

Stability of Isolated Populations of Terrestrial Mammals Inhabiting the Islands of the Peter the Great Bay, Sea of Japan

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Abstract—A comparative analysis of the dynamics of insular populations of terrestrial animals was performed. The stability of insular populations and the relationship between their viability and the type of dynamics are discussed.

Key words: terrestrial mammals, isolated populations, islands, dynamics of abundance.

One of the key problems in the insular biogeography of mammals concerns the formation of terrestrial theriofaunas on continental islands. The species composition of theriofauna and the distribution of species on the islands depend on the viability of isolated populations in a limited space. It is generally believed that stable populations are most viable. Although numerous definitions of population stability are known (Whittaker, 1980; Bykov, 1988; Gilyarov, 1990), this property is traditionally understood as the ability of a population to preserve its size at a relatively high and constant level, thereby avoiding the threat of extinction. It is well known that the size of the majority of populations (including insular ones) does not remain constant, being affected by various factors. According to MacArthur (1972), the greater the maximal possible size (density) of a given population, the less probable its extinction. Under conditions of limited space and isolation, the populations of those species that have spread over many (even very small) islands will be more viable than the populations of the species distributed only on large islands. The analysis of data on the dynamics of an animal's abundance or density makes it possible to compare the stability and viability of an insular population.

Recent genetic data indicate that the loss of heterozygosity may be the main factor responsible for the extinction of completely isolated small populations. The distribution of genotype frequencies is largely a random process, and the rate of heterozygosity loss during one generation is relatively high: $1/2N$, where N is the number of effectively reproducing individuals, which may be significantly smaller than the total number of individuals (Li, 1978). The distribution of genotype frequencies in generations also depends on specific features of population dynamics (Nei *et al.*, 1875). Although the examples providing evidence that the loss of heterozygosity is the direct cause of extinction of

certain populations are not numerous, there is a general agreement that viability increases with an increase in heterozygosity (Shaffer, 1989).

The purpose of this study was to reveal trends in the dynamics of animal abundance related to the viability of the populations of terrestrial mammals inhabiting the islands of the Peter the Great Bay.

MATERIAL AND METHODS

The Peter the Great Bay is located in the northwest of the Sea of Japan, near southern Primorye. There are more than 40 islands of continental origin, whose areas vary from 0.0045 to 93 km². Four of these islands are fairly large (12 km² and larger); the area of the others does not exceed 6 km², usually being much smaller. These islands completely separated from the continent during the last postglacial sea transgression, approximately 8000 years ago (Velizhanin, 1976). Currently, the insular populations of all species are completely isolated from the continental populations (Sheremet'ev, 2001).

This study is based on the published results of long-term investigations (including those performed under stationary conditions) on the islands of the Peter the Great Bay and in the continental part of southern Primorye (Shaposhnikov, 1938; Redkie..., 1981; Chislennost'..., 1981–1990; Chugunov and Katin, 1984; Yudin, 1984; Nesterenko, 1986, 1999; Katin, 1989; *Sovremennoe sostoyanie...*, 1992; Poddubnaya, 1995; Kostenko, 2000), as well as on the original material collected on the islands in 1999–2001 using the conventional methods of route and trap-line censuses. For the majority of small mammals, abundance was determined in relative values and recalculated per 100 trap-days (Novikov, 1953). The abundance of hedgehogs, ungulates, and predators was recalculated per 10 km of

Species composition and distribution of terrestrial mammals on the islands of the Peter the Great Bay

Species	Island*											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Erinaceus amurensis</i>	+	+	-	-	-	-	-	-	-	-	+	-
<i>Sorex caecutiens</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Sorex roboratus</i>	+	+	-	-	-	-	-	-	-	-	-	-
<i>Sorex taphaenodon</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Crocidura lasiura</i>	+	-	-	-	-	-	-	-	+	-	-	-
<i>Crocidura suavolensis</i>	-	+	-	-	-	-	-	-	-	+	+	-
<i>Tamias sibiricus</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Sicista caudata</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Apodemus agrarius</i>	+	+	+	-	-	+	-	+	+	+	+	-
<i>Apodemus peninsulae</i>	+	-	-	-	+	-	-	-	-	-	-	-
<i>Micromys minutus</i>	+	-	-	-	-	-	-	-	-	+	+	-
<i>Rattus norvegicus</i>	+	+	+	-	-	-	-	-	+	+	+	-
<i>Clethrionomys rufocanus</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Microtus fortis</i>	+	+	+	+	-	+	+	-	+	-	+	+
<i>Vulpes vulpes</i>	+	+	+	?	-	-	-	-	-	-	+	-
<i>Nyctereutes procyonoides</i>	-	-	-	+	-	-	-	-	-	-	-	-
<i>Kolonocus sibirica</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Cervus nippon</i>	-	-	-	-	-	-	-	-	-	+	+	-
<i>Capreolus capreolus</i>	+	-	-	-	-	-	-	-	-	-	-	-
Island area, km ²	93	12	6	5	1.5	3.3	0.9	2.4	0.08	14	22.5	0.0045–1.4

* Designations: (1) Russkii Island; (2) Popov Island; (3) Reineke Island; (4) Rikord Island; (5) Stenin Island; (6) Bol'shoi Pelis Island; (7) Matveev Island; (8) Furugel'm Island; (9) Vera Island; (10) Askol'd Island; (11) Putyatin Island; (12) Naumov, Malyi, Klykov, Skreb-tsov, Karamzin, Vkhodnye, Pervyi-Tretii Kamni Matveeva, Kentavr, De-Livron, Gil'debrandt, Durnovo, Antipenko, and Sibiriyakov islands; (+) reliable presence of the species, (-), reliable absence of the species, (?), unconfirmed data.

the route or, if comparable data were available, per 10 km² (Yudin, 1984; *Sovremennoe sostoyanie...*, 1992). The routes and trap lines were laid so as to cover all types of habitats existing on the islands. The field work amounted to more than 600 km of routes and 4867 trap-days; 651 terrestrial mammals were captured. In addition, the collections of the Institute of Biology and Soil Sciences (Far East Division, Russian Academy of Sciences) were used in this study. For the species with pronounced seasonal fluctuations of population size (insectivores and rodents), the maximal abundance recorded during the year is shown.

RESULTS AND DISCUSSION

The paleontologic data (Sheremet'ev, 2001) indicate that the populations of 18 out of the 19 mammalian species inhabiting the islands have been retained since the moment of island separation from the continent, and one species (the striped field mouse) has penetrated to the island recently, after the formation of sea straits.

With respect to the distribution on the islands, all terrestrial mammals are divided into two groups: species of limited distribution and widespread species.

Species of limited distribution occur on only a few islands (one to six, usually one to three).

Amur hedgehog *Erinaceus amurensis* Schrenk, 1859. On the islands where this species occurred, no more than two hedgehogs per 10 km of the route were found. Similar data were reported for the continental part of southern Primorye (Poddubnaya, 1995). According to Nesterenko (1999), the abundance of hedgehogs varies with the year; however, it has not increased in the study period.

Laxmann's shrew (*Sorex caecutiens* Laxmann, 1788). On Russkii Island, the maximal abundance of this shrew varies in different years from 4.5 to 6 ind./100 trap-days; on the continental part of southern Primorye, from 10 to 60 ind./100 trap-days (Nesterenko, 1999).

Flat-skulled shrew *Sorex roboratus* Hollister, 1913. On Russkii Island, the maximal abundance of these animals reaches 22.5 ind./100 trap-days. In some years, this species have not been recorded because of its low abundance. On the continental part of southern Primorye, the abundance of *S. roboratus* in different years is 1.2–5 ind./100 trap-days (Nesterenko, 1999).

Large-toothed shrew (*Sorex daphaenodon* Thomas, 1907). On Russkii Island, the abundance of this

species varies from 0.5 to 5.1 ind./100 trap-days; on the continental part of southern Primorye, it reaches 4.8 ind./100 trap days (Nesterenko, 1999).

Lesser white-toothed shrew (*Crocidura suaveolens* Pallas, 1811). On Askol'd Island, the abundance of this species reached 6 ind./100 trap-days; on Putyatin Island, 5 ind./100 trap-days; and on Popov Island, 2 ind./100 trap-days (Sheremet'ev, 2002). On the continental part of southern Primorye, this species is trapped very rarely (in some years, no more than 2 ind./100 trap-days) (Nesterenko, 1999).

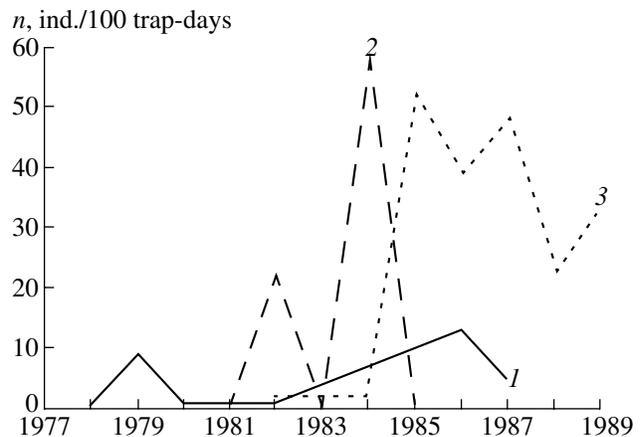
Ussuri white-toothed shrew (*Crocidura lasiura* Dobson, 1980). On Vera and Russkii islands, this species is very scanty (Nesterenko, 1999) and does not occur in catches in some years. On the continental part of southern Primorye, the maximal abundance of these shrews varies from 2 to 5 ind./100 trap-days (Nesterenko, 1999).

Siberian chipmunk (*Tamias sibiricus* Laxmann, 1769). On Russkii Island, this species was scanty. It did not occur in catches, and single individuals were detected only visually. On the continental part of southern Primorye, the maximal abundance of these animals in different years varies from 3 to 12 ind./100 trap-days (Kostenko, 2000).

Chinese birch mouse *Sicista caudata* Thomas, 1907. This species have been trapped very rarely both on Russkii Island and on the continental part of southern Primorye. The maximal abundance of *S. caudata*, recorded on Russkii Island, was 1.3 ind./100 trap-days. In depression years, this rodent has not been trapped. On the continent, the abundance of *S. caudata* may reach 5 ind./100 trap-days (*Sovremennoe sostoyanie...*, 1992).

Norway rat (*Ratus norvegicus* Berkenhout, 1769). According to the results of long-term studies (*Chislennost'...*, 1981–1990), the abundance of this species varies in different years from 1 to 21 ind./100 trap-days. No long-term depressions (lasting for two to three years) of the common rat population have been detected. In other islands inhabited by common rats, the abundance of this species during the census fell within the above range. On the continental part of southern Primorye, the abundance of rats varies insignificantly and, in natural biotopes, rarely reaches 2–3 ind./100 trap-days (Kostenko, 2000).

Old World harvest mouse (*Micromys minutus* Pallas, 1771). On the islands located in the Peter the Great Bay, only single *M. minutus* have been captured. On Russkii Island, the abundance of this species was 0.5 ind./100 trap-days; on Putyatin Island, 1 ind./100 trap-days; and on Askol'd Island, 2 ind./100 trap-days. According to the results of long-term studies (*Chislennost'...*, 1981–1990), the population of *M. minutus* on Russkii Island is subject to deep and long-term depressions, when the species does not occur in catches for four to five years. On the continental part of southern Primorye, the abundance of these animals is always low and in different years varies from 0.7 to 3 ind./100 trap-days.



Dynamics of insular populations (one island—one species) of mammals (according to Chugunov and Katin, 1984; *Chislennost'...*, 1981–1990): (1) *Apodemus peninsulae* (Stenin Island), smoothed dynamics; (2) *Apodemus agrarius* (Furugel'm Island), and (3) *Microtus fortis* (De-Livron Island), stepwise dynamics.

Korean field mouse (*Apodemus peninsulae* Thomas, 1906). On Stenin Island, the abundance of this species may remain fairly low for a long time (no more than 13.2 ind./100 trap-days). For this reason, this species has not been trapped in some years (Chugunov and Katin, 1984). On Russkii Island, the abundance of *A. peninsulae* in different years varies from 7 to 18 ind./100 trap-days (*Chislennost'...*, 1981–1990). On the continental part of southern Primorye, the abundance of *A. peninsulae* during three- to four-year cycles reaches 60–70 ind./100 trap-days; during a depression, no more than 3 ind./100 trap-days (Kostenko, 2000).

Large-toothed red-backed vole (*Clethrionomys rufocanus* Sandervall, 1846). According to the data obtained in long-term studies (*Chislennost'...*, 1981–1990), the abundance of this species, recorded in different years on Russkii Island, is 0–5 ind./100 trap-days. On the continental part of southern Primorye, it varies from 0.5 to 90 ind./100 trap-days in three- to four-year cycles (Kostenko, 2000).

Red fox (*Vulpes vulpes* Linnaeus, 1758). The frequency of foxes on the islands was 3.3 tracks per 10 km. Similar numbers were recorded on the continental part of southern Primorye (3 tracks per 10 km). At this abundance, annual fluctuations are not significant (*Sovremennoe sostoyanie...*, 1992).

Raccoon dog (*Nyctereutes procyonoides* Gray, 1834). Currently, the density of raccoon dogs on Rikord Island is 40–50 ind./10 km², which is close to the values recorded on the continental areas adjacent to the bay (38.2 ind./10 km²) (Yudin, 1984). Three years after the introduction of the raccoon dog into Askol'd Island, the number of these animals increased from 20 to 350 (Shaposhnikov, 1938), which corresponded to a density of 250 ind./10 km². To date, the raccoon dog has

disappeared from Askol'd Island, apparently as a result of its extermination.

Siberian weasel (*Kolonocus sibirica* Pallas, 1773). The frequency of Siberian weasel on Russkii Island is 33.3 tracks per 10 km. In adjacent continental areas (the Kedrovaya Pad' Reserve), these animals occur at a frequency of 5–17 tracks per 10 km in different years (*Sovremennoe sostoyanie...*, 1992).

Roe deer (*Capreolus capreolus* Linnaeus, 1758). The frequency of roe deer on Russkii Island is 22.5 tracks per 10 km. In the continental part of southern Primorye (the Kedrovaya Pad' Reserve), 50 to 350 tracks per 10 km in different years. In unprotected areas, this parameter is two to three times lower (*Sovremennoe sostoyanie...*, 1992).

Sika deer (*Cervus nippon* Temminck, 1838). Sika deer were kept in a park on Putyatin Island, both in enclosures and beyond them; by 1999, only about 100 out of several thousand deer remained in enclosures. According to our estimates, approximately 30–35 deer (20 to 22 ind./10 km²) inhabited Askol'd Island in 1999, whereas even in 1998 their number was at least 100 (60–70 ind./10 km²). According to Bromlei (1981), during the past decades (when the island was closed to visitors), the total number of sika deer exceeded 300 (200–220 ind./10 km²); in the early 20th century, when the deer were fed and protected, their number was approximately 2500 (1600–1700 ind./10 km²). On the continental part of southern Primorye (the Kedrovaya Pad' Reserve), the maximal abundance of this species in the first half of the 20th century was 22–23 ind./10 km² (*Sovremennoe sostoyanie...*, 1992).

Insular populations of five species of this group (ungulates and predators) are initially sparse, although some of them (e.g., raccoon dog and sika deer on Askol'd Island, which is inaccessible to visitors) may have a fairly high density. A relatively low abundance, without marked fluctuations, is characteristic of a species with low fecundity, whose life span is several times longer than the duration of reproductive cycle; it is characteristic of both insular and continental populations. The maximal sizes of the insular populations of three species (Laxmann's shrew, Korean field mouse, and large-toothed red-backed vole) are much lower than their continental populations. The insular populations of other insectivore and rodent species are slightly more numerous than the continental populations, but their relative density does not exceed 22.5 ind./100 trap-days. In general, the insular populations of all species of this group are characterized by smoothed dynamics at a relatively small fluctuation level. Depressions in the populations of some insectivore and rodent species may last for two to three years and even longer (figure, curve 1).

Widespread species occur on at least eight islands, including small islets (no more than 0.0045 km²).

Reed vole (*Microtus fortis* Buchner, 1889). The results of long-term studies (*Chislennost'...*, 1981–1990)

showed that the abundance of reed voles in the population inhabiting large islands in the Peter the Great Bay reaches 32 ind./100 trap-days; no long-term depressions of this population have been recorded. On small islands, where the reed vole is the only species of terrestrial mammal, its abundance may reach 50 ind./100 trap-days, and long (two to three years) periods of its high abundance are followed by long-term depressions (Katin, 1989). On the continental part of southern Primorye, the abundance of reed vole may exceed 90 ind./100 trap-days (Nesterenko, 1986).

Striped field mouse (*Apodemus agrarius* Pallas, 1771). According to the results of long-term studies (*Chislennost'...*, 1981–1990), the size of insular populations of this species undergoes dramatic fluctuations: even within the same season, it may increase dozens of times over, and depressions do not continue for more than one year. On the islands Bol'shoi Pelis and Furu-gel'ma, the abundance of striped field mice in different years varies from 0.7 to 59 and from 1 to 52 ind./100 trap-days, respectively; however, in the peak period it may reach 100 ind./100 trap-days (Chugunov and Katin, 1984). On Russkii Island, the abundance of this species in the study period was 13 ind./100 trap-days; Popov Island, 32; Reineke Island, 16; Askol'd Island, 16; and Putyatin Island, 12 ind./100 trap-days. In the absence of long-term depressions, the abundance of these rodents on the continental part of southern Primorye may also reach 100 ind./100 trap-days (Nesterenko, 1986).

A common feature of the insular populations of these two species is a stepwise mode of changes in animal abundance, which may reach more than 50 ind./100 trap-days in the periods of population growth. The only difference between them is that the cycles of insular populations of the reed vole are lengthened (figure, curves 2 and 3). Long-term depressions lasting for several years have no adverse effect on the insular populations of the reed vole, because this species has a reliable mechanism allowing it to preserve the reproducing part of population in unfavorable periods (Kotin, 1989).

The ability to reach a high abundance is also characteristic of the continental populations of the two species that are dominant among the rodents inhabiting open areas in southern Primorye.

Thus, a comparative analysis of the population dynamics of terrestrial mammals and the pattern of their distribution on islands shows that the extinction of populations on small islands is more probable because of insufficient number of animals in them. The abundance of some species (ungulates and predators) is permanently low, which makes them especially vulnerable. The insular populations of other species (insectivores and most rodents), whose size is normally small, undergo depressions lasting for two to three years or even longer. This has an adverse effect on the species with a short reproductive cycle.

CONCLUSIONS

The main characteristic feature of the population dynamics of mammals inhabiting numerous islands is that their abundance periodically reaches high values. Apparently, these population peaks are of principal importance for the distribution of genotype frequencies in generations and the maintenance of the required heterozygosity level in isolated populations. It should be noted that not only the height (maximal abundance), but also the frequency of these peaks are important.

Under conditions of limited space and isolation, those species are more viable whose insular populations can reach a large size, are not subject to long-term depressions, and have mechanisms for preserving the effectively breeding part of the population (in the case of depression). Less viable are species whose population have a relatively small size, which either remains fairly constant or manifests slight rises alternating with long-term depressions.

This concept of population viability applies both to the species inhabiting the archipelagoes of sea islands since the moment of their separation and to the immigrant species.

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