

Orthopterans in small steppe patches: an investigation for the best-fit model of the species-area curve and evidences for their non-random distribution in the patches

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Abstract – Distribution of orthopterans were studied in 27 steppe patches in the Buda Hills, Hungary. The smallest patches were about 300 m², the largest ‘continents’ were over 100 000 m². We collected 692 imagoes of 32 species and 1 201 imagoes of 28 species in July 1992 and July 1993, respectively. We found that the best-fit models for the species-area curves were both the power function and exponential models. The multivariate regression model incorporated area and distance from large patches as significant factors in determining the number of species. The correlation analysis revealed that the elevation and the height of grass vegetation also influenced the distribution of species. We applied three methods for testing whether the distribution of orthopterans was random or not. First, we compared the observed species-area curves with the expected curves. Second, we compared the small-to-large and large-to-small cumulative curves. Finally, we compared the observed species-area curves with the rarefaction curves. All three methods for both years showed that the occurrence of orthopterans in the steppe patches was not random. A collection of small islands harboured more orthopteran species than one or two large patches of the same area. © Elsevier, Paris

Orthopterans / habitat patches / species-area curves / pattern of distribution / conservation

1. INTRODUCTION

Changes in species number in relation to area is a basic question in ecology [35]. There are two main areas of interest: to find the best-fit mathematical formula for the graphical representation of the relationship; and to investigate the underlying biological mechanism for the relationship. Studies of the formulae date back to the beginning of the century. Arrhenius [1, 2] suggested a power function model, in which $\log(S)$ was linearly related to $\log(A)$ (S stands for the number of species, and A for the area), as the best-fit model. In contrast, Gleason [14, 15] proposed an exponential model (where S was linearly related to $\log(A)$) to describe the curve of the species-area relationship. After the emergence of the equilibrium theory [25, 26], which suggests the power function model, most ecologists ignored other models. However, Connor and McCoy [10] reviewed 100 data sets and found that in many cases, the power function was not the best-fit model.

There are at least three explanations that could account for the relationship between species numbers

and area: i) the random placement, or passive sampling theory; ii) fragmentation theories which include MacArthur and Wilson’s theory [25, 26]; and iii) habitat diversity theories (see references in e.g. [17, 28]). The important question, now, is to determine the relative contributions of these three processes to species-area relationships, for a range of ecological systems.

Steppe habitats are very valuable and rare in Europe, and threatened mainly by agricultural practices. From the point of view of a nature conservationist, knowledge of the distribution of a major insect taxon can bear important information for the management of the habitat.

We had three main goals: first to select the best-fit model for the species-area curves of orthopteran communities in selected steppe patches in the Buda Hills, Hungary, then to evaluate whether the distributions of species were random or not across patches. We did not attempt to select between fragmentation and habitat diversity theories, because of the lack of detailed habitat data. Finally, we evaluated the nature conservation values of orthopterans in the steppe patches.

2. STUDY AREA AND METHODS

Buda Hills are in the neighbourhood of Budapest, Central-Hungary (47°35' N, 18°55' E). The area is mainly forested (*Quercus cerris*, *Quercus petraea*). Our study area was on the Kutya Hill and Nagyszénás, where there were several steppe patches in the forest (240–520 m a.s.l.). The steppe vegetation was dominated by *Chrysopogon gryllus*, *Carex humilis*, *Festuca pallens*, *F. rupicola* and *Stippa* sp. in the patches. Altogether we sampled 27 study patches (appendix). The height of vegetation in each patches was estimated visually [5].

We collected orthopterans (Orthoptera: Tetrigidae, Acrididae, Tettigoniidae; Mantodea: Mantidae) by sweep-netting along previously marked 1-m wide transects [5]. A given transect was no longer than 50 m. The collected specimens were stored in alcohol. The transects were arranged to cover all habitats within a patch. We attempted to proportionately sample various habitat types, although the within patch habitat variation was small. The total length of transects in a patch depended on the size of the steppe patch. The transects on small patches were short, but covered relatively more area than on large patches. The sum of transects' lengths on large islands were at least 200 m. We calculated the density (individuals·m⁻²) of orthopterans to compare the samples. The samples were taken in July 1992 and 1993.

2.1. Choosing the best-fit model of the species-area curve

The best-fit model was determined by the examination of the residuals for systematic error [39]. We plotted the residuals against the independent variable (area), plotted the residuals against the expected values, and plotted the histogram of residuals. The best-fit model was determined by comparing these residual-plots of the four models (S-A, LgS-A, S-LgA, LgS-LgA) for non-linearity, non-constancy of variance and normality [39].

We applied correlation analysis between species number and the independent variables (listed in table I), and among the independent variables to detect the isolated effects of each variable [10]. We used stepwise multiple regression analysis to build a regression model. The two study years were pooled for these analysis.

2.2. Investigating the 'best-fit' theory

The random or non-random distribution of species on steppe patches was investigated in the three different ways proposed by Hart and Horwitz [17]: Coleman's method, Quinn and Harrison's procedure and the rarefaction method. Although the first and third methods are essentially the same (see e.g. [7, 40]), we used both to achieve results comparable with those of species-area and other studies obtained by applying only the widely-used rarefaction method. Below, we give a brief description of the techniques.

We used the method developed by Coleman [8] for the random placement hypothesis. This hypothesis states that all individuals were located at random, and the chance of finding any particular species was simply a function of the sample size and the number of individuals of that species in the community. We generated the species-area curves based on the expected number of species: $s(\alpha) = S - \sum(1 - \alpha)^{n_i}$, where s is the number of species in a sample, α the relative area of the sample, S the species number in all samples, n_i the number of individuals of the i th species. The expected curves were then compared with the observed number of species.

The small-to-large and large-to-small cumulative species-area curves were also compiled [34] as follows: beginning with the smallest island and adding successively larger islands; and beginning with the largest island and proceeding to the smallest. Both curves pass through the origin and a point representing the full biota of the total island area. A difference in the two curves indicates that random placement has not occurred.

Table I. Correlation among log₁₀ transformed data of independent variables measuring steppe patches. The acronyms are: area (A), distance to the nearest patch (D1), distance to the nearest large patch (D2), distance to the nearest 'continent' (D3), average height of grass vegetation (GH), and height above sea level (HASL). Two-tailed significances are given. *, $P < 0.05$.

	log(A)	log(D1)	log(D2)	log(D3)	log(GH)	log(HASL)
log(A)	1	0.060	-0.055	0.009	0.128	-0.434*
log(D1)		1	-0.155	0.308	0.352	0.131
log(D2)			1	-0.328	0.371	0.091
log(D3)				1	-0.322	0.515*
log(GH)					1	-0.247
log(HASL)						1

The rarefaction [38] and observed curves were compared to test for passive sampling. For rarefaction calculations, all observations were pooled. The assumption is that the number of individuals present in a patch represents a random sample from the pool of all species and individuals. For the analysis of rarefaction and cumulative curves, the largest patch was excluded.

We also studied the effects of environmental factors other than area. Remoteness of a given steppe patch was measured as the distance from i) the nearest island (D1), irrespectively of its size, ii) the nearest large island (D2), and iii) the nearest continent (D3). The height of grass vegetation was estimated on every patch. The average elevation of each patch was determined from 1:10 000 maps.

We applied the SPSS/PC+ program package for statistical analysis [32]. The variables were \log_{10} transformed to normalise their distribution.

3. RESULTS

We collected 692 adults belonging to 32 species in 1992, and 1 201 adults belonging to 28 species in 1993 (see *appendix* for a detailed species list.) The material is stored at the Hungarian Natural History Museum, Budapest.

As a first step, we evaluated our sampling design of non-equivalent effort on patches of different sizes. We found that our samples are good representations of the orthopteran communities, in that the distribution of sample sizes showed a lognormal distribution (*figure 1*), which is expected if large heterogeneous assemblies of species are sampled [24]. Second, we sampled the orthopteran community on one of our large patches (area = 101 700 m²) in a 50 × 50-m quadrat twice for another study. The comparison of the line and quadrat samplings revealed that the quadrat samples contained altogether thirteen species, whereas the line transects contained twelve species in 1992 and fourteen species in 1993. There was, however, an order difference between the sampled areas, 310 m² in the case of line transects and 2 500 m² for the quadrats.

3.1. The model of the species-area relationship

The power function and the exponential models were the best-fit models for orthopterans in the steppe patches. Neither of them violated the assumptions of lack of systematic error in residuals as a condition of best-fitting. Both models yielded a significant correlation between species number and area (exponential model: $S = -3.095 + 3.220(\log A)$, $r^2 = 0.740$, $F = 30.255$, $P < 0.0000$, $n = 27$; power function model:

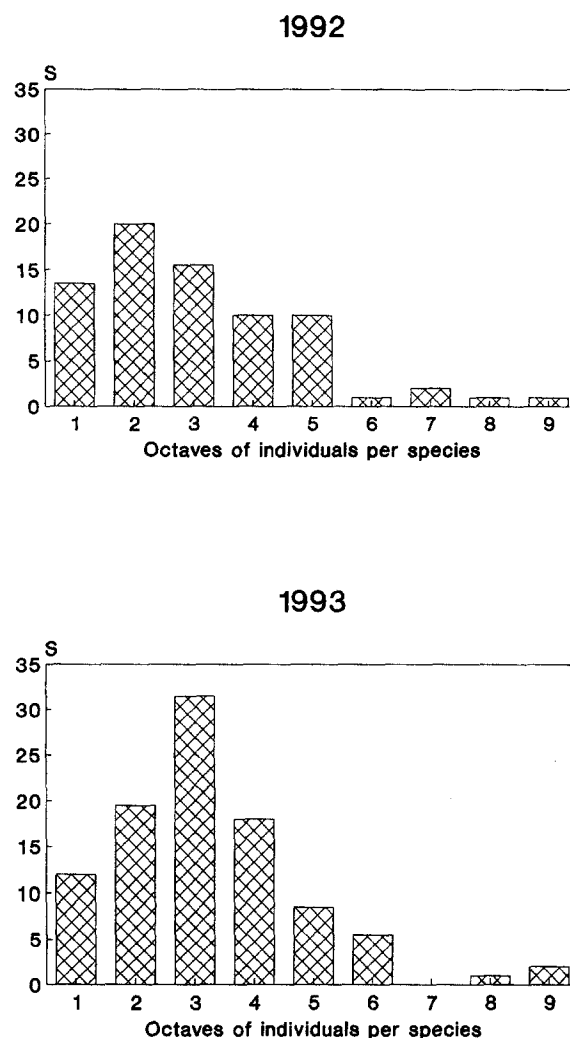


Figure 1. Distribution of sample sizes of orthopteran communities in steppe patches.

$\log S = 0.348 + 0.152(\log A)$, $r^2 = 0.723$, $F = 27.336$, $P < 0.0000$, $n = 27$). The slope of the power function model ($z = 0.152$) was less than the Prestonian slope $z = 0.262$ [33].

3.2. Correlation among the independent variables

The variables measuring landscape features were independent for almost all cases (*table 1*). Only the correlations of area and distance from steppe continent with height above sea level were relatively high. This is a consequence of the regional pattern, since the large meadows, considered as continents here, were situated at or near the foot of the hill.

Table II. Correlation coefficients between orthopteran species number and area, and other parameters. See *table I* for explanation of acronyms. *n* is given in parenthesis. Two-tailed significances are given. *, $P < 0.05$, **, $P < 0.001$.

	log(S)
log(A)	0.7227 (27)**
log(D1)	0.3009 (16)
log(D2)	0.3799 (22)
log(D3)	-0.0575 (24)
log(GH)	0.4154 (27)*
log(HASL)	-0.4128 (27)*

3.3. Relationships between species number and the independent variables

There was strong significant correlation between species number and area, and there were weaker, but yet significant correlations with the grass height and elevation (*table II*). Since the area and elevation are intercorrelated, this may be an indirect effect. The effects of elevation on species number may be mediated through area. Multiple stepwise regression analysis yielded a model which included two independent variables, namely the size of the steppe patch and its distance from the nearest large island (D2):

$$S = 0.125(\log A) + 0.117(\log D2) + 0.229$$

We excluded the distance from the smallest patch from this analysis, since the occurrence of species on a large island or continent ($> 10\,000\text{ m}^2$) may not be influenced by the vicinity of a small island ($< 1\,000\text{ m}^2$).

3.4. The non-random distribution of orthopterans

We found evidence that the distribution of orthopteran species was not random on the steppe patches. Coleman [8] showed that it is possible to compute the expected species-area curve and its variance for the random distribution of individuals based on a sample/species/abundance matrix. He suggested that if about two-thirds of the observed points fell within the band bounded by the plus and minus variance curves then the distribution was random. In our case, the majority of points were outside the band, which suggests a non-random distribution (*figure 2*). The position of the observed points in relation to the expected curves indicated that small islands harboured relatively more species, and large islands harboured relatively less species than expected under the random distribution.

The clear separation of the small-to-large and large-to-small cumulative curves (*figure 3*), and the rarefaction and observed species-area curves (*figure 4*) also suggest clear non-random pattern. In addition, the pat-

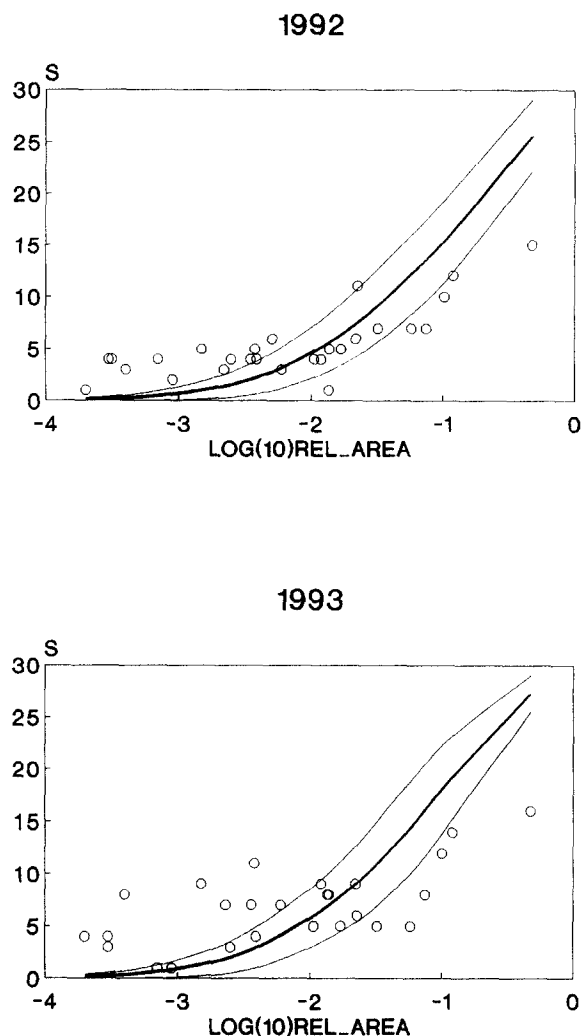


Figure 2. The expected species-area curves of orthopteran communities in steppe patches, the variances of the curves and the observed points. S: species number; log(10)Rel-Area: the logarithmically transformed relative area.

terns were similar in both years. The rarefaction curves lie above the observed points for large islands in both years, which reflect that the large patches are relatively impoverished in species. In the case of the cumulative curves, the small-to-large curves lie above the large-to-small ones which again indicate that the small fragments tended to contain a greater number of species than one large patch of similar size.

In summary for both years, all three methods suggested the same result, namely that the distribution of orthopteran species was not random, small islands were richer, and large islands were poorer in species than expected.

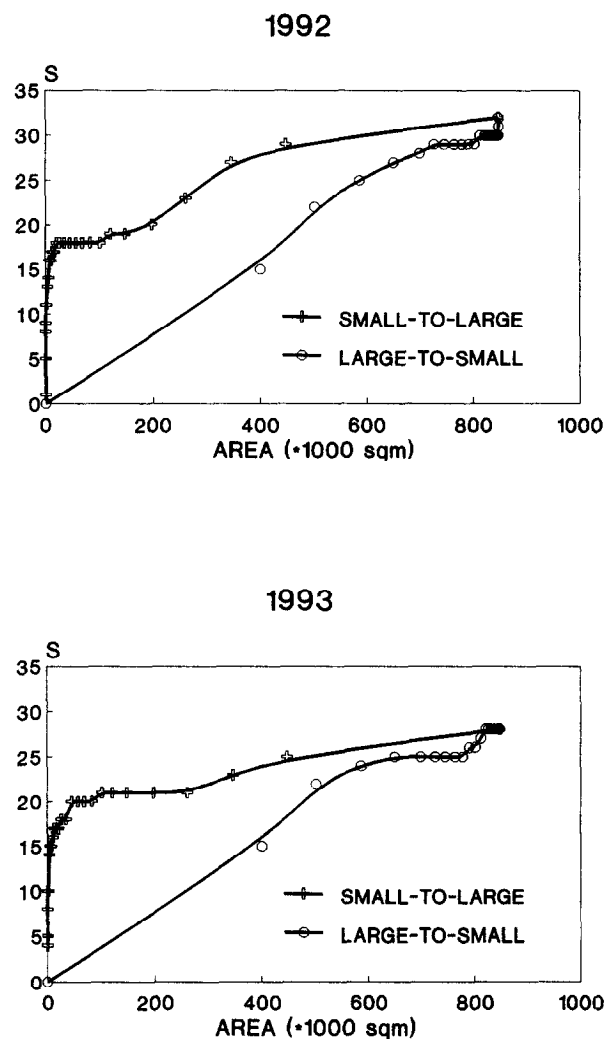


Figure 3. Small-to-large and large-to-small cumulative curves of orthopteran communities in the steppe patches of Buda Hills, Hungary.

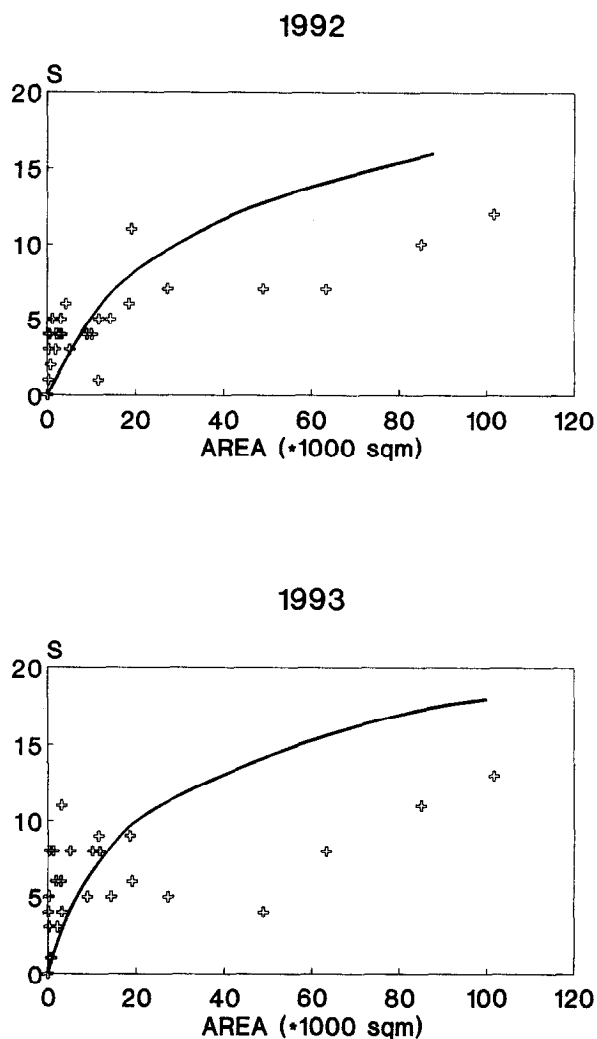


Figure 4. Rarefaction curves and observed points of the orthopteran species-area relationship in the steppe patches of Buda Hills, Hungary.

4. DISCUSSION

The species-area relationship is “one of community ecology’s few genuine laws...” [36]. However, the underlying mechanisms and processes are not understood yet (e.g. [10, 17, 28]). The possible generating mechanism of the species distribution is one of the most exciting problems in ecology. Nevertheless, many island biogeographical studies ignored the exact testing of possible hypotheses (random placement, fragmentation or habitat diversity theories, see [28]), only the fitting to MacArthur and Wilson’s equilibrium theory was studied. In the last decade, however,

new ideas challenged the outstanding role of the MacArthur-Wilson equilibrium theory (see [16, 17, 41]). As a consequence, alternative hypotheses became equally important. The next step was the identification of the underlying ecological mechanism. For example, Newmark [30] studied the distribution of mammals in North American national parks. He found that the equilibrium theory was an important predictor of species richness, while habitat diversity proved to be far less powerful. However, he did not test the null-hypothesis of random distribution. Nilsson et al. [31] considered the possibility of random distribution, but did not analytically test it. Recently, Martin et al. [27] conducted a study on the effects of island size and isolation on bird species richness. Although they made

quantitative censuses, they evaluated the random placement hypothesis theoretically, but missed the mathematical calculations. Quinn and Harrison [34] suggested a method to identify fragmentation effects (see Methods). Recently, Hart and Horwitz [17] published a proposal to test between random placement, fragmentation (area per se) and habitat diversity hypotheses. However, the investigation for the generating mechanism has a great drawback; namely, it requires quantitative data, thus, the conventional qualitative species lists are insufficient. Very few studies contain information on the number of individuals of each species [17].

The few investigations on distribution patterns and generating mechanisms of the species-area relationships have different results. Hart and Horwitz [17] showed an example of bird species of northern peat-bogs, and they found a random pattern. Coleman et al. [9] also found, that the distribution of birds was random. Báldi and Kisbenedek [4] found that fragmentation effects were present in the distribution of breeding birds in reed-bed islands, and that many small reed islands contained more species than one large island with the same area. The habitat diversity hypothesis was suggested by Douglas and Lake [11] for stone-inhabiting stream invertebrates.

Steppe patches for orthopterans are almost real islands, because only few species preferred the edges of steppe patches (*Pholidoptera* (Wesmael, 1831) spp., *Euthystira brachyptera* (Ocskay, 1826)), all others avoided the shady margins. Therefore, they are good objects for studying the effects of habitat patchiness.

What factors may contribute to the non-random distribution of species? Rosenzweig [35] suggests that habitat diversity is the key factor determining species numbers on islands. However, grasshoppers (Orthoptera: Acrididae), are usually polyphagous and the niches are overlapping [21, 22], therefore, their habitat specificity is not strong. In our study, the vegetation height was the only measurement we made on the habitat, and it significantly correlated with species number. We showed [5] that grassland naturalness significantly affects orthopterans, which points also to the role of vegetation. These indicate that habitat diversity hypothesis may have a key role in influencing species numbers.

Increased predation may also contribute to the relative impoverishment of orthopteran communities in large patches, because the main vertebrate predator of orthopterans, the red-backed shrike (*Lanius collurio* L., 1758), occurred only on large patches and continents (pers. obs., [13]). The effects of invertebrate predators may be less important [6].

We did not find any interpretable pattern in the distribution of species across islands of different sizes. That is, the visual inspection of the *appendix*, where

the islands were listed in decreasing order of size, did not reveal any clear pattern, suggesting patch-size dependent distribution of rare and/or abundant species.

Orthopterans have a key role in grassland management, because they are the major biomass components of arthropods [37]. They affect the whole biotic community by modifying the vegetation structure through grazing and serve as a main food resource for many invertebrate and vertebrate species. The dolomitic steppe meadows of the Buda Hills are rich in arthropods [3, 12], especially in orthopterans [29]. Two orthopteran species are listed in the IUCN Red List of Threatened Animals [20]: the predatory bush cricket (*Saga pedo* (Pallas, 1771)), and the *Stenobothrodes eurasius* (Zubowsky, 1898). During our recent and previous surveys ([23] and unpubl. data), we detected the predatory bush cricket a few times, but only on large islands. Our study suggests that a system of small patches can increase species number, but it seems that large patches are required for threatened species. This hypothesised pattern is very similar to the one we found with birds in a reed archipelago [5], and reflects the need to describe and understand species-area relationships for management purposes.

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Appendix. Area of the steppe patches in the Buda Hills, Hungary, the total length of the 1-m wide transects in the patches, and the list of collected orthopteran species and their abundances for 1992/1993. We followed the nomenclature of Harz [18, 19]. The patches are listed in decreasing order of size.

Area (m ²)	Steppe patches																													
	13	15	13a	27	21	5	22	21a	12	9	20	12a	21b	11	7	26	14	3	6	4	17	19	18	2	4a	16	23			
>400000	101 170	85 100	63 300	49 000	27 300	19 100	18 600	14 400	11 800	11 500	10 200	9 000	5 100	4 300	3 300	3 200	3 000	2 100	1 900	1 300	800	600	300	300	250	250	180	180		
Transect (m)	200	310	200	145	150	100	100	130	65	110	91	85	50	65	70	50	70	75	35	60	42	30	39	40	60	30	30	30		
Species 1992/1993	1/3	4/1	1/1	2/1	2/1	1/1	1/1	2/1	3/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1		
<i>Manis religiosa</i> (L., 1758)																														
<i>Plataneperla fulvata</i> (Poda, 1761)	1/1																													
<i>Leptophyes albivittata</i> (Koll., 1833)	1/3	2/3	4/6	1/1	1/1	1/3	2/1	1/1	1/1	1/1	1/1	1/1	1/1	1/3	1/1	1/2	1/1	1/1	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1		
<i>Mecanema thalassinum</i> (Deg., 1773)	2/1			1/1																										
<i>Conocephalus discolor</i> (Thbg., 1815)	1/4																													
<i>Conocephalus discolor</i> (Lair., 1804)	1/1																													
<i>Tetrigonia viridissima</i> (L., 1758)																														
<i>Decticus verrucivorus</i> (L., 1758)		1/4		1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Platycleis grisea</i> (F., 1781)	10/21		2/5																											
<i>Platycleis fessellana</i> vintaei (Charp., 1825)	1/4	2/1	1/1	1/1	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Menoptera</i> (<i>Bicolorana</i>) <i>bicolor</i> (Phil., 1830)																														
<i>Pholidoptera aptera</i> (F., 1793)			4/1																											
<i>Pholidoptera fallax</i> (Fusch., 1853)	1/3																													
<i>Pholidoptera griseoptera</i> (Deg., 1773)																														
<i>Sega pedo</i> (L., 1758)		1/1																												
<i>Tetrix mutans</i> (Hgb., 1822)	1/5	1/1	1/1	1/1	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Callipterus italicus</i> (L., 1758)	1/1			3/1	1/1	1/1	3/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Oedipoda coerulescens</i> (L., 1758)																														
<i>Eulysitra brachyptera</i> (Ocskay, 1826)																														
<i>Onocentrus</i> (<i>Dreohius</i>) <i>haemorrhoidalis</i> (Charp., 1825)	1/1	1/6	1/7					1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Onocentrus</i> (<i>Dreohius</i>) <i>petraeus</i> (Bris., 1855)		1/1																												
<i>Onocentrus ventralis</i> (Zett., 1821)	4/3																													
<i>Stenobothrus crassipes</i> (Charp., 1825)	31/21	3/7	8/10	4/2	1/16	13/7	5/3	8/18	11/7	9/25	2/7	1/2	1/2	1/6	6/1	3/8	9/7	4/4	1/3	1/5	8/2	1/1	4/1	5/5	1/1	1/1	7.5	1/1	1/1	
<i>Stenobothrus lineatus</i> (Panz., 1796)	13/15		2/1	1/4	4/4	1/1	3/2	1/3	2/1	1/5	1/5	1/3	1/3	3/3	1/1	2/8	1/2	1/5	1/2	1/1	1/1	1/1	2/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Stenobothrus nigromaculatus</i> (H.S., 1840)	1/1				1/6	3/1	1/2	12/19	2/5	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	6/3	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Chorithippus</i> (<i>Glyptobothrus</i>) <i>apricianus</i> (L., 1758)	1/11		1/9																											
<i>Chorithippus</i> (<i>Glyptobothrus</i>) <i>vagans</i> (Ex., 1848)	9/1	1/1	1/1																											
<i>Chorithippus</i> (<i>Glyptobothrus</i>) <i>mollis</i> (Charp., 1825)	1/3																													
<i>Chorithippus</i> (<i>Glyptobothrus</i>) <i>brunneus</i> (Thbg., 1815)	3/2	1/2	1/1	1/2		3/1	1/1	1/2	2/1	1/1	1/1	1/1	1/1	1/2	1/1	1/1	1/1	1/1	1/5	1/5	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
<i>Chorithippus</i> (<i>Glyptobothrus</i>) <i>biguttatus</i> (L., 1758)	2/1																													
<i>Chorithippus albomarginatus</i> (Deg., 1773)	36/12	1/1																												
<i>Chorithippus dorsatus</i> (Zett., 1821)	1/2	2/3																												
<i>Chorithippus parvulus</i> (Zett., 1821)	68/94																													
<i>Chorithippus montanus</i> (Charp., 1825)	1/3																													
<i>Euchorippus pubivittatus</i> (F. W., 1846)	5/2																													
<i>Euchorippus declivus</i> (Bris., 1848)	42/149	2/3	7/4	1/1	1/1	1/1	1/2	2/2	1/1	1/10	1/1	1/1	1/1	1/2	1/1	2/3	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	