
Species and genetic diversity of vole populations of Antalieptė Reservoir islands

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Results of a study of vole species diversity of 20 islands of the Antalieptė Reservoir and the genetic diversity of bank vole *Clethrionomys glareolus* in four of those islands are presented. Four species of small rodents were caught in the islands. 90% of all species captured in the islands and 59% of those captured on the mainland were formed of bank vole. Total of 8 enzyme loci were studied for the genetic diversity of bank vole. All the loci studied exhibited allelic polymorphism. The number of alleles per locus varied from 2.1 ± 0.3 in Beržai Island to 3.4 ± 0.2 in Arkliai Island. The mean heterozygosity varied from 0.243 ± 0.08 to 0.334 ± 0.14 in different populations. Genetic distance between isolated populations varied in a range of 0.091 to 0.315. A high proportion of loci showed significant departures from the Hardy–Weinberg equilibrium in all populations of Antalieptė Reservoir islands.

Key words: fragmentation, vole species diversity, *Clethrionomys glareolus*, allozymes, genetic diversity

INTRODUCTION

The destruction and modification of continuous areas of natural habitats due to anthropogenic impact reduces biodiversity and therefore is one of the most important reasons for species extinction (due to population splitting, migration barriers) [33]. The area of an island is one of the main factors influencing the number of species on it. About 30% of species undergo extinction, if the area of the island reduces up to ten times [29].

In a fragmented area the population undergoes a strong influence of stochastic processes on the survival and reproduction of its individuals (demographic waves, predators, food resources, environmental and genetic factors); besides, a restricted process of colonisation induces a greater extinction probability [16].

It has been long since it was recognised that genetic diversity and variation are important in maintaining high levels of fitness and allowing populations to survive in changing environmental conditions.

Destruction of natural habitats can decrease the genetic diversity of populations. A number of studies indicate a low level of genetic variation and inbreeding depression in island populations [2, 7, 9]

as a result of their finite size [10]. In small isolated populations genetic variation is stronger influenced by gene drift (more often fixed harmful alleles) [18], migration rates and gene flow which brings up new variants of genes to gene pool [13]. On the islands removed far from the mainland or completely isolated from it genetic variation is very poor [15]. Besides, as a consequence of isolation, genetic separation of subpopulations can be caused. Studies of voles show that the main factor in differentiating island races from their mainland ancestors is the chance genetic composition of the founding animals [2].

This pilot study of Antalieptė Reservoir islands aims at quantifying the species and genetic diversity of the vole populations. Data describing their genetic diversity may help to understand the structure and relationships of the populations.

MATERIAL AND METHODS

Sampling site

The Antalieptė “sea” is an artificial water reservoir (Fig. 1). It is located 15 km SW of the Zarasai town (55°37' N, 26°02' E) of Lithuania. The reservoir was formed in 1959 near Antalieptė town due

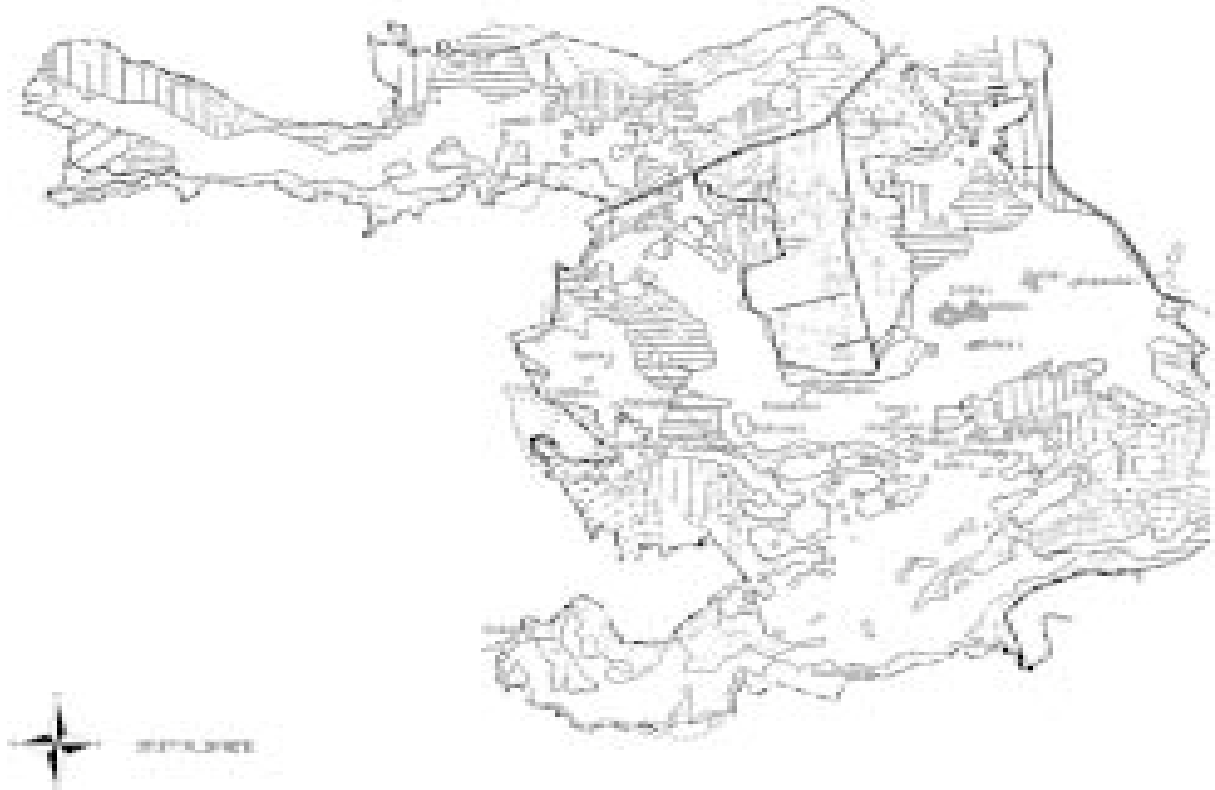


Fig. 1. Relations between area of islands and species number in them

to damming of River Šventoji. The area of 800 ha was flooded, 26 lakes were merged. From the tops of the hills of the former landscape there were formed from 80 to 90 islands. Later, some of the islands were transformed to peninsulas and now the Antalieptė Reservoir covers approximately 1911 ha and has only 50 islands of various sizes left [11]. The area of islands varies from 0.05 ha to 6.3 ha and the distance from the mainland shore varies from 15 to 500 m (Table 1). Only two of the islands (Lapuočiai* and Bebrai) are very old and existed in Lake Dusetos before the flooding. In most cases the biotope on the islands is represented by different kinds of forests (pine, deciduous and mixed) [26].

The names of the islands used in the article are used according to [26].

Sampling

Sampling of small rodents from 20 islands of the Antalieptė reservoir was carried out in the fall of 1999, and there were found several small rodent species, – *Apodemus flavicolis*, *Clethrionomys glareolus*, *Microtus arvalis*, *M. agrestis* (Table 2). The distribution of small rodents on the islands was une-

Table 1. Island area and distance from the bank. Islands marked with an asterisk were analyzed genetically

	Island	Are, ha	Distance from the bank, m
1	Absoliutas	0.41	130
2	Ajeras	0.41	200
3	Arkliai*	6.30	140
4	Bebrai*	0.56	250
5	Beržai*	0.87	500
6	Didžioji	3.17	70
7	Genio kalvė	0.39	40
8	Kandžiai	0.21	15
9	Karšis	0.25	180
10	Lapuočiai	0.45	460
11	Malkos	0.45	210
12	Nakvynės	2.33	60
13	Paminkas	0.12	80
14	Pietūs	0.17	40
15	Priešzubrinė	0.16	30
16	Pušynėlis	0.37	50
17	Saulėlydis	0.74	15
18	Šešėliai*	0.73	40
19	Varnos	0.99	230
20	Vėžiai	0.06	350

qual. Bank voles inhabited 16 of the 20 islands visited by us and could be found almost on every island. Because of such domination, bank voles were chosen for a pilot study on genetic diversity. Specimens were trapped following the standard methods described by Flowerder [8] with some modifications. Two lines of 25 traps with 5 m intervals were placed on a biotope on each island and in the mainland. The exposition lasted two days with checking twice a day. A bit of bread with sunflower-seed-oil was used as a bait. The standard capture methods were applied on islands bigger than 1 ha, while on a middle-size (0.26–1 ha) and smaller islands (0.05–0.25 ha) the pattern of trap placement was adequate to the space available, placing on a middle-size islands two lines with 10 traps and on smaller ones two lines with five traps.

The biodiversity of the populations in the mainland and on the islands was under investigation in the summer of 1999 (July–August) and in the fall (September–October) of the same year. In addition to the above investigations which were still continued at that time, a pilot study of genetic diversity of some vole populations on the islands was carried out. A total of 1155 traps per day were placed on the islands of the Antalieptė reservoir in the fall of 1999. The number of traps placed on the islands varied from 20 to 220.

Enzyme electrophoresis

Samples of bank vole liver tissue were homogenised and homogenates analysed using polyacrilamide gel electrophoresis (PAAG), following Davis [6] and Brewer [5] with some modifications. The enzymes screened were as follows (isozyme, abbreviation, E. C. number, and corresponding structural gene loci in parentheses): glucose-6-phosphat dehydrogenase (GPD, 1.1.1.49, *Gpd-1*), non-specific esterase (EST; 3.1.1.-, *Est-2,-3,-4*) and malic enzyme (ME; 1.1.1.40, *Me-1,-2*). Three enzyme systems and non-specific proteins (NP) were resolved using multilayer 5% and 7.5% PAA gels with a Tris-EDTA-borat buffer (pH 8.3–8.4) system. Gels were prepared using the protocol of Harris & Hopkinson [12]. The fractionating of isozymes was performed at 110–130 mA (260–380 V) depending on a system analysed. Staining of the enzymes was undertaken following Show & Prasad [25]. Allelic variants were resolved by direct side-by-side comparison of migrating allozymes on the same gels. The genotypes at polymorphic loci were determined in each specimen according to the

principles of enzyme electrophoresis [24]. In some individuals, however, the genotypes could not be determined for the entire set of loci due to insufficient quality of resolution.

Statistic analysis

Species diversity on islands was determined by two coefficients – the Shannon coefficient for biodiversity and the coefficient of Simpson for domination [1].

When the number of species is large, the Shannon coefficient is close to the maximal value. $H = 0$ when only one species is captured and $H = \max$ when the same number of individuals of all species is captured. The Shannon coefficient was calculated based on the following formula:

$$H = \sum p_i \log_2 p_i$$

where $p_i = n_i/N$, with n_i – number of individuals of one species, $N = \sum n_i$ – all catches.

The Simpson coefficient was used for dominance quantity:

$$\lambda = \sum (n_i/H)^2$$

The number of individuals for 100 traps per day was defined according to the first day's catch. Species diversity on the islands was defined according to 2-day capture results.

Genetic diversity on the islands was quantified by the mean number of alleles per locus (A), the proportion of polymorphic loci (P) ($P_{0.95}$; frequency of the most common allele < 0.95), the mean observed heterozygosity (H_0) and Hardy–Weinberg expected heterozygosity (H_E) [22] for each locus and averaged over all loci using BIOSYS-2 software [30].

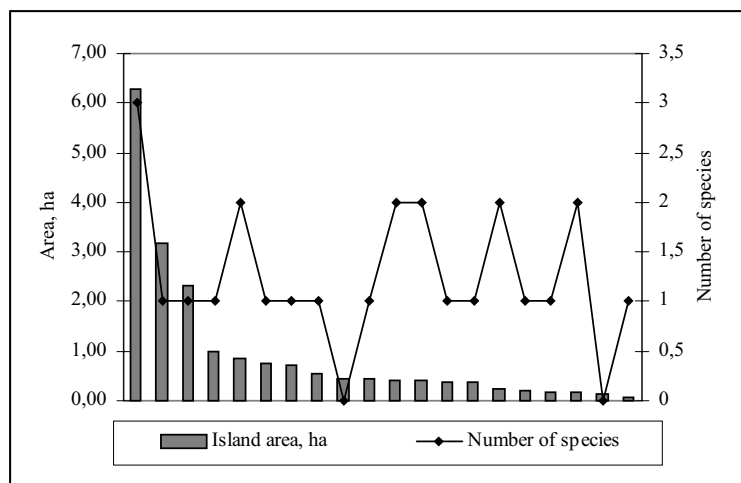


Fig. 2. Relations between area of islands and species number in them

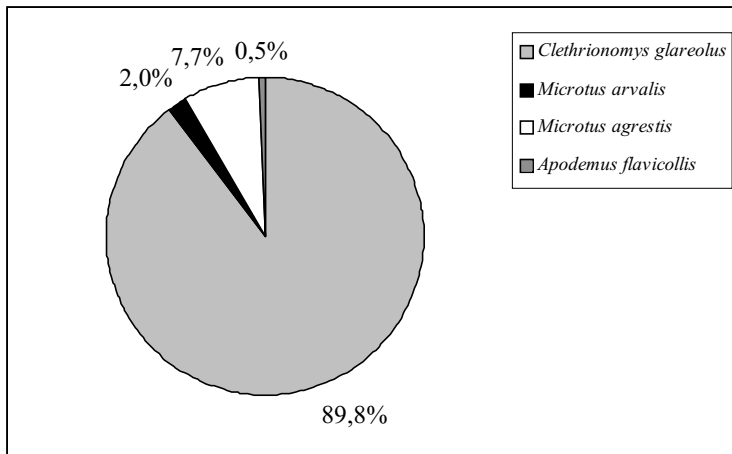


Fig. 3. Species structure of small rodents in islands studied in 1999

Deviations from the Hardy–Weinberg equilibrium were tested using chisquare analysis [32] with the significance value assigned by Monte Carlo permu-

tation process with 1000 replicates in the TFPGA program [20]. Nei's genetic distance (D) was calculated between all pairs of the five populations analysed [21]. A dendrogram based on genetic distance was constructed using the unweighted pair-group arithmetic average (UPGMA) cluster analysis by TFPGA.

RESULTS

Species diversity on islands

In 1999, 20 islands of the Antalieptė Reservoir were studied for the biodiversity and genetic structure of the populations.

Only one island (Arkliai) was inhabited by three species of small rodents, the other five islands screened were inhabited by two species, and twelve islands were inhabited by only one species with the

Table 2. Species structure of islands of the Antalieptė Reservoir in the fall of 1999. Islands analyzed for genetic variability are marked with an asterisk

Island	Species				Total number of species caught	Total number of individuals caught
	<i>Apodemus flavicollis</i>	<i>Clethrionomys glareolus</i>	<i>Microtus arvalis</i>	<i>Microtus agrestis</i>		
	Total number of individuals caught in island					
Absolutas	–	1	–	1	2	2
Ajeras	–	10	–	2	2	12
Arkliai*	1	42	–	3	3	46
Bebrai*	–	26	–	–	1	26
Beržai*	–	9	3	–	2	12
Didžioji	–	19	–	–	1	19
Genio Kalvė	–	3	–	–	1	3
Kandžiai	–	12	–	–	1	12
Karšis	–	2	–	3	2	5
Lapuočiai	–	–	–	–	0	0
Malkos	–	18	–	–	1	18
Nakvynė	–	19	–	–	1	19
Paminklas	–	–	–	–	0	0
Pietus	–	–	–	3	1	3
Priešzubrinė	–	1	1	–	2	2
Pušynėlis	–	2	–	–	1	2
Saulėlydis	–	6	–	–	1	6
Šešėliai*	–	5	–	–	1	5
Varnos	–	1	–	–	1	3
Vėžiai	–	–	–	3	1	3
Species composition	1	176	4	15	4	196
Shenon's coefficient, H						0.882
Simpson's coefficient, λ						0.646

dominance of bank vole. There were no inhabitants on two of the islands studied at all.

The number of individuals caught on the islands varied from 0 to 46. The density for 100 traps/day varied from 0 to 65 individuals. The common abun-

dance of small rodents on islands was 16.6 ± 3.48 specimen 100 traps/day.

It was established that the species diversity depended on the area of the island, and it was as follows: islands bigger than 1 ha inhabited 1–3 spe-

Table 3. Allele frequencies, deviations from Hardy–Weinberg equilibrium (< 0.05), proportion of polymorphic loci ($P_{0.95}$), mean number of alleles per locus (A) with standard errors in parentheses, mean heterozygosity observed (Ho) and expected (He) (standard errors in parentheses) for populations of *Clethrionomys glareolus* on four islands and peninsula of n – number of individuals screened. Significant deviations from Hdy–Wbg are marked in bold

Locus	Allele	Populations				
		Arkliai	Bebrai	Ber=ai	Šešėliai	Peninsula
n		32	22	7	5	6
<i>Gpd1</i>	a	0.156	0.000	0.000	0.000	0.083
	b	0.406	0.182	0.357	0.400	0.083
	c	0.375	0.545	0.643	0.600	0.167
	d	0.063	0.273	0.000	0.000	0.667
<i>HdyWbg</i>		0.000	0.062	0.197	0.011	0.531
n		29	16	8	5	6
<i>Est2</i>	a	0.000	0.031	0.000	0.000	0.000
	b	0.052	0.125	0.188	0.100	0.000
	c	0.759	0.719	0.750	0.900	0.917
	d	0.190	0.125	0.063	0.000	0.083
<i>HdyWbg</i>		0.083	0.082	0.888	1.000	1.000
n		36	25	8	5	6
<i>Est3</i>	a	0.444	0.280	0.375	0.000	0.167
	b	0.444	0.580	0.438	0.900	0.833
	c	0.083	0.140	0.188	0.100	0.000
	d	0.028	0.000	0.000	0.000	0.000
<i>HdyWbg</i>		0.013	0.018	0.162	1.0000	0.739
n		29	19	8	5	6
<i>Est4</i>	a	0.190	0.184	0.000	0.200	0.417
	b	0.500	0.368	0.375	0.300	0.500
	c	0.310	0.447	0.625	0.500	0.083
<i>HdyWbg</i>		0.000	0.000	0.002	0.261	0.637
n		33	23	8	4	5
<i>Me1</i>	a	0.061	0.100	0.000	0.000	0.000
	b	0.530	0.850	0.938	0.500	0.700
	c	0.409	0.050	0.063	0.500	0.300
<i>HdyWbg</i>		0.000	0.134	1.000	0.021	0.131
n		20	11	8	5	6
<i>Me2</i>	a	0.050	0.000	0.000	0.200	0.000
	b	0.425	0.591	1.000	0.400	1.000
	c	0.050	0.136	0.000	0.000	0.000
	d	0.475	0.273	0.000	0.400	0.000
<i>HdyWhb</i>		0.000	0.000		0.846	
n		36	25	8	5	6
<i>Np1</i>	a	0.000	0.000	0.313	0.300	0.333
	b	0.278	0.400	0.688	0.700	0.667
	c	0.667	0.600	0.000	0.000	0.000
	d	0.056	0.000	0.000	0.000	0.000
<i>HdyWbg</i>		0.000	0.009	0.024	0.131	0.006
$P_{0.95}$		100	100	85.7	100	85.7
A		3.4 (0.2)	3.0 (0.2)	2.1 (0.3)	2.4 (0.2)	2.3 (0.4)
Ho		0.285 (0.097)	0.311 (0.0888)	0.334 (0.136)	0.314 (0.137)	0.243 (0.80)
He		0.564 (0.036)	0.521 (0.048)	0.383 (0.089)	0.383 (0.079)	0.73 (0.085)

cies (Arkliiai), on middle size islands 1–2 species were found (Beržai, Bebrai), and 0–2 species were found living on islands of smaller size (Fig. 2).

Bank vole was dominating on 89.8% of all islands studied (Fig. 3). On 10 of 20 islands (50%) bank vole was the only one species inhabiting the island.

On the shore of the Antalieptė Reservoir 93 individuals were caught. Bank vole composed the total of 59% of all small rodents caught on the mainland. Low rodent density varied from 3 to 15 individuals per 100 traps/day. The Shannon coefficient in the mainland $H = 2.00$, Simpson's coefficient $\lambda = 0.35$.

Genetic structure of bank vole *Clethrionomys glareolus* in five island populations

Four islands (Arkliiai, Bebrai, Beržai, and Šešėliai) and the peninsula selected in the present study for genetic analysis cover a wide range of geographic distances and insularity. A total of 8 enzyme loci were studied for allozymic variation in five populations of bank vole (Table 3). All the loci studied exhibited allelic polymorphism ($P_{0.95}$). The number of alleles per locus varied from 2.1 ± 0.3 on Beržai Island to 3.4 ± 0.2 on Arkliiai Island. Significant deviations of the genotypes from Hardy–Weinberg equilibrium were found in 2 (Šešėliai Island) to 6 loci (Arkliiai Island) analysed (in Table 3 marked in bold). There was no significant deviation from Hardy–Weinberg equilibrium (except *Np1* locus) for peninsular population of bank vole.

The genetic distance (Table 4) $D = 0.091$ between Arkliiai and Bebrai Island populations of bank vole was small. The differences were biggest between the Arkliiai Island and peninsular bank vole populations ($D = 0.315$).

Table 4. Matrix of genetic distance among the vole populations of four islands and peninsula studied

	Population	1	2	3	4	5
1	Arkliiai	*****	0.091	0.265	0.220	0.315
2	Bebrai	0.203	*****	0.132	0.182	0.206
3	Beržai	0.366	0.273	*****	0.190	0.199
4	Šešėliai	0.319	0.324	0.297	*****	0.174
5	Peninsula	0.396	0.343	0.335	0.315	*****

DISCUSSION

Small mammal communities of the Antalieptė Reservoir islands were detected to be very poor. The Shannon coefficient on the islands ($H = 0.92$) indicates a poor biodiversity of the islands investigated.

The Simpson coefficient was high ($\lambda = 0.7$) due to dominance of bank vole on all islands.

The genetic diversity of Arkliiai Island population based on the mean number of 3.4 alleles observed per loci was the highest of all islands studied, but the most common genotypes in all loci were homozygous ($H_o = 0.285$) (results not shown). Also, a significant heterozygote deficiency ($p < 0.000$) was observed in all loci studied, except for *Est-3*, showing a possibility of high inbreeding rates on the island. On Bebrai Island the mean number of alleles observed per locus was 3.0. The biggest number of shared alleles was established between the Bebrai and Arkliiai populations. On Bebrai Island, the genetic diversity based on the mean of observed heterozygosity was 0.311. Deviations from Hardy–Weinberg equilibrium occurred in four of the seven allozyme loci, mostly due to heterozygote deficiency ($p < 0.000$) like in Arkliiai Island. Such a similar genetic structure of both populations results in a genetic similarity $D = 0.091$ of Arkliiai and Bebrai islands (Table 4, Fig. 4) and suggests that the heterozygous genotypes cannot survive under the pressure of selection.

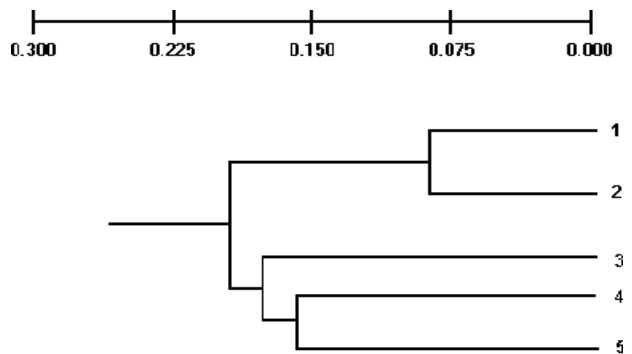


Fig. 4. UPGMA tree derived from allozyme data (Nei (1972) genetic distance) for island (1 to 4) and peninsula (5) populations of *Clethrionomys glareolus*: 1 – Arkliiai, 2 – Bebrai, 3 – Beržai, 4 – Šešėliai, 5 – peninsula

In the Beržai Island population which is most isolated, the genetic diversity was exhibited by a mean of 2.1 allele per locus, confirming that ‘distant islands exhibit a reduced genetic diversity’ [15]. However, a big proportion of the loci studied confirmed the Hardy–Weinberg equilibrium ($p > 0.05$).

Alleles with low frequencies are absent in a number of screened loci (Table 3) of Beržai and Šešėliai vole populations (*Est^a*, *Me1^a*, *Np^d*). The mean heterozygosity was found to be 0.334 and 0.314 in Beržai and Šešėliai populations, respectively. Allelic loss occurs more rapidly than loss of genic heterozygosity. Rare alleles are lost especially rapidly [19]. Occurrence of some alleles with low frequencies in

samples suggests the stochastic background, producing novel alleles at different sites [28].

The genetic diversity of Šešėliai Island was quite similar to that of the peninsular population, based on the mean number of alleles per locus (2.4 and 2.3, respectively). Only two loci (*Gpd1* and *Me1*) of the enzymes screened didn't conform to Hardy–Weinberg equilibrium on Šešėliai Island, showing the stability of the population. The bank vole peninsular population is the only one where all loci are in Hardy–Weinberg equilibrium (except *Np1*). This means that the population is in a stable state, too. Therefore the genetic distance between the populations of Šešėliai Island and the peninsula was 0,174 (Fig. 4). From the genetic point of view, on middle-size islands (from 0.26 to 1 ha) the populations were more stable than in bigger ones.

In this fragmented system, bank vole moving from one island to another must cross water barriers, and the dispersion rate depends on species mobility. *Clethrionomys* species are known to be not very good dispersers [17]. In fact, there may be very few individuals dispersing from one island to another on the Antalieptė Reservoir islands. So, the reason of such likeness could be similar environmental conditions. Small mammals are suitable species for analysing the effect of “genetic fragmentation” of the landscape, because it is possible to get an appropriate sample size in a short time.

ACKNOWLEDGEMENTS

We are very grateful to Doc. Dr. A. Paulauskas and Dr. L. Balčiauskas for their advice and methodical-technical assistance.

Received 18 September 2001

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PELĖNŲ RŪŠINĖ IR GENETINĖ ĮVAIROVĖ ANTALIEPTĖS TVENKINIO SALOSE

S a n t r a u k a

Tirta smulkiųjų graužikų rūšinė įvairovė 20 ir rudojo pelėno genetinė įvairovė 4 Antalieptės marių salose. Jose pagautos 4 smulkiųjų graužikų rūšys. 89,8% visų salose sugautų rūšių ir 59% krante sudarė rudasis pelėnas. Genetinės rudojo pelėno penkių salų populiacijų įvairovės vertinimas atliktas išanalizavus 8 fermentinius lokusus. Visi tirti lokusai polimorfiniai. Alelių skaičius lokuse kito nuo $3,4 \pm 0,2$ Arklių iki $2,1 \pm 0,3$ Beržų saloje. Vidutinis heterozigotiškumas lokusui populiacijose svyravo nuo 0,243 ($\pm 0,08$) iki 0,334 ($\pm 0,14$). Genetinės distancijos tarp salų kito nuo 0,091 iki 0,315. Visose tirtose salų populiacijose nustatytas patikimas nuokrypis nuo Hardžio-Vainbergo dėsnio.

Raktažodžiai: fragmentacija, pelėnų rūšinė įvairovė, *Clethrionomys glareolus*, alozimai, genetinė įvairovė