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Response of Orthoptera species (Tettigoniidae and Acrididae) to wildfires in a Central European dry grassland

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Abstract

The effects of wildfires on the Orthoptera fauna of extensive dry grasslands were investigated at 25 random sites in a military training area in Eastern Austria. Using a space-for-time substitution, a time span of 1 to about 20 y after fire was considered. Fire-induced trajectories of habitat characteristics such as microclimate proved to have a determining effect on the occurrence of most acridids and some tettigoniids. Dispersal capacity and fire-shelter characteristics of egg deposition sites did not significantly influence postburn occurrence patterns of the investigated species. Of a total of 20 species, seven were favored by wildfires, two were adversely affected by fire and eleven did not show significant responses to postburn age. Four species, amongst them *Celes variabilis*, which is highly endangered in Central Europe, can be considered fire-dependent in the study area. Therefore, fire can have beneficial effects for the conservation of acridid grasshoppers in particular. A reconsideration of the present legal ban on the use of prescribed burning in Central Europe is recommended.

Key words

Fire ecology, burning, species composition, conservation

Introduction

Besides grazing and mowing, burning is the most important form of disturbance in grassland ecosystems. Hence there is a broad array of literature dealing with the effects of fire on grassland vegetation and fauna in general (for reviews see Collins & Wallace 1990, Daubenmire 1968, Swengel 2001, Vogl 1974, Whelan 1995), and on Orthoptera in particular (*e.g.*, Bock & Bock 1991, Chambers & Samways 1998, Evans 1984, Porter & Redak 1996).

In central Europe, legal constraints restrict research on, as well as the application of, prescribed burning, to a few exceptional cases, despite the fact that fire has played a significant role in the historical management of open landscapes (Goldammer *et al.* 1997a). Due to the cessation of traditional management regimes, some, at least partly, fire-shaped habitats, such as heathlands and dry grasslands, have severely deteriorated and many of the affected sites are targets of conservation efforts (*e.g.*, Paar *et al.* 1993). Since alternative management methods are not available or are expensive, some conservation biologists favor fire as a means of maintenance and restoration of open landscapes (Goldammer *et al.* 1997b). Thus there is a growing need for research on this topic.

However, there is a considerable lack of knowledge about the effects of fire on flora and fauna of central European ecosystems (Goldammer *et al.* 1997b). In particular, well-replicated studies are scarce because most investigations are limited to the assessment of the impact of an accidental single fire. The last review of the orthopterological literature of central Europe (Ingrisch & Köhler 1998) refers to only one study dealing with the effects of fire on some Orthoptera species (Handke 1988). A bibliography of central European research on fire ecology (Goldammer & Page 1997) contains a single further reference (Retzlaff & Robrecht 1991), and a survey of the recent orthopterological literature revealed a third paper with a focus on fire ecology of Orthoptera (Hochkirch 1997).

The present study focuses on the responses of 20 Orthoptera species to wildfires in a steppe grassland in the pannonic region of eastern Austria. By using a space-for-time substitution (Pickett 1989), a time span from 1 to about 20 y after fire was considered in order to address the following questions: 1) Do different species of Orthoptera show a different distributional pattern with regard to postburn age? 2) If so, are these patterns due to differences in egg survival and dispersal capacity or are they rather, responses to fire-induced habitat modifications? 3) Is fire detrimental or favorable to Orthoptera conservation in the study area?

Methods

Study area.—This study was conducted in the military training area "Großmittel" in eastern Austria, some 35 km south of Vienna (lat 47°53′ N, long 16°19′ E; elevation 218 to 271 m above the Adriatic sea). The expanse of the study area, which is the artillery shooting range of the training area, is 850 ha. Mean temperature of the study region is 9.4°C and annual precipitation averages 614 mm, indicating a subcontinental (pannonic) climate. During the growing season there is a considerable water deficit (Bieringer & Sauberer 2001). The shallow, dry and nutrient-poor soils originated from a limestone gravel surface deposited during the Pleistocene. Due to the flat relief and the low ground-water table there is little variation in soil type and soil texture over the whole study area. Dry grassland dominated by *Stipa* spp., *Festuca stricta* and *Bromus erectus* is the natural vegetation of this region (Sauberer & Bieringer 2001) and covers today more than 1500 ha in Großmittel. Part of it has never been ploughed and can hence be regarded as virgin steppe. The investigated area is almost free of trees and shrubs. Military training activities (artillery shooting) are the only form of land use.

Most fires are triggered by military shooting, but lightning-caused fires occur as well. Prescribed burning, however, is not performed. Thus all fires are more or less accidental. Owing to changes in the dryness of the vegetation, the fires show a bimodal distribution with peaks in early spring and late summer.

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Sampling design.—To achieve an approximately even distribution over the range from one to at least 20 years after burning, the sampling was stratified: four postburn age classes (1 - 5, 6 - 10, 11 - 15 and >15 years after burning) were considered, and out of each, at least five sites were selected randomly. This resulted in a total of 25 sampling sites, with nine for the first age class, five for the second, six for the third and five for the fourth. Each random point was assigned to a certain post-fire age by the detailed fire reports of the military garrison command. Only fires extending over at least 1.0 ha were considered. Points which were less than 100-m removed from the nearest forest edge were not included in the sample to avoid possible edge effects on the orthopteran species composition (Bieringer & Zulka in prep.). All field work was done in 1998.

Orthoptera.—A relative index of abundance was obtained by timed species counts (Sutherland 1996). This method is based on the assumption that common species are on average noted prior to rare ones. A circle of 0.1 ha (about 35 m diameter) around the marked center of each site was observed for a period of 10 min. The time at which each species was first seen was recorded. Species which were recorded within the first 1-min interval were allocated a score of 10, the second interval a score of 9 and so on. If a species was not seen but merely acoustically recorded it was scored as 1. These counts were done three times (18 July, 15/16 August and 30 August), and a mean score across all three counts calculated. Since this method has not yet been established for Orthoptera, an evaluation of its reliability was performed. The results of the timed species counts were compared with counts of singing males (Fischer *et al.* 1997) of two species with conspicuous songs and marked differences in biology, ecology and abundance. All singing males of the large, Orthoptera-predating tettigoniid *G. glabra,* and the middle sized, grass-feeding acridid *S. nigromaculatus,* were recorded for a 5-min period at each site on 26 July. These data highly correlated with the mean scores of the respective timed species counts (*G. glabra*: Kendall's $\tau = 0.67$, $p < 0.001$; *S. nigromaculatus*: $\tau = 0.65$, $p < 0.001$).

As a measure for the dispersal capacity, the ratio of wing length to body length of females was calculated (see Appendix 1). Different egg deposition site characteristics are likely to also differ in their susceptibility to fire. To indicate the shelter of eggs against fire, egg deposition sites were allocated scores from 1 to 3 according to their vertical location (soil = 1, surface = 2, vegetation = 3) (Appendix 1). Information about wing and body length and egg deposition sites were taken from Detzel (1998), Harz (1969, 1975) and Ingrisch & Köhler (1998).

Habitat variables.—On 31 March three randomly chosen soil samples were gathered at each site. At the Bundesamt und Forschungszentrum für Landwirtschaft (Federal Office and Research Centre for Agriculture, Vienna) soil water content (%), pH, total N and mineral nitrogen (NO_3 and NH_4), phosphor (P_2O_5) and potassium (K_2O) were assessed. For further analyses, mean values of the three samples were calculated.

Soil temperature sums were assessed by the polarimetric sucrose inversion technique of Pallmann *et al*. (1940). The inversion of sucrose to fructose and glucose is an exponential function of temperature (Schmitz & Volkert 1959), as are many physiological responses. Since sucrose has other polarimetric properties than fructose and glucose, the degree of inversion can be determined by a polarimeter. At each site three plastic tubes containing 20 ml of sugar solution were buried at about 5 cm depth from 28 February to 13 April. Rotation angles were measured before starting and after the end of exposure with a circular polarimeter (Atago Polax-D). The mean rotation angle differences of the three replicates were used for further analyses (see Schmitz & Volkert 1959). Higher rotation angle differences indicate higher temperature sums.

The percentage of bare ground was assessed on 26/27 June by horizontally placing a rule of 1-m length on the vegetation and counting the centimeter-units which were not covered by living plants or litter. This was done on three random points at each site. An estimation for the overall density of the vegetation was obtained by vertically placing a 0.5-m broad and 1-m high panel with a chequered pattern (each square 10 X 10 cm) in the vegetation. From a distance of 0.5 m the percentage of the area of each square which was covered by plant material was estimated. The sum of the obtained values of all squares was calculated to characterize the site.

For the measurements of plant material three squares of 20 X 20 cm were randomly placed at each site. On 1 March, litter was gathered and the vegetation clipped at these plots. Litter was dried at 40°C to weight constancy and weighed by a laboratory scale (Mettler PM 4600). A mean value was calculated from the three replicates. On 20 June the vegetation was clipped again and dried and weighed as described for the litter, to estimate primary production. On 26 June one previously unclipped random square per site of the standing crop was harvested, sorted for forbs and grasses, dried and weighed.

Snow catch was assessed as a measure of water availability after thaw. The mean value of snow depth was calculated from measurements on seven random points at each site taken on 8 December.

Within a (5 X 5 m) square, placed in the center of each site, all vascular plant species were recorded by a vegetation ecologist on 21/22 May. The coverage of each species was estimated according to the method described by Braun-Blanquet (1964).

Statistical analysis.—For all Orthoptera species weighted averages of postburn ages of the inhabited sites were calculated (Jongman *et al.* 1995). The products of the respective postburn ages and scores of timed species counts of all inhabited sites were calculated and summed. This sum was divided by the sum of the scores of timed species counts.

To obtain uncorrelated descriptors of habitat characterisitics a principal component analysis (Manly 1998) was performed using the statistical package SPSS. Since it is uncertain whether the relationships between the habitat variables are linear, all variables were rank-transformed before analysis (Bortz 1993). Only principal components with an eigenvalue above 1.0 were considered. For these a varimax rotation with Kaiser normalization was calculated (Manly 1998).

All tests for correlations were done by Kendall's coefficient of rank correlation. Despite the large number of single tests a Bonferroni-type error adjustment was not performed, since this form of error adjustment is appropriate only for relatively large samples. Due to the small sample size the power of the tests was already low. An even lower type I error rate would thus have lead to extremely high type II errors (Bortz 1993). The interpretations were based on a testwise significance level of 0.05. However, the number of significant single tests (19 out of 100) suggests that the rejection of the general H_0 is justified (Bortz *et al.* 1990).

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Table 1. Correlation analysis (Kendall's τ) of the relationship between timed species counts and postburn age as well as the four extracted principal components. Significant correlations (P < 0.05) are printed in bold (taxonomy follows Heller *et al.* 1998).

	postburn age	PC 1	PC 2	PC 3	PC 4
Tettigoniidae					
Conocephalus discolor Thunberg 1815	0.16	-0.24	-0.29	-0.04	0.04
Decticus verrucivorus (Linnaeus 1758)	-0.22	**0.36**	0.05	-0.12	-0.03
Gampsocleis glabra (Herbst 1786)	-0.18	0.21	-0.01	0.01	-0.28
Metrioptera bicolor (Philippi 1830)	0.11	-0.05	0.22	-0.08	0.01
Platycleis montana(Kollar 1833)	**-0.43**	**0.34**	-0.19	0.19	0.15
Platycleis albopunctata (Goeze 1778)	-0.10	-0.04	-0.05	**0.35**	-0.15
Platycleis vittata (Charpentier 1825)[=veyseli]	0.24	-0.29	-0.14	-0.09	-0.14
Tettigonia viridissima Linnaeus 1758	0.24	-0.26	0.16	-0.16	0.09
Gryllus campestris Linnaeus 1758	-0.20	0.20	-0.15	-0.04	0.08
Acrididae					
Calliptamus italicus (Linnaeus 1758)	**-0.43**	0.30	-0.08	**0.34**	0.05
Chorthippus mollis (Charpentier 1825)	**-0.33**	**0.35**	-0.18	-0.01	-0.06
Euthystira brachyptera (Ocskay 1826)	0.16	-0.19	0.24	0.11	-0.16
Myrmeleotettix maculatus (Thunberg 1815)	**-0.43**	**0.39**	-0.21	-0.01	0.16
Omocestus haemorrhoidalis (Charpentier 1825)	-0.25	0.26	0.20	0.01	**0.31**
Omocestus petraeus (Brisout de Barneville 1856)	**-0.37**	0.33	-0.01	0.30	-0.22
Stenobothrus crassipes (Charpentier 1825)	**0.36**	**-0.45**	-0.05	-0.13	-0.10
Stenobothrus lineatus (Panzer 1796)	**0.51**	**-0.50**	-0.04	-0.21	0.01
*Stenobothrus nigromaculatus (*Herrich-Schäffer 1840)	**-0.49**	**0.59**	-0.14	-0.09	-0.22
Celes variabilis (Pallas 1771)	**-0.47**	**0.40**	0.01	0.27	-0.16
Oedipoda caerulescens (Linnaeus 1758)	-0.28	0.26	0.11	0.01	0.26

Results

Occurrence patterns of Orthoptera species.—The species differed markedly in the mean postburn age of the inhabited sites (see Fig. 1). Weighted averages showed a sequence from 1.53 y (*O. petraeus*) up to 13.5 y (*S. crassipes*). Four species were entirely restricted to sites with a postburn age of 5 y at most (*O. petraeus*, *C. variabilis*, *M. maculatus* and *C. italicus*). One species (*S. crassipes*) was not recorded from sites between the first and the third year after fire. Three species were recorded in all sites (*M. bicolor*, *G. campestris*, *C. mollis*), and five species were found only once (*C. discolor*, *P. vittata*, *T. viridissima*, *E. brachyptera*, *O. caerulescens*).

The abundances of seven species were negatively correlated with postburn age, two species correlated positively and 11 species, including those that were recorded only once, showed no significant correlations (Table 1).

PCA of habitat variables.—The PCA of the habitat variables revealed four principal components with an eigenvalue higher than 1.0 (see Table 2). PC 1 can be interpreted as an axis of openness and warmth. This axis is a composite of the following habitat variables: amount of litter, percentage of bare ground, soil temperature sums, snow catch, primary production and species richness of grasses and forbs. PC 1 is significantly correlated with postburn age (τ = -0.670, $p < 0.001$). PC 2 represents the variables soil moisture, soil nutrient content and vegetation density and can be characterized as a moisture-nutrient-axis. It is not correlated with postburn age (τ = -0.098, p = 0.515). PC 3 is an indicator of forb to grass ratio since it is positively correlated with biomass and coverage of forbs and negatively correlated with the respective parameters of grasses. It shows no correlation with postburn age (τ = 0.181, p = 0.230). PC 4 reflects mineral nitrogen content and pH of the soil and can therefore be considered a soil chemistry axis. It is also not correlated with postburn age (τ = -0.023, p = 0.881).

Determination of species occurrence patterns.—Correlation analysis between the abundances of the Orthoptera species and the four extracted principal components (Table 1) suggested a high influence of the openness-warmth axis (PC 1). Six species are positively correlated with the first principal component, two negatively. This means that most species which showed clear responses to postburn age are also significantly correlated with PC 1 as well. For *C. italicus* and *O. petraeus,* error probabilities exceed 0.05 and are therefore considered not significant in Table 1, but are below 0.1 in both cases. Two species showed significant correlations with forb to grass ratio (PC 3), one with soil chemistry (PC 4) and none with the moisture-nutrient axis (PC 2) (Table 1).

Mean postburn age of inhabited sites correlated neither with the wing length to body length ratio of females (τ = -0.166, p = 0.475) nor with the score of egg deposition sites (τ= -0.039, p = 0.831) of respective species.

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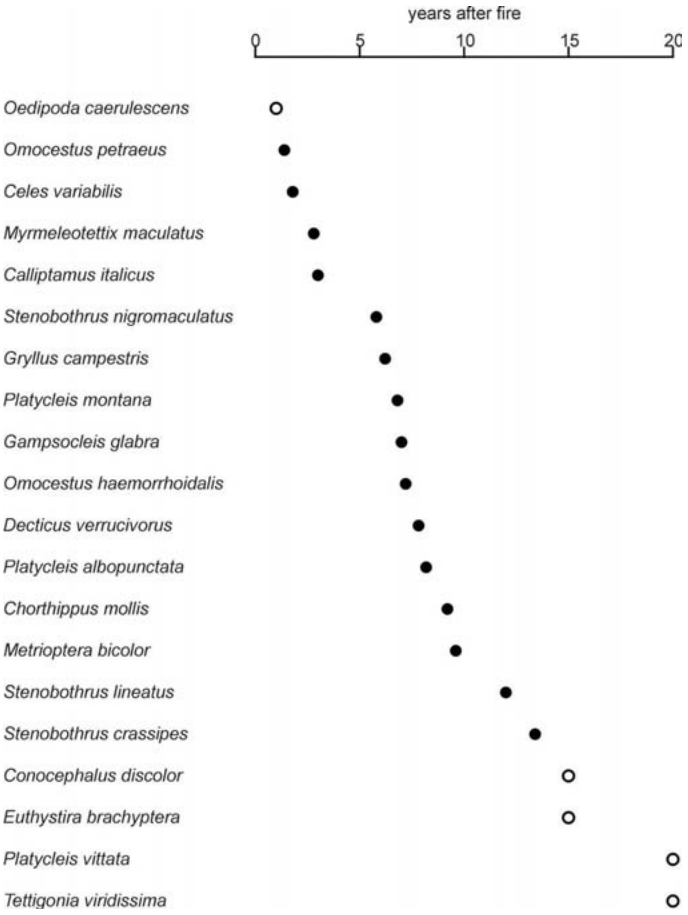


Fig. 1. Weighted averages of postburn age of the sites inhabited by the respective species. Open circles indicate species that were recorded only once.

Discussion

Fire can influence orthopteran species composition in two main ways. First, fire directly damages eggs, nymphs and adults. The species composition following fire is therefore dependent on the species' ability to survive fire or to recolonize burnt sites. Some studies suggest that species which place their eggs in the soil have an advantage over surface or vegetation breeders since their eggs are better protected from heat and suffer lower mortality rates (Handke 1988, Hochkirch 1997). Species with high dispersal capacity also seem to be favored and often dominate the first one or two seasons after a fire (Retzlaff & Robrecht 1991). Despite these strong effects the original species composition mostly recovers within a few years (*e.g.*, Porter & Redak 1996). Second, fire alters habitat conditions and thus indirectly favors species with certain habitat requirements. Bock & Bock (1991) reported a higher abundance of species preferring bare ground and herbaceous food in the first year post-fire, and Evans (1984) found that the relative abundance of grass feeders increased after fire, since fire led to a higher proportion of grasses in his study area. Chambers & Samways (1998) concluded that grasshopper species composition after fire depends on the trajectory of plant succession.

As could therefore be expected, fire proved to have a significant effect on most species considered in the present study. Out of 15 more regularly recorded species, abundances of nine are either positively or negatively correlated with postburn age. The majority of Orthoptera species have their main occurrence in sites younger than 10 y post-burn. Four species can actually be considered fire-dependent under the special circumstances of the study area since they are restricted to the youngest post-burn stages. One species was not recorded from sites younger than 4 y post-burn and hence may be detrimentally affected by fire. However, fire obviously does not evenly influence species belonging to different taxonomical groups. Of the nine species the abundances of which were significantly correlated with postburn age, eight are acridids, while five of the six regularly occurring species which showed no clear response to fire are tettigoniids. Thus acridids seem more directly affected by fires in the study area than tettigoniids. The occurrence patterns of most tettigoniids cannot be assigned to fire effects.

Fire-triggered habitat modifications seem to be of overriding importance for the determination of the postburn Orthoptera fauna. The highly fire-correlated openness-warmth axis (PC 1) was a significant indicator of the occurrence patterns of eight species. Six species prefered an open, species-rich vegetation and high temperatures, while two species prefered the relatively cooler microclimate and the higher amount of litter at sites that remained unburnt for many years. Due to their high intercorrelation, the effects of the habitat variables summarized in PC 1 cannot be separated.

However, the different response of acridids and tettigoniids suggests that temperature is likely to be a key factor. While tettigoniid development is buffered against temperature influences by its complex regulation (Ingrisch 1986a, b, c; Helfert 1980), embryonic

Table 2. Eigenvalues of the principal components and factor scores of the 18 habitat variables considered. The highest factor score of each variable is printed in bold.

	principal components			
	PC 1	PC 2	PC 3	PC 4
habitat variables				
bare ground	**0.88**	-0.18	-0.12	0.17
litter	**-0.86**	0.29	-0.09	0.06
soil temperature sum	**0.81**	-0.13	0.27	-0.00
primary production	**0.72**	-0.07	-0.02	0.07
snow catch	**-0.71**	-0.13	0.03	-0.09
number of grass species	**0.69**	-0.14	-0.03	-0.18
number of forb species	**0.61**	-0.02	0.30	-0.22
soil water content	-0.20	**0.80**	-0.00	-0.04
total nitrogen	-0.31	**0.70**	-0.18	0.28
phosphor	-0.10	**-0.67**	0.05	0.22
vegetation density	-0.36	**0.66**	-0.18	0.02
potassium	0.48	**0.62**	0.23	-0.08
phytomass grasses	-0.08	0.12	**-0.87**	-0.13
coverage of forbs	0.03	-0.09	**0.62**	0.08
coverage of grasses	0.45	-0.31	**-0.58**	0.30
phytomass forbs	0.49	-0.04	**0.50**	-0.06
mineral nitrogen	-0.25	0.09	0.04	**0.88**
pH	0.33	-0.26	0.13	**0.75**
eigenvalue	5.14	2.76	02.06	1.72

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as well as postembryonic development of acridids is much more directly influenced by temperature (Cherrill & Begon 1989, Willott & Hassall 1998, van Wingerden *et al.* 1991).

Only three species were significantly influenced by habitat characteristics not related to postburn age (PC 2, PC 3 and PC 4). *P. albopunctata* and *C. italicus*, which showed positive correlations with PC 3, are mixed feeders (Ingrisch & Köhler 1998) and may therefore be favored by a higher proportion of forbs. The correlation of *O. haemorrhoidalis* with the soil chemistry axis (PC 4) cannot readily be interpreted.

In the present study no influence of dispersal capacity and egg deposition site characteristics could be found. However, it is unlikely that these parameters have no influence on species occurrence patterns. Maybe the temporary resolution of the sampling design was not fine enough to detect such effects. In a long-term examination these factors seem to be outweighed by other parameters determining the species composition.

Conservation implications.—Overall, fire appears to play an important positive role influencing species occurrence in the study area. Seven species were favored by wildfires while two were adversely affected by fire. Moreover, the existence of four species in the study area depended on the availability of recently burnt sites, while only one species was absent from the youngest postburn stages. Among the fire-dependent species, *C. variabilis* deserves special consideration. In the study area this steppe species reaches the northwestern range of its distribution. In Central Europe *C. variabilis* has become extinct at most of its formerly reported sites of occurrence (Berg & Bieringer 1998, Kocarek *et al.* 1999, Liana 1992, Matvejev 1992). The suggestion by Retzlaff & Robrecht (1991), that on burnt sites rare or endangered species are absent, can thus not be supported by this study. On the contrary, fire may improve habitat conditions for some thermophilous species which reach the border of their range in Central Europe (see also Clausnitzer 1994). Under special circumstances, fire can be a valuable instrument of Orthoptera conservation. Therefore, a reconsideration of the present general ban on the use of fire in research and nature conservation is recommended. However, since fire is apparently detrimental to some species, the undifferentiated use of prescribed burning must be avoided. A scientific assessment on a case-by-case basis seems advisable.

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Appendix 1. Wing-length to body-length ratio (calculated from measurements by Harz 1969, 1975) and egg deposition sites (taken from Detzel 1998 and Ingrisch & Köhler 1998) of all species recorded in the present study.

	wing-length/body-length	egg deposition site
Tettigoniidae		
Conocephalus discolor	1.02	vegetation
Decticus verrucivorus	0.88	soil
Gampsocleis glabra	0.98	soil
Metrioptera bicolor	0.34	vegetation
Platycleis montana	0.92	soil surface
Platycleis albopunctata	1.16	soil surface
Platycleis vittata	0.46	soil surface
Tettigonia viridissima	1.49	soil
Gryllus campestris	0.63	soil
Acrididae		
Calliptamus italicus	0.53	soil surface
Chorthippus mollis	0.73	soil
Euthystira brachyptera	0.18	vegetation
Myrmeleotettix maculatus	0.80	soil surface
Omocestus haemorrhoidalis	0.69	soil surface
Omocestus petraeus	0.77	soil surface
Stenobothrus crassipes	0.23	soil surface
Stenobothrus lineatus	0.67	soil surface
Stenobothrus nigromaculatus	0.62	vegetation
Celes variabilis	0.80	soil surface
Oedipoda caerulescens	1.06	vegetation

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