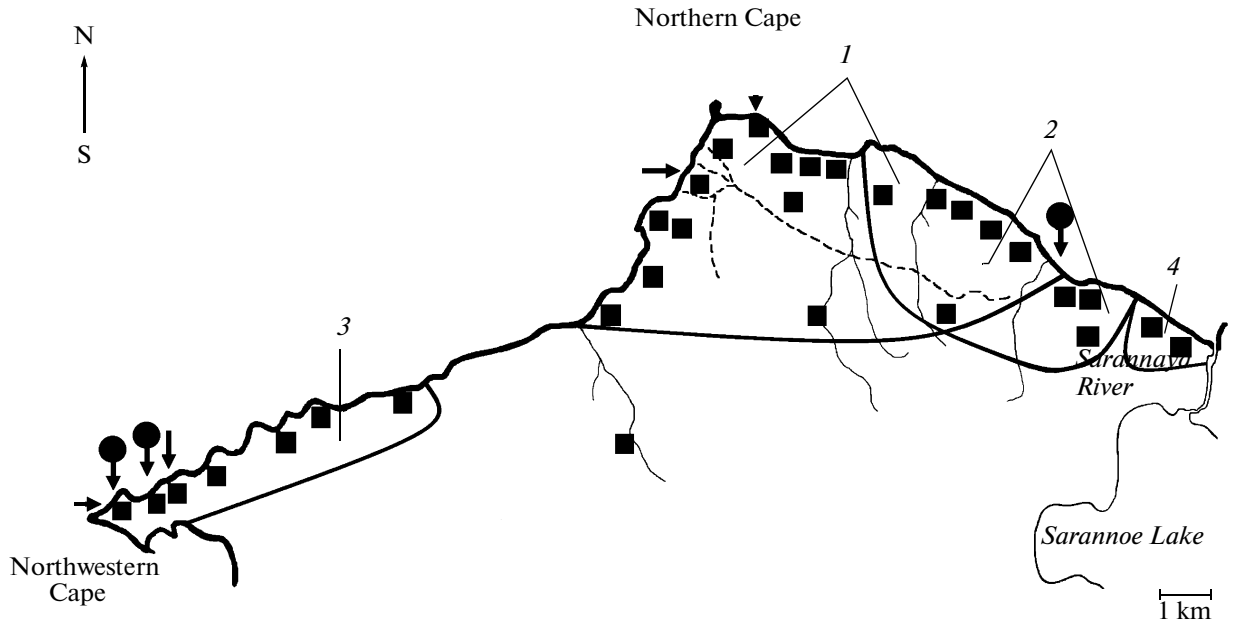

Fig. 4. Use of concentrated food sources by Arctic foxes in the northern extremity of Bering Island. The lines involve parts of the coast where the following food remains were found near Arctic fox dens: (*1*) northern fur seal cubs from the Northern rookery; (*2*) cormorants from the colony in Pasenyuk Bay; (*3*) sea birds from colonies on the territory of the Northwestern rookery; and (*4*) blueback salmon from the mouth of the Sarannaya River. The rest of the designations are as in Fig. 1.

How is the food transported if the entire coast is occupied by family plots of Arctic foxes? One of the main routes is the laida. Many times, we encountered Arctic foxes on the laida, who did not manifest any elements of territorial behavior at our appearance and tried to hide as quickly as possible. These were probably nonresidents that were passing through the territories of the neighboring plots.

In addition, we found "arterial" pathways of Arctic foxes that stretched along the island's coastline to the east and southwest from the Northern rookery (Figs. 1, 2). These pathways are at a distance of 1.5–2 km into the island and pass behind the family plots of Arctic foxes concentrated along the shoreline. Judging by the beaten paths on the waterlogged surface of the tundra and abundance of fresh tracks, they are used very intensively by Arctic foxes. At the same time, we did not find any signal tussocks even once along the entire extent of the main paths, the excrement lay right on the path. In the area of the Northern rookery, the branching path passed strictly along the boundaries of plots of families 1h and 2h and families 2h and 3h, as the male from plot 2h that vigorously barked at us did not once transgress these paths. We think that the laida and main routes, which do not cross the plots of the residents, allow Arctic foxes from more remote plots to get into the rookery of northern fur seals.

DISCUSSION

In the northern extremity of Bering Island, the dens of Arctic foxes are located mainly on elevated points, which are convenient for observation. Such a position of dens is characteristic of Arctic fox colonies everywhere. In the European North, the majority of dens are located on tops of hills, slopes and river banks (Skrobov, 1960). In the north of Alaska, the dens are found mainly along the banks of rivers and streams, on lake shores, and on hills (Chesemore, 1969; Eberhardt et al., 1983). A similar pattern of den location was registered in northern Yamal (Tsetsevinskii, 1940), on Wrangel Island (Ovsyanikov, 1993), and on St. Lawrence Island (Fay and Stephenson, 1989). The position of dens on slopes and elevated places is determined by the better draining conditions of these places during the melting of snow, especially in the areas of permafrost (Skrobov, 1960; Chesemore, 1969). In the conditions of the high density of Arctic fox colonies on Being and Mednyi islands, which has been preserved steadily for decades and hundreds of years, the position of dens on elevated places intensifies their signal significance as a supporting network of visual reference points of the biological signal field (Naumov, 1973, 1977). The multiyear use of the dens often leads to the appearance of high grassy vegetation around them (Il'ina, 1950; Chesemore, 1969; Mochalova, 2008). The degree of the zoogenic change of the plant cover depends on the type of soils and surrounding vegetation, but in small bush tundras and tundra–meadow communities, these changes significantly intensify the visibility of Arctic fox dens (Mochalova, 2008).

The network of pathways that form on a family plot leads to the dens. On the pathways and in places of ter-

ritorial demonstrations of the Arctic fox on family plots of Bering Island, as well as on Mednyi Island, special tussocks have formed. These tussocks are very noticeable and are, apparently, of considerable importance in the formation of the biological signal field. Such tussocks in Arctic fox colonies were described for the first time for Mednyi Island (Naumov et al., 1981) and are still known only for the Commander Islands (Goltsman et al., 2003, 2005a). The tussocks are formed owing to the fact that Arctic foxes mark the same places with excrement. The soil becomes saturated with nitrogen and phosphorus, which leads to a transformation of the vegetation and, first of all, to an overgrowth of gramineous plants. The formation of similar signal tussocks in Arctic fox colonies on Bering and Mednyi islands is apparently associated with the similarity in the ecology of island populations, namely, in the prolonged use of small family plots with a very conservative spatial structure located next to highly predictive and long-standing sources of food resources (Goltsman et al., 2005a, 2005b).

The greater part of Arctic fox dens in the studied region was attached to the coastline and only a few dens were situated deep in the tundra. The same was discovered in the southern part of the Bering Island (our unpublished data). This is natural, since the main part of food resources of the islands (rookeries of sea mammals, bird colonies, and sea wastes) are concentrated along the coastline. Such a character of Arctic fox den location on Bering Island was noted by Il'ina (1950) and is typical also of the other islands of the Bering Sea: Mednyi (Naumov et al., 1981; Goltsman et al., 2003, 2005b), St. Lawrence (Fay and Stephenson, 1989), and Saint Paul islands (White, 2001). If we consider the Arctic fox population of Bering Island on the whole, the greatest contribution during the period of breeding of the offspring is made by shoreline colonies, whereas the density of Arctic foxes in the middle of the island is small.

As in Mednyi Island (Goltsman et al., 2005b, 2010), in the studied Arctic fox colony on Bering Island, the density of reproductive dens is associated with the available sources of food of the habitat. However, an important difference exists between the two island populations in this relation. As it was in the period of island animal farming in the first half of the 20th century on Bering Island (Il'ina, 1950), the density of Arctic fox family plots is especially high next to the rookeries of northern fur seals. On Mednyi Island, after the passing of the Arctic fox population through a demographic bottle neck, the density of reproductive plots of Arctic foxes in the area of northern fur seal rookeries has remained low for more than 30 years already (Goltsman et al., 2010). These interisland differences in the structure of Arctic fox colonies correspond well with differences in the foraging ecology, which appeared in recent decades.

On both islands, the range of potential food objects of the Arctic fox is quite wide and depends on the season and local conditions (Cherskii, 1920; Barabash-Nikiforov, 1939; Zagrebel'nyi, 2000a; Goltsman et al., 2010). As a rule, Arctic foxes turn to abundant and easily accessible sources of food, such as corpses of whales and other sea mammals beached by the sea or food dumps near human settlements (Il'ina, 1950; Kapel, 1999; White, 2001). On both islands, in summer, Arctic foxes use colonies of sea birds the most intensively (Zagrebel'nyi, 2000a; Goltsman et al., 2010). Our data also show that in spite of the almost complete absence of sea bird colonies and the presence of two northern fur seal rookeries in the northern extremity of Bering Island, bird remains are found more often on the dens of Arctic foxes than those of northern fur seals. At the same time, the products of rookeries are used by many Arctic fox families. In this respect, the contrast in the use of food resources between the populations of Mednyi and Bering islands is very significant. On Mednyi Island, northern fur seal rookeries are not currently an important source of resources for the reproductive families of arctic foxes. Even those few families that raise their pups near the rookery feed them mainly sea colonial birds and hardly use the products of the rookery. The disappearance of the tradition of using northern fur seal rookeries on Mednyi Island and its preservation on Bering Island is, apparently, associated with differences in the modern history of these populations and the passing of the Mednyi population through a demographic bottleneck (Goltsman et al., 2010).

Only some of the families studied by us on Bering Island had a rich source of food directly on their plot, whereas the majority of plots were poor in food (table). However, judging by the food remains near the dens, Arctic foxes actively used sources of food that were located outside the territory of their plots, often many kilometers away from them (Fig. 4). As the main routes, Arctic foxes used the laida and pathways that stretched for large distances across uninhabited areas of the tundra (Figs. 1, 2). Transportation of the remains of northern fur seals to a distance of up to 5 km from the rookeries on Bering Island was also observed by Il'ina (1950).

Since adult animals can obtain food without difficulty outside the territory of the family, the feeding value of the family plot becomes important only after the grown cubs pass on to solid food. In this period, the adults are no longer able to bring a sufficient amount of food to the den from remote sources and the family territory should be located either immediately on the "food spot" or include part of the laida where the cubs can gather amphipods and various sea wastes. Both types of plots were found in an Arctic fox colony in the northern extremity of Bering Island. The third possible variant is when easily accessible food (in our case, the humpback salmon) appears during the period when the cubs pass to independent feeding, which allows Arctic foxes to locate the breeding den deep in the island and not to take the cubs out onto the laida

(plots 16c and 17c, Fig. 1). Only the plot of family 2c, which was situated 1.5 km from the Northern rookery and did not have any way out onto the laida, was an exception, and this family was the only one in which the brood died out completely of hunger. However, the correlation between the accessibility of food on the family plot and the survival of cubs did not reach the threshold of reliability, which was, apparently, associated with the small size of the sample included in the analysis.

The high density of Arctic fox colonies around the northern fur seal rookery may be associated with the collective use of a constant concentrated source of food, which allowed the exploitation of the rookery by 17 Arctic fox families simultaneously (Fig. 4). On Mednyi Island, such joint use of concentrated food resources on rookeries was observed at the end of the 1960s, when on a 4.5 km stretch of the shore occupied by the Southeastern northern fur seal rookery, up to 30 inhabited Arctic fox dens were counted, while the number of Arctic foxes that were observed simultaneously on the rookery reached 65 (Chelnokov, 1970, 1982). The possibility of using concentrated food sources that lie outside the protected family territory collectively with a large number of Arctic fox families impedes using sociobiological models of relation of the family structure with the size of the inhabited plot and abundance of resources located directly on it (see a discussion of such models, for instance, in Macdonald, 1983; Johnson et al., 2002).

The structure and composition of Arctic fox families on Bering and Mednyi islands are very similar. In both populations a considerable proportion of families includes more than two adult animals. The average sizes of broods on Bering Island are slightly larger than on Mednyi Island (6.7 ± 0.7, $n = 13$ on Bering Island *vs.* 4.4 ± 0.23, $n = 60$ on Mednyi Island), while the fraction of complex families is smaller (30.8% on Bering Island vs. $47.7 \pm 1.6\%$, min = 30, max = 67 on Mednyi Island; Goltsman et al., 2003). Given that both these parameters vary considerably by years and that the sampling of Bering Island is small and reflects the situation for only one year, we cannot verify to what degree the differences between the populations of the two islands are pronounced.

Thus, the study performed by us revealed noticeable similarities and some currently existing differences in the use of space and obtaining of food by Arctic foxes of two Commander subspecies in the environs of the Northern rookery on Bering Island and the Southeastern rookery on Mednyi Island. A higher population density, joint use of concentrated food sources, and greater significance of northern fur seal rookeries as a food source during the breeding period are characteristic of the Bering Island Arctic foxes. For a more comprehensive and representative comparison of the demographic characteristics, it is necessary to perform a longer and larger study of the Arctic fox population of Bering Island. This is especially important as this is one of the two most ancient isolated island populations that remain on earth, and as the Arctic fox is the only aboriginal land predator on Bering Island.

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