

# ‘Island syndrome’ in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island

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## Abstract

Comparative analysis of the biology of insular and mainland populations has demonstrated a number of differences in characteristics of insular populations, termed the ‘island syndrome’. A subspecies of Arctic fox on the Commander Islands (*Alopex lagopus semenovi* on Mednyi Island) has been isolated for an evolutionarily significant time in small territories at the periphery of the species’ range. The number of foxes on Mednyi had been observed to be very high since the islands were discovered in 1741, but a drastic decline in population density in the late 1970s, owing to mange, has left the population low. The aim of the study was to determine whether the Mednyi Arctic fox population exhibited the features expected in an isolated insular population, such as difference in body size, increased population density, larger social groups, lower tendency to disperse and lower fertility, and whether any behavioural changes were evolutionarily reinforced or were a temporal response to current ecological factors on the island. Eight predictions were identified based on the island syndrome, of which the Mednyi Arctic foxes conformed to seven. We suggest a new prediction, namely that the tendency for increased sex dimorphism in dispersal may also be a distinguishing feature of insular populations. All the features displayed by the insular population on Mednyi – conservative use of space, increased tendency to form complex groups, decreased fertility and dispersal – seemed to be preserved regardless of the currently comparatively low populations. Thus, although foxes have been below carrying capacity for at least 10 generations, island syndrome characteristics have persisted.

## INTRODUCTION

Islands have often been at the centre of ecological and evolutionary studies, offering exceptional situations for investigating the biogeography of organisms and allowing the testing of hypotheses. Much of island biology has been focused around biodiversity and speciation, with less attention on the changes within a population following isolation. Once a population becomes isolated on an island it is generally recognized that population-level changes may take place. Comparative analysis of the biology of insular and mainland rodent populations has demonstrated several differences in the characteristics of insular populations, termed the ‘island syndrome’ (Adler & Levins, 1994). The dominant characteristics in rodents are: (1) increased body size of individuals; (2) higher population density and stability; (3) increased survival rate and decrease in fertility; (4) decrease in territory size, reduction of territorial defence and increase in territory overlap; (5) lower dispersion.

The suggested explanation for island syndrome (reviewed by Stamps & Buechner, 1985; Adler & Levins,

1994) is that islands are more often characterized by a simpler ecosystem structure, with increased food resources and reduced competition allowing for increased population density and stability. Emigrating individuals often represent a non-random sample of the population and, as a result, dispersal potentially provides a powerful selective force on individuals. Within insular populations, areas of finite size are generally confined by insurmountable barriers, thus limiting the possibility of dispersal and dramatically changing the directions of selection.

These factors may lead to a decrease in territory size and a strengthening of links between neighbours at the same time, while increased intraspecific competition may lead to greater body size, and higher population density to a decrease in fertility through reduced litter sizes and delayed sexual maturation. Also, the reduction in dispersal distances is predicted to increase the viscosity of gene flow, creating greater population substructure compared with mainland populations (Roemer *et al.*, 2001).

While different explanations have often been offered for the separate components of the island syndrome and for different taxa, the observed regularity suggests that theoretical explanations will account for observed island patterns and that these explanations should be independent of taxon (Williamson, 1981; Adler & Levins, 1994). This

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regularity compels us to search for a single common mechanism related to insularity that produces island, mainland and inter-island variations (Adler & Levins, 1994).

Generally the more isolated the population and the smaller the island area, the more pronounced the effects of island syndrome. Although these tendencies have been found in different classes of vertebrates (Stamps & Buechner, 1985), most data have been obtained for rodents (Adler & Levins, 1994). Insular populations of carnivores are much less studied in this respect; however, a recent study by Meiri, Dayan & Simberloff (2004b) has suggested that the observed differences between insular carnivore species and their mainland conspecifics are more complex than those suggested by the island syndrome and neither follow an apparent pattern nor are easily predictable. For example, by measuring skulls and teeth of the order Carnivora, Meiri *et al.* (2004b) hoped to establish a negative correlation between relative size of island individuals (the ratio between a species insular and mainland sizes, averaged for all populations) and their body mass, termed the 'Island rule' by Van Valen (1973). The Island rule predicts that, on islands, small mammals such as rodents will tend towards gigantism (Foster, 1964), whereas larger mammals such as lagomorphs, carnivores and artiodactyls will tend towards dwarfism (Foster, 1964; Van Valen, 1973). Characteristics of the island syndrome (Adler & Lever, 1994) such as competitive release, resource limitation (Lomolino, 1985), dispersal ability (Lomolino, 1983), lighter predation pressure (Heany, 1978; Michaux *et al.*, 2002) and the hypothesis of optimal mammalian size (Brown, Marquet & Taper, 1993; Damuth, 1993; Marquet & Taper, 1998) have been suggested to explain these patterns of variation in body size of island species. However, Meiri *et al.*'s (2004b) results indicate that carnivores do not tend towards dwarfism on islands. For example, puma *Felis concolor* found on Vancouver island are larger than their mainland conspecifics, despite the absence of their mainland competitor, the lynx *Felis lynx* and the dwarfism of the pumas' common prey, the black-tailed deer *Odocoileus hemionus columbianus*: Shackleton, 1999 on the island. Red foxes *Vulpes vulpes* are bigger in Britain than they are in Belgium, and Eurasian otters *Lutra lutra* are smaller in Sri Lanka than in India (Meiri *et al.*, 2004b) which is in accordance with Bergmann's rule that states an intra-specific increase in body size occurs towards higher latitudes (Bergmann, 1847). However, in other carnivore species this pattern is not apparent, e.g. the Eurasian otter is smaller in Britain than in north-west Europe and leopard cats *Felis bengalensis* are smaller in Java than on the more equatorial Sumatra, even though all the above species follow Bergmann's rule on the mainland (Cavallini, 1995; Meiri *et al.*, 2004a,b). In general, their study has emphasized the need to consider the effects of the island syndrome and, in particular, the evolution of body size, separately for each mammalian order (as defined by Foster, 1964) rather than focusing on a single mechanism irrespective of order. Insular populations of Arctic fox *Alopex lagopus* are, therefore, of much interest in this respect.

Subspecies of Arctic fox on the Commander Islands (*A. l. semenovi* on Mednyi Island and *A. l. beringensis* on Bering Island) are isolated throughout the year by the waters of the Bering Sea. These fox populations have been isolated for an evolutionarily significant time in small territories at the periphery of the species range (*c.* 10° to the south of the southern border of the remaining part of Arctic fox distribution range) in ecological conditions unusual for the Arctic fox. Under these circumstances one can expect evolutionary changes to be especially fast (Gould & Eldredge, 1977).

Research was carried out on Mednyi Island where four major factors define the ecological conditions. The first factor is the impossibility of migration and strict limitations on mobility in a 'saturated' environment. Insular isolation creates not only virtually no emigration and immigration, but also severely limits natal dispersal opportunities. While mainland Arctic foxes are able to travel hundreds of km in search for a new habitat, the habitat choice is extremely limited on the island, which is 0.3–7.5 km wide and *c.* 53 km long. Since the island is narrow, all paths cross the home ranges of resident foxes, which may thus influence the use of the paths and, consequently, the migration process. The second factor is the presence of rich food resources with a completely predictable spatial and temporal distribution. There are no rodents on Mednyi Island, and the Arctic fox's food resource does not consist of fluctuating numbers of lemmings and voles, but marine resources (sea birds and marine mammal carcasses, fish and invertebrates), which are relatively stable all year round. During the reproductive season, rich and highly predictable additional food sources are available through sea bird colonies and sea mammal rookeries, which have a conservative spatial distribution. The third factor is comparatively low requirements in the location and structure of reproductive dens because of small seasonal temperature changes. This contrasts sharply with the conditions in the major part of the Arctic fox range, where winter temperatures are extremely low and, since cubs are born in spring, requirements of the dens are high. The fourth factor is the absence of other terrestrial mammals as potential predators or competitors.

The number of foxes on Mednyi had been observed to be very high in comparison to mainland populations since the islands were discovered in 1741 (Goltsman, Kruchenkova & Macdonald, 1996). Up to the second half of the 20th century, the population density remained extraordinarily high compared to other arctic fox populations (see below).

It is possible to hypothesize that if high population density persisted over evolutionarily significant time intervals, then the insular population is adapted to a highly saturated environment. A drastic decline in population density occurred in the late 1970s, however, because of an outbreak of mange. For several years, cub mortality reached 90% (Goltsman, Kruchenkova & Macdonald, 1996; Goltsman & Kruchenkova, 2001). After this catastrophic decline and passing through a 'bottleneck', the population stabilized, although numbers were much

lower than before. Thus, during recent decades the Mednyi Arctic foxes, adapted to 'overpopulation', found themselves in the unusual conditions of low population density. The number of foxes was about one-tenth of its previous value on the island, without any visible decline in food resources.

This unique natural experiment presented an opportunity to distinguish between features of fox biology that are an evolutionary adaptation to stable conditions of long-term insular isolation, and those that are responses to the current shorter-term ecological situation. For example, decrease in fertility could be a direct social response to density increase (Creel & Macdonald, 1994), and the size of reproductive groups and dispersal tendency could depend on food resource distribution and population density. Changes in territorial behaviour might also be a response to the short-term ecological situation.

The previously saturated nature of the island population combined with the high densities, induce higher levels of intraspecific interactions compared to mainland populations. Direct observations of Mednyi foxes have shown a system of territorial defence that is typical of all Arctic fox populations. It is characterized by display, mobbing, and direct aggression against an intruder, combined with territorial barks, expressive postures and urine and faeces markings performed many times a day during the breeding season and if provoked by meetings with fox or human intruders (Naumov *et al.*, 1981; Frommolt, Goltsman & Macdonald, 2003; Kruchenkova, Goltsman & Frommolt, 2003). Owing to the small home ranges, neighbouring families are at short distances and barking is used frequently as communication within and between family groups (Frommolt *et al.*, 2003). As demonstrated by playback experiments (Frommolt *et al.*, 2003), the Arctic foxes of Mednyi Island are able to distinguish the barks of their own family group from those of other individuals.

The goal of this work was: (1) to determine whether the Mednyi Arctic fox population exhibited the features expected in an isolated insular population, such as difference in body size, increased population density, larger social groups, lower tendency to disperse and lower fertility compared to mainland populations; (2) to determine whether any behavioural changes were evolutionarily reinforced or were a temporal response to current ecological factors.

## METHODS

The study was conducted on Mednyi Island, in the Commander Island Biosphere Reserve. The Commander Islands are located at the western extreme of the Aleutian island chain and lie 175 km east of Kamchatka between 55°25' to 54°31'N and 165°04' to 168°E in the Pacific Ocean, in the south of the ice-free Bering Sea. Mednyi Island covers an area of 187 km<sup>2</sup>. The mountains of Mednyi, covered with mountain tundra, are up to 700 m high. Hills divided by narrow valleys with shallow brooks form steep cliffs with a narrow seashore. The winters on the island are relatively mild with a mean daily

temperature of -4 °C in January–March. In summer, the highest temperature is *c.* 11 °C in August, with strong winds, almost permanent fog, and drizzle (Ponomariova & Isachenkova, 1991).

Our research stations were maintained in the southern part of Mednyi, near to the south-east fur seal rookery and in the central part of the island. Field studies were conducted for a total of *c.* 20 months, consisting of 1.5–3 months between June and September in each year from 1994 to 2002. Foxes on Mednyi are largely restricted to a narrow strip along the coastline where food sources are concentrated. Annual surveys of foxes and their food covered the southern half of the island between Korabelny–Vodopadsky Capes and Southern Cape, which comprised a coastal strip of *c.* 70 km long. All fox breeding dens were mapped during exhaustive searches. Breeding dens are most commonly located under stones, in scree and crevices along the shoreline and those located in mountain tundra are < 300 m from the shore. Numerous paths connect breeding burrows with dens and shelters on the shore, and stretch to rich feeding areas within each home range, with major arterial paths connecting different home ranges. Conspicuous mounds – the accumulated scent posts of resident foxes – concentrate in the tundra around breeding burrows (see below), and this makes the burrows easier to locate. In 1994, a survey of foxes covering the whole island showed that the number of foxes and breeding dens in the southern part of the island, which is studied annually, is 1.6 times higher than in the northern part. Additional surveys of some areas of the northern part were carried out in 1995, 1997 and 2001. They confirmed that the number of foxes and breeding dens in the north is 1.6–2.0 times lower than in the south. For years when the north was not surveyed, the number of foxes on the entire island was estimated, taking into account the size difference in northern and southern parts, as  $(N + N/1.6)$ , where  $N$  is the number of foxes in the south.

Foxes were trapped near dens or trails, using box traps (0.4 × 0.4 × 1 m); cubs, at the age of *c.* 2 months, were caught by hand. Traps were baited with carcasses of sea birds, or canned meat. Traps were checked every 2 h and closed overnight. The captured animals were placed in a textile bag and weighed. Animals were marked with plastic ear tags sized 3.5 × 1 cm (D 400 Rototag-Ohrmarken, Fa. Horn, Horn-Tierzuchgeräte, Germany, Dülmen). The tags were placed in the cartilaginous part of the pinna of animals using Rototag-forceps (D 410 Fa. Horn) after disinfecting the ears. The whole handling process took < 10 min. In total, between 1994 and 2002, 95 adult foxes and 274 cubs were tagged.

Arctic foxes displayed little fear of people, so they could be observed at 5–60 m, either at dens or while following them on foot while they foraged. A total of 1825 h of observations was gathered. The composition of each family was logged in terms of the numbers of adults of each sex and numbers of lactating and non-lactating females. Age, sex, status and identity of individual foxes were assessed during capture and tagging. Non-tagged adults could often be sexed, because foxes can usually be approached

**Table 1.** Comparative body weight (kg) in Arctic foxes *Alopex lagopus* from different populations

Study site	Weight of males (summer)			Weight of males (winter)			Weight of females (summer)			Weight of females (winter)			Authors and comments
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	
Arctic fox populations in Pacific islands													
Mednyi Island	5.0	0.47	30				4.1	0.49	32				Our data
				7.22	1.35	21				6.21	0.86	18	Cherskyi, 1919
				6.55						5.80			Iljina, 1950. p. 122.
				6.38						5.58			Data of 1931–32
				8.1						6.9			Barabash-Nikiforov, 1937
													Marakov, 1964.
													Total no. of weighed males and females 630.
Bering Island				5.58	1.22	108				4.52	0.93	86	Cherskyi, 1919
				5.37						4.60			Barabash-Nikiforov, 1937
Arctic fox populations except Pacific islands													
Iceland	3.58***	0.45	478	4.23***	0.6	338	3.14***	0.38	514	3.69***	0.55	245	Hersteinsson, 1984
Delta of the Lena river (East Siberia)				3.82***	0.78	118				3.09***	0.75	114	Tavrovsky, 1939
Yakutia (East Siberia)				3.19		320				3.09		270	Cha, 1953
Chukotka				3.40***	0.57	12				3.00***	0.62	11	Novikov, 1983
Svalbard, Norway				3.60***	0.58	317				3.03***	0.61	267	Prestrud & Nilssen, 1995

Values significantly different from the mean value of the Mednyi Arctic fox are indicated with an asterick: \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ , two-tailed Student's  $t$ -test.

closely, and they can sometimes be individually identified by natural marks. Lactating females were recognized by distended teats. Sex of cubs was determined only when tagging the animals. To establish family composition, each family was repeatedly observed. Overall, 107 families with cubs were recorded, although family composition was not established in all of them. Hence, when analysing various parameters of families (the number of adults, lactating females, additional adults) we used 75 families for which all these parameters were identified. The number of cubs emerging from the den, at *c.* 4 weeks, was scored for each group and taken as a measure of litter size (no data were obtained for pre-emergence mortality).

Mapping data were processed with GIS-program MapInfo 5.0 (MapInfo Corporation). For statistical comparisons Zar (1999) and Statistica for Windows (StatSoft, Inc., 1995) were used.

For the period preceding our study, data were used on population numbers that existed for the years between 1928 and 1963 (Iljina, 1950; annual survey reports of S. Marakov). During these years, the entire population was surveyed annually. In addition, there were data on the number of foxes trapped annually from 1867 to 1964 (trapping ceased in 1965). Data for 1964 to 1975 were obtained from S. Marakov (pers. comm.) who carried out fox surveys on Mednyi Island between 1951 and 1975. Data for 1993 were taken from Rajzanov (2002). Our own research provides data for 1976 and 1978 (Naumov *et al.*, 1981; Goltzman, Kruchenkova & Macdonald, 1996) and for 1994 to 2002.

## RESULTS

### Body size

The average weight of 30 Mednyi Arctic fox males in June–July 1994–99 was 5.0 kg (range 4.2–6.0, SD = 0.47), and the weight of 32 females averaged 4.1 kg (range 3.2–5.1, SD = 0.49). We have no recent data for winter weight; however, data from previous studies at the beginning and middle of the 20th century (Table 1) report average winter weights of 6.4–8.1 kg for males, and 5.6–6.9 kg for females.

Body weights and sizes of Mednyi Island Arctic foxes were higher than those of Arctic foxes from other areas (Tables 1 and 2). Foxes from an adjacent large island (Bering Island, 1667 km<sup>2</sup>), *A. l. beringensis*, were smaller than Mednyi foxes (Ognev, 1931; Zalkin, 1944), but larger than foxes from non-Pacific populations. Comparison of skull parameters showed the same patterns, with male skulls from Mednyi being 6.2% longer, and female skulls 4.7% longer, than the average measurements (CBL) of foxes from other populations (Table 2).

### Population density

Trapping data from 1867 to 1927 showed that, in some years (e.g. 1886), the population reached 1500. On average, 491 foxes per year were trapped (SD = 281,  $n = 38$ ), and no indications were found in the literature that the number ever fell exceptionally.

**Table 2.** Comparative skull size in Arctic foxes *Alopex lagopus* from different populations CBL, condylobasal length; ZB, zygomatic breadth

Study site	CBL males			ZB males			CBL females			ZB females			Authors
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	
Arctic fox populations in Pacific islands													
Mednyi Island	129.5	5.1	33	70.4	3.1	32	123.5	3.8	17	67.0	2.0	17	Zagrebelnyi, 2000
Bering Island	129.2	4.3	92	70.0	2.5	91	124.1	3.7	58	66.9	1.7	58	Zagrebelnyi, 2000
Arctic fox populations except Pacific islands													
Iceland	119.8***	4.2	438	70.1	2.2	412	114.7***	4.0	342	66.9	2.1	329	Hersteinsson, 1984
Svalbard	117.7***	4.8	56	68.7***	2.6	54	113.4***	4.6	49	65.7	2.7	44	Frafjord, 1992b
Yakutia	122.2		93				117.9		103				Cha, 1953
Chukotka	122.5***	3.3	52	69.4	2.3	52	117.6***	2.5	62	66.8	2.1	62	Zagrebelnyi, 2000
Canada	119.6***	6.5	467	68.5***	2.2	466	115.5***	3.9	383	65.7**	2.0	383	Hall, 1989
European North of Russia	122.6***	3.1	12	69.3	3.2	13	119.9***	2.7	21	67.6	1.3	19	Shiljaeva, 1974
Yamal Peninsula	123.0***	3.1	110	69.8	1.1	115	121.8	3.6	145	66.6	2.1	112	Shiljaeva, 1974
Delta of the Yenisey river	122.7***	3.5	76				117.6***	2.6	77				Shiljaeva, 1974

Values significantly different from the mean value of the Mednyi Arctic fox are indicated with an asterisk: \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ , two-tailed Student's *t*-test.

The mean number of foxes reported in annual winter censuses between 1928 and 1963 was 768 (minimum number ranging between 301 and 1150,  $SD = 248.0$ ,  $n = 34$ ; data missing for 2 years).

S. Marakov (1983, pers. comm.), who carried out summer fox surveys from 1951 to 1975, claims that the average number of foxes during the period 1965–75 was *c.* 600 and did not fluctuate. Numbers declined sharply after 1975 coinciding with the outbreak of mange and, by 1978, fewer than 120 animals survived (Goltsman, Kruchenkova & Macdonald, 1996).

For the past 10 years the Mednyi population has been relatively stable at *c.* 15% of its former abundance. Mean abundance between 1993 and 2002 was 90 (range 52–120,  $SD = 20$ , median = 89,  $n = 10$ ).

The number/100 km<sup>2</sup> of breeding dens in the annual survey area in the southern part of the island averaged 16.66 (range 11.43–20,  $SD = 3.35$ ) between 1994 and 2002. The density for the whole island (187 km<sup>2</sup>) in 1994 was 12.30. The estimated density for the whole island between 1995 and 2002 was 9.89 (range 6.95–12.30,  $SD = 2.02$ ). Breeding dens seemed to be present at densities that were 10–15% of those before the population declined. For example, in 1951, 149 dens were found on the entire island (*i.e.* 79.6 dens/100 km<sup>2</sup>). In 1968 on the southern end of the island near the northern fur seal rookery, there were 30 active breeding dens (Chelnokov, 1970) but, during the period of our research, there were between zero and three breeding dens. In 1938, in the area of Glinka Bay (12–15 km north of the south-eastern end of the island), there were 21 active breeding dens (Poljakov, 1933–38), and in 1952 there were 26 breeding dens (S. Marakov, pers. comm.), but during our research there were no more than three to four breeding dens.

### Composition and size of reproductive groups

Families of Mednyi Arctic foxes almost invariably comprised one male and up to four females, although one family was observed with five females. Of 75 Arctic fox reproductive groups with known sex composition studied between 1994 and 2002, 36 involved two members, 23 comprised three, 12 four members, and four comprised five members. In four complex families, a single male had a home range encompassing two breeding dens, each with a female group including one or two lactating females and, in two cases, one female helper. In three of these groups, the male guarded and brought food to cubs at both dens. The fourth family consisted of a male, a mother and daughter (both lactating), a female helper and another female of indeterminate status, and jointly used two breeding dens in which there were litters of seven and four cubs.

Communally breeding females shared a den and jointly fed their litters in 24 families. Seven breeding groups included two males; in four of these, both provided cubs with food. In 23 groups, helpers fed cubs. In most families there was only one helper, a non-reproductive female. In five cases the family included two yearling helpers, in three of these, the helpers comprised one female and one male, and in the remaining two the helpers were both females. In eight groups, the periphery of the home range was used by non-reproductive animals (usually females, who did not approach the den or the cubs).

A tendency to polygamy was also reflected in the sex ratio of the population (Table 3). The sex ratio (female/male) in breeding adults averaged 1.29 ( $\pm 0.12$   $SD$ ,  $n = 9$ ). The skew towards females was already evident among 1- to 2-month-old cubs ( $1.50 \pm 0.91$   $SD$ ,  $n = 9$ ).

**Table 3.** Arctic fox *Alopex lagopus* sex ratio in 1994–2002

Age group	Mean sex ratio (female/male) <sup>a</sup>	SD	Range
Adults in total ( $n = 471$ )	1.24	0.25	0.85–1.75
Breeding adults ( $n = 229$ )	1.29	0.12	1.13–1.45
Non breeding animals excluding helpers ( $n = 201$ )	1.04	0.51	0.5–2.25
Cubs ( $n = 274$ )	1.50	0.91	0.79–3.5

<sup>a</sup> Data only for animals where the sex was determined with certainty.

### Fertility

The mean litter size on Mednyi was 4.6 (range 1–13,  $SD = 2.2$ ,  $n = 57$ ). The mean number of cubs per lactating female was 3.7 ( $SD = 1.4$ ,  $n = 56$ ) (this value is smaller than the mean litter size owing to the reduced sample size as the status of one female was unknown). The mean number of cubs per adult in the family (including reproductive adults and helpers) was 1.8 ( $SD = 0.8$ ,  $n = 57$ ).

The initial age of reproduction was determined for 21 females (Fig. 1a). Three started to breed at age 1 year, 13 at age 2 years, three at age 3 years, and two at age 4 years. All the three breeding yearlings (of 49 yearling females: 37 tagged as cubs and 12 as yearlings) lived in complex families. In each of these families there was an older lactating female and the possibility of induced lactation cannot be excluded. One male started to breed at 1 year of age, but most (10) were 2 years old, and 2 were 3 years old (Fig. 1b).

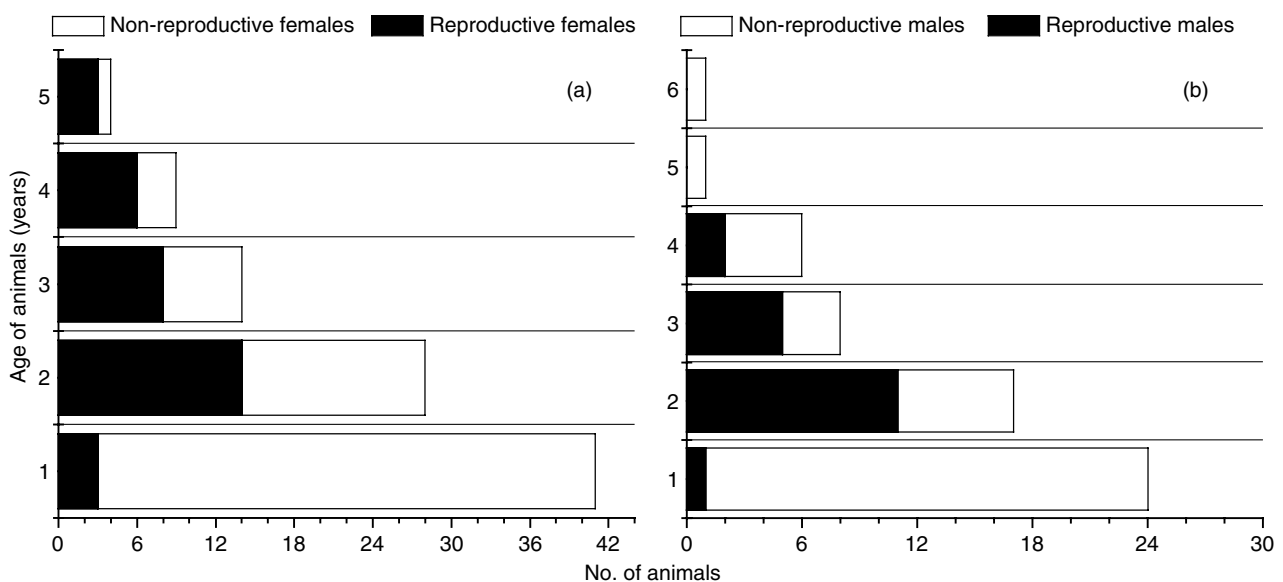
The number of cubs in Arctic fox litters (post-emergence) recorded on Mednyi Island before this study, according to published data, is between 6.4 (in 1931–33, Barabash–Nikiforov, 1938) and 4.1 (in 1937; Iljina, 1950).

According to Poljakov's report, average litter size in 1933 was 3.7 ( $n = 73$ ). In 1938, the average size of 93 litters at six sites on the island was  $5.0 \pm 0.63$  SD (range of means for each site: 4.4–5.9 cubs;  $n = 93$ ) (Poljakov, 1933–38). This figure is similar to the mean of 4.6 observed in this study.

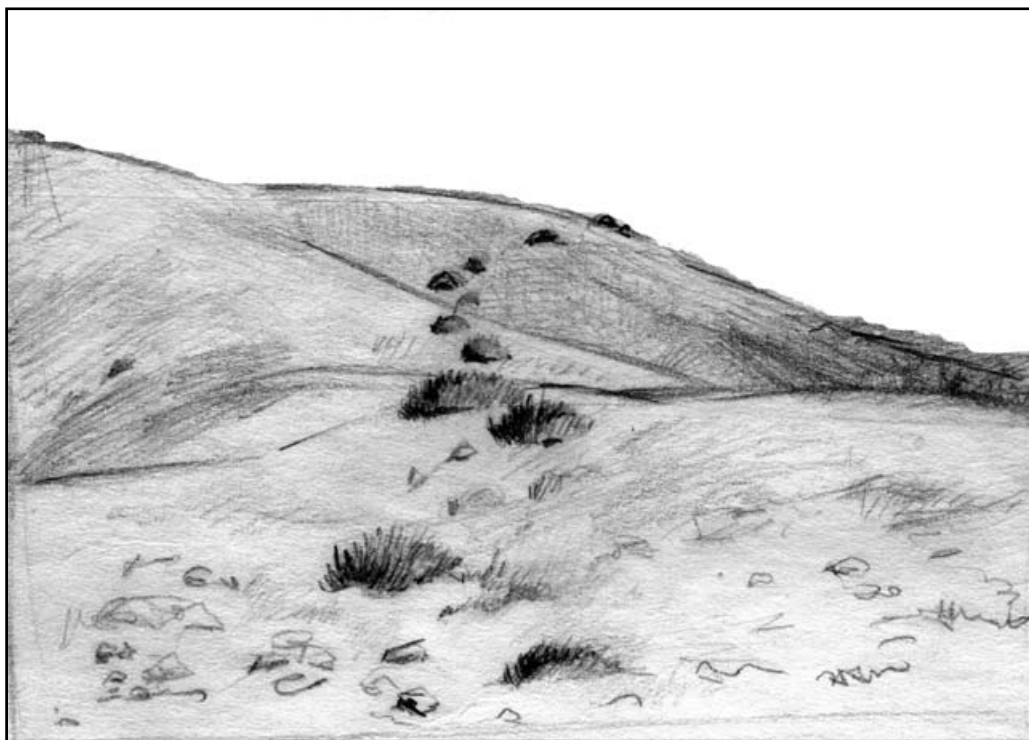
### Dispersal and territoriality

The small size of the island limited the distance that the foxes could travel, and all those marked as cubs and seen as yearlings were within 14 km of their natal home range. Of these, 37 were females, of which 19 remained on their natal ranges, 10 were seen in adjacent areas, four were located 5–8 km from their natal ranges and the locations of four were uncertain. The average dispersal distance for females that left their natal range was  $2.99$  km  $\pm$  1.90 SD ( $n = 14$ ). Of 31 males, only three remained in their natal range as yearlings, six moved to adjacent areas, 14 left for more distant areas and there were no data for eight of them. Males dispersed farther than females, the average dispersal distance of males was  $5.81$  km  $\pm$  3.82 SD ( $n = 20$ ). (Mann–Whitney  $U$ -test  $Z = 2.31$ ,  $P = 0.02$ ).

By the time of first breeding, these differences in philopatry were pronounced. Eleven females had their first litters in their natal ranges, seven in adjacent home ranges, and only three bred in areas at a distance of 5–8 km. Of the 11 males were marked at weaning and who subsequently reproduced, only one remained in his natal home range, and one in an adjacent area. Of the males whose fate could be determined a year or more after the reproduction, 15 remained in the same home range for a period of 1–4 years after breeding was first recorded, four moved to an adjacent unoccupied area, and one male changed his home range, forming a new family, using a den at a distance of *c.* 3 km.



**Fig. 1.** The proportion of breeding individuals among Arctic foxes *Alopex lagopus* of different ages: (a) females, (b) males.



**Fig. 2.** The string of the Arctic fox *Alopex lagopus* mounds on a fox track. Drawing by V. Smirin.

The mean extent of fox home ranges along the seashore in 1994–99 was 2.0 km (range 1.0–5.0 km,  $SD = 1.1$ ). This affected the mean nearest neighbour distances between breeding dens, which was 2.23 km ( $SD = 1.60$ ,  $n = 72$  den/years). Usually the home range was a narrow strip, < 1 km wide, along the shoreline.

The same dens, paths and territorial display areas were used by many generations of foxes. In three home ranges where families of Arctic foxes were observed in 1976–78 and 1994–2002, territorial advertisements (vocalization, expressive postures, urine and faecal markings), were seen in similar locations.

In tundra, unique ‘signposts’ are formed (Naumov *et al.*, 1981) along fox trails and near breeding dens where foxes traditionally mark their territory. These comprise mounds of about 30 cm high and 30–80 cm in diameter, which are formed by the tussocky growth of grasses (*Agrostis clavata*, *Poa malacantha* (syn. *P.komarovi*), *Festuca rubra*) and sedges (*Carex spp*) owing to constant organic enrichment of soil over generations of Arctic foxes (Naumov *et al.*, 1981; O. Mochalova, pers. comm). In our study, mounds were found to mark fox paths, sometimes on barren tundra devoid of other vegetation (Fig. 2). As many as 25 of these mounds (average 11.8 mounds,  $SD = 6.7$ ,  $n = 29$ ), each separated by an average nearest neighbour distance of 7.9 m ( $SD = 5.0$ ,  $n = 116$ ), formed chains that stretched along the fox paths and became denser near dens and sites of territorial dispute. Between May and June there were fox faeces on or within 50 cm (as the faeces are sometimes washed away from the mounds) of  $70.1 \pm 24.5\%$  mounds in 10 mound chains.

Territorial displays involving barks, expressive postures, urine and faecal marking were performed many times a day during the breeding season. Vocalizations occurred at an average rate of  $2.59 \pm 0.27$  per h of observation (440 h) in one family in 1976 and  $1.06 \pm 0.20$  (253 h) in a second family (Kruchenkova *et al.*, 2003). Barks were audible to us at 1.0–1.5 km. A territorial bark induced multiple responses with members of the same family and the neighbours participating in interactive ‘counterbarking’. These displays were performed several times a day, especially in the morning and evening.

Even though only few instances of intruders coming to an occupied home range in the presence of residents were directly observed, they were always violently attacked by residents or fled when the residents appeared (i.e. 18 cases in 1994–2000). Aggression towards intruders was displayed by five males, three female helpers, six lactating females, four members of non-reproductive groups. On one occasion, two lactating females together attacked the intruder and in three cases the resident male, who came running at the bark of a resident female, expelled the male intruder.

If a resident did not attack an intruder directly (e.g. when the resident was a young fox and the intruder a large male), mobbing was the usual reaction. It was also usual when a human appeared in the home range. During mobbing, the resident followed an intruder, making long, loud cries interspersed with serial barks. Of 153 occasions when people passed close to 22 dens with cubs (data from 1996 and 1998), there was one or more adult resident at the den in 79.1% of cases and, in 74.4% of these, mobbing

occurred. In 26.3% of the 20 instances of mobbing, the cries were followed by the appearance at the den of another family member.

## DISCUSSION

### Body size

The larger body size of Mednyi foxes mirrors results for island rodents (Adler & Levins, 1994). Levins & Adler (1993) explain the large body mass of insular mammals as a consequence of reduced reproductive effort and delayed sexual maturity in response to increases in densities, with long-term directional selection for increased body size explained as a response to increased intraspecific competition. There are, however, cases where fox populations on islands contrast with both our data and that of general island syndrome theory. For example, populations of the island fox *Urocyon littoralis* are a dwarf form compared to that of its progenitor, the mainland grey fox *U. cinereoargenteus* Wayne *et al.*, 1991; Crooks, 1994).

The decrease in the body size of the California Channel island fox and the increase in the size of the Mednyi arctic fox clearly contradict the Island Rule of a negative correlation between relative size of island individuals and body mass (see above) since the California Channel foxes are much smaller (average body mass 1.89 kg,  $SD = 0.24$   $n = 202$ ; Roemer *et al.*, 2001) than the Mednyi Arctic foxes, and would appear to be more likely to increase in size. The opposite body size evolution of foxes on California Channel Islands and Mednyi Island confirms the conclusion of Meir *et al.*, (2004b) that the size of carnivores is subject to a number of selective pressures, which lead to different results in different environments.

We suggest that the differences in foraging ecology between these island fox populations and their mainland conspecifics (or the congener of the California Island foxes) are the most likely explanation for these variations in their body size evolution. The food resources of island Arctic foxes are much more stable and abundant than those of mainland Arctic foxes that depend on populations of rodents. This allows them to satisfy higher energy requirements of a larger body size. In addition, food items of Mednyi Arctic fox (beached carcasses of marine mammals, seashore animals, eggs and nestlings of colony birds) by contrast to those of mainland Arctic foxes are motionless, often heavy, and are protected by strong skin or hard shells. This might favour a strong skull and greater body mass, while having little influence on agility. By contrast to the Mednyi Arctic foxes, the California island foxes seem to have similar diets with the mainland population of grey fox. Their diet consists predominantly of insects, mice and fruits, although, compared with the grey fox, island foxes show less dependence on vertebrate prey (Roemer *et al.*, 2001).

Other factors such as presence of predators and competitors may also play a significant role in determining body size. On California Channel Islands the golden eagle may predate on the foxes. There are, however, no large

raptors on the Mednyi Island, so a reduction in agility and a larger body size does not increase the risk of predation.

### Population density

Even before the population crash in the 1970s, foxes on Mednyi were culled, making direct comparisons with dynamics of other populations impossible. However, at present, Mednyi foxes remain one of the densest and most stable populations of Arctic foxes with the highest density of natal dens reported in the literature (Table 4). Angerbjorn, Hersteinsson & Tannerfeldt (2004) acknowledged methodological differences. On the Kanin Peninsula (in European Russia) densities of Arctic fox dens (active and non-active) ranged from 0.7 to 5.8 per 10 km<sup>2</sup> in 1945–47 (Shibanov, 1951); in the Bolshezemelskaya and Malozemelskaya Tundra (Barents Sea coastal plain, and the delta of the Pechora River) the densities of Arctic fox dens were *c.* 2.9–5.6 (mean 4.4) per 10 km<sup>2</sup> in 1953–56 (Scrobov, 1960); in Siberia from 0.2 to 2.9 per 10 km<sup>2</sup> (Chirkova, 1967). However, the density of active breeding dens is unlikely to exceed 5–30% of these figures (e.g. Skrobov, 1960; Smits & Slough, 1992). Nonetheless, the density of active Arctic fox breeding dens on Mednyi Island is high.

A reduction in major density-depressing factors (e.g. competition, predation and habitat diversity) is often advanced as the explanation for elevated island densities (Williamson, 1981). On Mednyi, the comparatively benign climatic conditions, the absence of competitors and predators and rich, reliable food resources, all contribute to the manifestation of the island syndrome (Adler & Levins, 1994).

### Composition and size of reproductive groups

Traditionally it was assumed that the Arctic fox reproductive unit was a pair (e.g. Chirkova, 1967; Waser & Jones, 1983; Garrott, Eberhardt & Hanson, 1984; Angerbjorn, Tannerfeldt & Erlinge, 1999). Even for families known to contain three or more adults, it is rare to see them together in the vicinity of the den (Frafjord, 1991; Kruchenkova & Goltsman, 1994). However, studies in Iceland (Hersteinsson & Macdonald, 1982), Norway (Frafjord, 1991; Strand *et al.*, 2000), and Wrangel Island (Ovsjanikov, 1993) reveal larger social groups.

On Mednyi, family units often consisted of a pair of reproducing adults and a non-breeding female helper, with families of more than one lactating female also common. Even on St Paul Island (Pribilof Islands, Bering Sea), where the proportion of complex families is also high (33% in 1990 and 37% in 1991), the occurrence of two lactating females in one group was exceptional (White, 1992). Thus, the tendency to form complex groups on Mednyi seems to be greater than is typical in mainland populations even when population density is low. This has been attributed to the patchy nature of their food (Goltsman, Kruchenkova, Sergeev *et al.*, 2005).



**Table 4.** Comparative densities of active Arctic fox *Alopex lagopus* natal dens in islands and adjacent mainland ranges

Location	Years	No. of active dens per 100 km <sup>2</sup>	Study area (km <sup>2</sup> )	Authors
<b>Arctic fox populations in Pacific islands</b>				
Mednyi Island	1938	68.9	187	Iljina, 1950; Poljakov, 1933–38
Mednyi Island	1951	79.6	187	C. V. Marakov (pers. comm.)
Mednyi Island	1994–2002	11.42–20.00 <sup>b</sup>	70	This study
St. Paul Island (Pribilof Islands)	1990–91	27.2–44.0	125	White, 1992
<b>Arctic fox populations except Pacific islands</b>				
Aberdeen Lake area, Northwest Territories, Canada	1961–63	1.07–2.14	2147	Macpherson, 1969
Keewatin district, NWT, Canada	????	0–1.74	518	Speller, 1972
Prudnoe Bay, Alaska	1975–79	1.11–4.44	450	Eberhardt <i>et al.</i> , 1983
Colville River Delta, Alaska (75 km W. Prudnoe Bay)	1976–80	0.12–1.35	1700	Eberhardt <i>et al.</i> , 1983
Yukon-Kuskokwin Delta, Alaska	1985–90	0–13.5	37–52	Anthony, 1996
Yukon Coastal Plain, Northern Yukon, Canada	1984–89	0–0.04	2449	Smits & Slough, 1992
Kola Peninsula	1994	2.5	109	Angerbjorn <i>et al.</i> , 1999
Olenekskyi Bay	1994	1.11	90	Angerbjorn <i>et al.</i> , 1999
Yana Delta	1994	13.43 <sup>a</sup>	67	Angerbjorn <i>et al.</i> , 1999
Indigirka/Lopatka	1994	12.31 <sup>a</sup>	130	Angerbjorn <i>et al.</i> , 1999
Kolyma Delta	1994	2.73	110	Angerbjorn <i>et al.</i> , 1999
Herschel Island, Northern Yukon, Canada	1984–90	1.98–6.93	101	Smits & Slough, 1992
Faadeyevskiy, New Siberian Islands	1994	14 <sup>a</sup>	100	Angerbjorn <i>et al.</i> , 1999
Kotel'nyy, New Siberian Islands	1994	14.29 <sup>a</sup>	35	Angerbjorn <i>et al.</i> , 1999
Ayon Island	1994	4	50	Angerbjorn <i>et al.</i> , 1999
Wrangel Island	1981–84	0.96–8.7 <sup>a</sup>	310	Ovsjanikov, 1986

<sup>a</sup> The peak phase of population densities.

<sup>b</sup> The estimated density in whole island (187 km<sup>2</sup>) is 9.35 per 100 km<sup>2</sup>, SD = 1.88, Min = 6.42, Max = 11.23, *n* = 9.

### Fertility

Litter sizes in Arctic foxes are the largest of carnivorous mammals (e.g. Chirkova, 1967; Tannerfeldt & Angerbjorn, 1998) and, judging by the number of placental scars, can contain > 20 cubs (Cha, 1953; Chirkova, 1967). Average litter sizes vary widely, from 2.8 on Rat Island, Alaska (Berns, 1969) to 9.6 on Wrangel Island (Ovsjanikov *et al.*, 1991; Ovsjanikov, 1993), and 11.2 in Norway (Frafjord, 1992a) (Table 5).

Both the level and predictability of food resources determine litter sizes (Tannerfeldt & Angerbjorn, 1998) which, in areas where rodents are present, average 9.2 cubs, considerably higher than 5.9 in areas where rodents do not form a significant part of the foxes' diet (Frafjord, 1993). Chirkova (1967) notes that in the increase phase when food is abundant, litters of 8–12 cubs are born, but in the decrease phase this drops to three to five, particularly in the inner regions of mainland tundra. Litter sizes on Pacific Islands are on the lower part of the scale.

The reproductive output of Mednyi foxes was further reduced as mainly foxes between 2 and 3 years of age reproduced. In comparison, in mainland populations, yearlings commonly reproduce (Chirkova, 1967; Macpherson, 1969; Novikov, 1983), and in fox farms they produce litters as large as those of older animals up to 6 years (Tavrovsky, 1946).

The co-adapted traits of sexual maturation and reproductive capacity are often negatively related to maximum body size (Stearns, 1976). Intraspecific competition

favours such traits (Kaweki, 1993) although there is a trade-off with reproduction effort (Lidicker & Ostfeld, 1991; Hansson, 1992) – larger animals exhibit a lower reproduction effort. Alternatively, however, conditions where the probability of offspring survival is increased might favour large offspring and lower reproductive success (since in situations of high survival, many offspring do not need to be produced). Thus, both litter size and offspring size may be subject to selection in response to variation in mortality. Promislow & Harvey (1990) recognized the circularity of this argument and distinguished between intrinsic and extrinsic mortality. In populations that experience high levels of extrinsic mortality (mainland populations co-occurring with diverse density depressing factors) individuals increase fecundity, while the converse is true for the same species subjected to lower extrinsic mortality (insular populations with reduced density depressing factors). The situation on Mednyi conforms to that predicted by the island syndrome, with reduced fecundity in comparison to mainland populations (Stearns, 1976).

### Dispersal and territoriality

Despite its small size, the Arctic fox is exceptionally mobile, often dispersing tens of km (Hersteinsson & Macdonald, 1982; Tannerfeldt & Angerbjorn, 1996; Anthony, 1997; Strand *et al.*, 2000) or even hundreds of kilometres (Chirkova, 1967; Garrott & Eberhardt, 1987).

**Table 5.** Comparison of Arctic fox *Alopex lagopus* litter sizes in Pacific islands and other ranges

Locations	Litter size		SD	<i>n</i>	Authors
	max	mean			
Pacific island populations					
Rat Island (Aleutian islands)	5	2.8		16	Berns, 1969
St Paul Island (Pribilof Islands)					
1990		4.3		21	White, 1992
1991		2.3		38	White, 1992
Bering Island (Commander Islands)		4.0	1.8	359	Poljakov, 1933–38
1937–38					
Mednyi Island					
1931–33	10	6.4	1.3	17	Barabash-Nikiforov, 1938
1933		3.7		73	Poljakov, 1933–38
1937		4.1			Iljina, 1950
1938		5.0		93	Poljakov, 1933–38
1994–2002	13	4.6	2.2	57	This study
Arctic fox populations except Pacific islands					
Iceland	10	4.2	1.5	309	Hersteinsson, 1984 <sup>a</sup>
Sweden	16	6.3	3.3	164	Angerbjorn <i>et al.</i> , 1995
Norway	13	11.2		5	Frafjord, 1992 <sup>a</sup>
Finland					
1964–1974	12	6.6		10	Kaikusalo, 1991 (from
1985–1991	5	2.4		28	Tannerfeldt & Angerbjorn, 1998)
Svalbard, Norway	8	5.3	1.7	35	Prestrud, 1991, 1992 (cited in
	8	5.8	1.6	5	Tannerfeldt & Angerbjorn, 1998)
					Frafjord, 1992 <sup>a</sup>
Yugorsky Peninsula	16	7.8	3.2	117	Shilajeva, 1985
Kildin Island	13	6.5	2.2	48	Lavrov, 1932
Kara tundra	22	7.1			Chirkova, 1967
Taymyr Peninsula					
1975		5.0			Yakushkin, 1985
1976		6.5			
1977		5.2			
1978		5.9			
1979		6.4			
Wrangel Island	15	9.6		19	Ovsajnikov <i>et al.</i> , 1991
Alaska	10	5.5	3.1	4	Underwood, 1971, 1991 (cited in
					Tannerfeldt & Angerbjorn, 1998)
NWT, Canada	14	6.7	3.3	27	Macpherson, 1969
	14	6.1		11	Speller, 1972
	12	7.6	3.5	9	Hall, 1989
Herschel Island, Northern Yukon, Canada	7	5.0	1.2	5	Smits & Slough, 1992

Mednyi foxes dispersed over shorter distances than typical of mainland foxes (the distances recorded were minimum average distances since the whole island was not surveyed here), but differences between male and female dispersal rates remain pronounced. We suggest that pronounced female philopatry on Mednyi is related to a shift from monogamy to polygyny, that is linked in turn with the pattern of distribution of food resources, which are abundant, stable and clumped in summer but less predictable in winter.

Over 9 years, only three of 17 instances where females reproduced in areas 5–9 km from their natal range were observed. On St Paul Island, where five yearling females and two males were followed during dispersal, three females left their natal ranges (one possibly died), as did

both males (White, 1992). Pronounced female philopatry may be a distinctive feature of the Mednyi population or may indeed be a distinguishing feature of insular populations where the pattern of food resource distribution promotes a tendency toward polygyny.

Despite the larger body sizes of Mednyi Arctic foxes, their home ranges are much smaller than those of Arctic foxes in other parts of the species' range (usually exceeding 10 km<sup>2</sup>) (Hersteinsson & Macdonald, 1982; Frafjord & Prestrud, 1992; Angerbjorn, Stroeman *et al.*, 1997; Anthony, 1997; Strand *et al.*, 2000). This contradiction to the general allometry relating home-range size and body size (Gittleman & Harvey, 1982) has been described for other island populations (Stamps & Buechner, 1985; Roemer *et al.*, 2001).

**Table 6.** Distinguishing features of the insular population of Arctic fox *Alopex lagopus*

Trait	Authors	Confirm by our data
Larger body mass	Adler & Levins, 1994 for review	Yes
Greater population stability, no apparent long-term cycle	Adler & Levins, 1994 for review	Yes
Increased sociality	Macdonald, 1983	Yes
Delayed sexual maturity	Adler & Levins, 1994 for review	Yes
Smaller litter size	Adler & Levins, 1994 for review	Yes
Lower territoriality and aggression	Stamps & Buechner, 1985	No, retain a strict territorial system
Smaller home ranges	Stamps & Buechner, 1985	Yes
Reduced dispersal	Adler & Levins, 1994 for review	Yes

Insular systems typically have higher resource densities and reduced levels of interspecific competition owing to a depauperate fauna. On this basis, Roemer (2004) predicted an expected increase in both territory holders and non-territorial floaters. The prediction is for an increase in floaters to lead to increased defence costs for territory holders and ultimately to a reduction in territorial behaviour. This reduction in territoriality could be manifested as: (1) reduced territory size; (2) increased territory overlap; (3) acceptance of subordinates within the territory; (4) reduced intraspecific aggression (Stamps & Buechner, 1985). Contrary to these predictions, the small family home ranges of Mednyi foxes are intensively guarded by large family units. The island foxes on Santa Cruz Island (California Channel islands) also retain a strict territorial system despite high population density and small home-range size (Roemer *et al.*, 2001). Island syndrome suggests that the restriction of dispersal selects for a more sedentary lifestyle (*sensu* Tamarin, 1978; Cromwell, 1983) increasing social stability and reducing aggressive interactions through greater neighbour familiarity and kin recognition (Kawata, 1990; Lambin & Krebs, 1991). Our observations on Mednyi do not conform to these predictions.

## CONCLUSIONS

Eight predictions based on the island syndrome were identified. The Mednyi Arctic foxes conform to seven of these (Table 6). In addition, a new prediction is suggested, namely that the tendency for increased sexual dimorphism in dispersal distances (pronounced even against a background of very short dispersal distances) may also be a distinguishing feature of insular populations where the pattern of food resource distribution promotes a tendency toward polygyny.

All the features displayed by the insular population on Mednyi (conservative use of space, increased tendency to form complex groups, decreased fertility and dispersal), seem to be preserved regardless of the currently comparatively low populations. For 10 or more generations, foxes have been below carrying capacity, yet island syndrome characteristics have persisted.

Although the traits that change rapidly in temporarily fluctuating populations are also those that are associated

with the island syndrome, different processes may be responsible (Adler & Levins, 1994). Adler & Levins (1994) distinguish between short-term changes observed in fluctuating populations and newly insularised populations and those observed in established island populations that are apparently a result of long-term changes. Short-term changes may largely be reaction norms over a range of environmental conditions. Long-term changes may represent directional selection over generations. Since ecological and evolutionary time overlap, distinguishing between the driving forces of selection may be difficult. The failure of mainland populations to continue from the short-term reaction norm processes to the long-term evolutionary processes seen in island populations may be because of gene flow through dispersal and stabilizing selection pressures.

Much research on the island syndrome has been undertaken on rodents (Adler & Levins, 1994) and often predation is identified as the greatest factor contributing to the syndrome. In carnivores, predation may be less important but other density-depressing factors may be reduced on islands.

Finally if the island syndrome is widespread among diverse groups of organisms, as it seems to be (Stamps & Buechner, 1985), an understanding of the responsible mechanisms would be valuable in managing populations in increasingly fragmented landscapes where habitats exist as discrete patches or islands.

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