

## Molehills as important larval habitats for the grizzled skipper, *Pyrgus malvae* (Lepidoptera: HesperIIDae), in calcareous grasslands

MERLE STREITBERGER and THOMAS FARTMANN

Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Robert-Koch-Straße 28, 48149 Münster, Germany; e-mails: m\_stre05@uni-muenster.de; fartmann@uni-muenster.de

**Key words.** Lepidoptera, HesperIIDae, *Pyrgus malvae*, butterfly, disturbance, ecosystem engineer, molehill, *Agrimonia eupatoria*, habitat requirement, larval ecology, microclimate, oviposition site selection, calcareous grassland, vegetation structure

**Abstract.** Small-scale soil disturbance, such as animal mounds created by subterranean ecosystem engineers are important microhabitats for species of conservation concern. There are many studies on the effects of ecosystem engineers on plant species diversity and soil properties, but the influence of such organisms on other taxa, such as insects, are rarely analyzed. In this paper, we demonstrate for the first time the role of molehills produced by the European Mole (*Talpa europaea*) (Linnaeus, 1758) as a larval habitat for a threatened butterfly species within central European calcareous grasslands. We selected the grizzled skipper (*Pyrgus malvae*) (Linnaeus, 1758) as a study species as previous studies revealed that it prefers warm and open microhabitats for oviposition. Our study clearly showed that host plants occurring on or in the close vicinity of molehills were regularly occupied by immature stages of *P. malvae*. Occupied host plants at these disturbed sites were characterized by a more open vegetation structure with a higher proportion of bare ground or stones and a lower cover of the herb layer compared with available host plants (control samples). Among molehills those were preferred that had the highest cover of host plants, especially *Agrimonia eupatoria*. Molehills are important larval habitats for *P. malvae* in calcareous grasslands on deeper soils. At these sites succession occurs rapidly and the amount of bare ground is usually low, even when they are managed. In contrast to other known breeding sites in calcareous grasslands, molehills with a high cover of host plants provide ideal conditions for the successful larval development of *P. malvae*: (i) sufficient food during the larval period and (ii) warm microclimatic conditions.

### INTRODUCTION

Disturbance is an important determinant of biodiversity (White & Jentsch, 2004). According to Pickett & White (1985) disturbance affects local species and population structure by altering the physical environment. Such disruptive events are either natural or man-made and the disturbance regime within an ecosystem is influenced by the frequency, intensity and spatial extent of such events (Walker, 2012).

In heavily industrialized countries human activities may have severe effects on the extent of natural disturbances (cf. Walker, 2011). In extreme cases a modification of the disturbance regime can lead to the loss of natural habitats and species diversity, as it has, for example, occurred on most central European floodplains due to human flood control (Tockner & Stanford, 2002). In contrast, nature conservation mimic natural disturbances or use traditional forms of land use to conserve a wide range of different habitats and species (Jentsch, 2007). For example, local mechanical soil disturbance is used in degraded open habitats in Europe to promote low-competitive plant species (Jacquemart et al., 2003; Tschöpe & Tielbörger, 2010; Ödman et al., 2012; Fleischer et al., 2013). However, such sites not only support plant species richness. Due to the warm microclimatic conditions at locally disturbed sites with sparse vegetation and bare ground, they also provide microhabitats for many threatened insect species, especially for the development of their larvae

(e.g. Gröning et al., 2007; Warren & Büttner, 2008; Salz & Fartmann, 2009; Wunsch et al., 2012).

Nonetheless, small-scale soil disturbance with altered soil conditions and a reduction of plant biomass may also be created naturally by mound building ecosystem engineers. In general, ecosystem engineers are defined as organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials (Jones et al., 1994). Classic examples of mound building engineering species are subterranean herbivores or insectivores, such as pocket gophers or moles (Canals & Sebastià, 2000; Reichman, 2007; Seifan et al., 2010). The effects of ecosystem engineers have been extensively studied in natural or semi-natural grasslands, especially in terms of plant species diversity and soil properties (e.g. King, 1977; Zhang et al., 2003; Zaitlin & Hayashi, 2012; Sasaki & Yoshihara, 2013). In contrast, the influence of engineering organisms on other taxa, such as insects, is rarely analyzed. There are a few studies that show that mounds of burrowing rodent species have an effect on insect community structure and promote species diversity (Davidson & Lightfoot, 2007; Yoshihara et al., 2010). However, there are no detailed studies on the significance of animal mounds as important larval habitats for insects.

The objective of this study is to determine the importance of small-scale disturbances caused by the European Mole (*Talpa europaea*) (Linnaeus, 1758) (Insectivora: Talpidae) for the threatened butterfly *Pyrgus malvae* (Linnaeus, 1758) (Lepidoptera: HesperIIDae) in central

European calcareous grasslands. As *P. malvae* prefers warm and open microhabitats for oviposition (Krämer et al., 2012) we assume that molehills are important larval habitats for this species. In general, the requirements of the immature stages of butterfly species exceed those of the adult stages (Thomas, 1991). Therefore, autecological knowledge of the pre-adult stages of butterfly species is essential for their conservation (García-Barros & Fartmann, 2009).

## MATERIAL AND METHODS

### Study organism

The grizzled skipper *P. malvae* (Linnaeus, 1758) (Lepidoptera: HesperIIDae) has a Palearctic distribution ranging from the British Isles to Korea, and from the Mediterranean region to middle Finland (65°N) (Ebert & Rennwald, 1991). In the northern half of Germany, *P. malvae* is relatively rare. In North Rhine-Westphalia it is listed as endangered (Settele et al., 1999), in Hesse (Settele et al., 1999) and the whole of Germany it is considered as near threatened (Reinhardt & Bolz, 2011). In our study area, the Diemel Valley, *P. malvae* is a univoltine species that hibernates as a pupa and adults are on the wing between the end of April and end of June (Fartmann, 2004). In general, *P. malvae* colonizes a wide range of different open habitats, such as woodland fringes, clear-cuts or different types of grassland (Wagner, 2006). A key resource of its habitats is an open vegetation structure with a certain cover of bare ground (Ebert & Rennwald, 1991; Krämer et al., 2012). In the Diemel Valley semi-dry calcareous grasslands represent the most important habitat of *P. malvae* (Fartmann, 2004). Different species of *Rosaceae* serve as host plants for larvae of *P. malvae*. In the Diemel Valley *Agrimonia eupatoria* and *Potentilla tabernaemontani* are the main host plants (Krämer et al., 2012).

### Study area

The Diemel Valley is located in central Germany, at the border of North Rhine-Westphalia and Hesse (51°22'N/8°38'E and 51°38'N/9°25'E). The region is characterized by a sub-oceanic climate (Müller-Wille, 1981). The majority of the area consists of limestone and calcareous grasslands are widespread (Fartmann, 2004). The Diemel Valley represents the region with the greatest area of calcareous grasslands in the northern half of Germany (Fartmann, 2006). A high percentage (approx. 55%) of the calcareous grasslands within the study area is still actively managed, mainly by traditional rough sheep grazing (Fartmann, 2004). Next to *T. europaea*, *Lasius flavus* (Fabricius, 1782) (Hymenoptera: Formicidae) is a further mound building ecosystem engineer occurring frequently within the calcareous grasslands (own observation).

A detailed description of the study area is given by Fartmann (2004).

### Sampling design

Sampling was carried out from 21st to 25th June 2011, involved 24 person-days, on nine calcareous grassland patches (mean value  $\pm$  SD = 1053  $\pm$  1318 m<sup>2</sup>; median = 770 m<sup>2</sup>, MIN = 180 m<sup>2</sup>; MAX = 4500 m<sup>2</sup>) where molehills and *P. malvae* were abundant. All patches were situated at the foot of slopes or on the tops of hills as only there was the soil deep enough for moles. To avoid confusion with eggs of *Pyrgus serratulae*, only those patches where this sibling species was absent were selected. In every patch we systematically searched for molehills featuring at least one potential host plant either directly on the molehill or within a 10 cm wide zone around the hill by pacing out each patch in sinuous lines with an interval of 2.5 m

between each line. Potential host plants growing in the patches included *Agrimonia eupatoria*, *Fragaria viridis*, *Potentilla erecta*, *P. tabernaemontani* and *P. sterilis* (Fartmann, 2004; own observation). Every individual potential host plant occurring on or close to (10 cm wide zone) a molehill was then searched for immature stages of *P. malvae* (egg, egg shell or caterpillar). If pre-adult stages of *P. malvae* were detected on a host plant occurring on or in close vicinity of a molehill (within a 10 cm wide zone around the hill) ( $N = 83$ ), vegetation structure and microclimatic conditions (see below) were ascertained within a radius of 20 cm around the occupied plant, which hereafter is referred to as an "occupied molehill". Additionally, each patch was covered by a 10  $\times$  10 m grid. Samples of unoccupied molehills ("unoccupied molehill",  $N = 62$ ) were systematically selected by searching from the centre of the grid for the next molehill with a potential host plant, either directly on the molehill or in the 10 cm circle around the hill, on which there were no immature stages of *P. malvae*. In order to document the complete range of available host plants, 85 control samples were systematically recorded for every host plant that was closest to the centre of the 10  $\times$  10 m grid. Here, sampling took place according to the method described above.

The following vegetation structure parameters were estimated for every sample: cover of herb, cryptogam and litter layer, cover of bare ground and stony surface, as well as the total and single cover of potential host plant species. Furthermore, the vegetation height was measured and the aspect, inclination and geographical coordinates were recorded in order to calculate the heat load index according to McCune & Keon (2002).

### Statistical analysis

Differences between the parameters were tested using generalized linear mixed models (GLMMs: lmer, Bates et al., 2008). Proportional binomial GLMMs were applied in cases of cover data. For other data (vegetation height and heat load index) we used Gaussian (vegetation height) and Poisson (heat load index) models.

Two binomial GLMMs were applied to ascertain which vegetation structure parameters determine the use of a molehill as a larval habitat by *P. malvae* (model a, occupied and unoccupied molehills as the dependent variable) and which vegetation structure parameters possess the highest explanatory power for the occurrence of *P. malvae* on molehills in general (model b, occupied molehills and control samples as the dependent variable).

Prior to the regression analyses, two principal component analyses (PCA) were carried out in order to merge strongly inter-correlated variables (correlations with Spearman rank correlations [ $r_s$ ] values  $>|0.7|$ ) into one component. In both cases cover of herb layer and bare ground were summarized into one component (hereafter called 'vegetation structure'), which was incorporated into the models as an independent variable. The two components were positively correlated with the cover of the herb layer (model a:  $r_s = 0.95$ ,  $P < 0.001$ ; model b:  $r_s = 0.97$ ,  $P < 0.001$ ) and negatively with the cover of bare ground (model a:  $r_s = -0.96$ ,  $P < 0.001$ ; model b:  $r_s = -0.83$ ,  $P < 0.001$ ). The eigenvalue of the component of model a was 1.9 and explained 97.9% of the variance in the data set, the eigenvalue of the component used for model b was 1.8 and explained 90.5% of the variance in the data set.

The selection of the final GLMMs was based on backward selection using likelihood ratio tests with a significance level of  $\alpha = 0.05$ .

In all GLMMs *patch* served as the random factor. Analyses were carried out using R.15.0.

TABLE 1. Mean values  $\pm$  SD of all the parameters of occupied ( $N = 83$ ) and unoccupied molehills ( $N = 62$ ) and control samples ( $N = 85$ ). Comparison between groups was done using GLMMs with *patch* as a random factor. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , n.s. not significant.

Parameter	Occupied molehills ( $N = 83$ )	Unoccupied molehills ( $N = 62$ )	$P$	Control samples ( $N = 85$ )	$P^a$
Host plant cover (%)					
<i>Agrimonia eupatoria</i>	7.4 $\pm$ 8.7	2.5 $\pm$ 3.1	**	5.4 $\pm$ 6.7	n.s.
All host plants	8.7 $\pm$ 8.5	3.7 $\pm$ 3.2	**	8.8 $\pm$ 6.1	n.s.
Vegetation structure					
Cover of different layers (%)					
Herb layer	54.6 $\pm$ 30.2	46.6 $\pm$ 36.2	n.s.	73.1 $\pm$ 19.7	*
Cryptogams	3.2 $\pm$ 6.8	3.0 $\pm$ 8.4	n.s.	14.9 $\pm$ 15.7	*
Litter	6.0 $\pm$ 6.6	5.0 $\pm$ 4.1	n.s.	11.2 $\pm$ 7.2	n.s.
Bare ground	39.6 $\pm$ 32.7	49.6 $\pm$ 38.4	n.s.	8.4 $\pm$ 6.0	***
Stony surface	1.3 $\pm$ 2.5	2.0 $\pm$ 2.7	n.s.	0.1 $\pm$ 0.4	n.s.
Vegetation height (cm)	5.6 $\pm$ 3.7	4.6 $\pm$ 2.7	n.s.	5.8 $\pm$ 3.6	n.s.
Climate					
Heat load index	0.8 $\pm$ 0.1	0.8 $\pm$ 0.1	n.s.	0.8 $\pm$ 0.1	n.s.

<sup>a</sup> Occupied molehills and control samples were tested against each other.

## RESULTS

Immature stages of *P. malvae* were found on 83 of the 1073 molehills with potential host plants, which is an occupancy of 7.7%. *A. eupatoria* was the most frequent host plant (85.4% of the cases) with the other host plants far less frequently used (*F. viridis* 11%; *P. tabernaemontani* 2.4%; *P. erecta* 1.2%).

Vegetation structure and microclimate (heat load index) of occupied and unoccupied molehills did not differ (Table 1). In contrast, the cover of host plants was significantly greater at occupied than unoccupied molehills.

The vegetation structure on occupied molehills differed greatly from that of the control samples (Table 1). Occupied molehills were significantly more open having a

lower cover of herbs and cryptogams, and higher cover of bare ground.

The likelihood of a molehill being accepted as a larval habitat (occupied vs. unoccupied molehills) increased only with the cover of host plants (Table 2a). In contrast, occupied molehills differed in their vegetation structure from that of control samples (Table 2b): The likelihood of a site being selected as a larval habitat was positively correlated with the cover of stony surface and negatively with vegetation structure, and cover of cryptogams and litter (Table 2b). The negative correlation with the variable “vegetation structure” implies that microhabitats with a low cover of the herb layer and high cover of bare ground were preferred.

TABLE 2. Statistics of GLMM: (a) binomial, prediction of the use of a molehill as a larval habitat of *P. malvae* ( $N = 83$  occupied molehills vs.  $N = 62$  unoccupied molehills). (b) binomial prediction of larval habitat preferences of *P. malvae* ( $N = 83$  occupied molehills vs.  $N = 85$  control samples). Strongly inter-correlated parameters (cover of herb layer and bare ground) were summarized by a PCA into one component (“vegetation structure”), which was used as an independent variable in both models. The following variables entered into the analysis were not significant: (a) vegetation height, cover of cryptogams, litter, stony surface, vegetation structure, (b) vegetation height, cover of host plants. Non-significant predictors were excluded from the models by stepwise backward-selection ( $P > 0.05$ ). \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Variance of the random intercept: (a) 0.12639, (b) 0.56498.

Variable	Estimate	SE	Z	P
(a)				
Total host plant cover	0.27616	0.06241	4.425	***
Pseudo $R^2$ [Nagelkerkes] <sup>a</sup> = 0.17				
(b)				
Cover of cryptogams	-0.12048	0.02752	-4.378	***
Cover of litter	-0.11116	0.04000	-2.779	**
Cover of stony surface	1.26494	0.39076	3.237	**
Vegetation structure	-1.45967	0.54735	-2.667	***
Pseudo $R^2$ [Nagelkerkes] <sup>a</sup> = 0.43				

<sup>a</sup> Random term included in null model.



Fig. 1. Characteristic molehill with *Agrimonia eupatoria* used for oviposition by *P. malvae* in a semi-dry calcareous grassland.

## DISCUSSION

This study clearly showed that host plants on molehills were regularly occupied by immature stages of *P. malvae*. Occupied molehills were characterized by a more open vegetation structure with a higher proportion of bare or stony ground and a lower cover of the herb layer compared with that at control sites. Among molehills those that were preferred had the highest cover of host plants, especially *A. eupatoria* (Fig. 1).

It is very likely that molehills are preferred as breeding sites by *P. malvae* as they offer suitable microclimatic conditions for larval development. Generally, larval development is enhanced by a warm microclimate (Weiss et al., 1988; Roy & Thomas, 2003). In fact, higher soil temperatures were measured within pocket gopher (*Geomys pinetis*) mounds than in the surrounding vegetation (Simkin & Michener, 2004) and these disturbed microsites are similar to the mounds formed by *Talpa europaea*. Besides a reduced vegetation cover, the slopes of the mounds are more exposed to solar radiation and mound soil is better drained, which are thought to account for the higher temperatures within the mounds (Simkin & Michener, 2004). In addition, the dark colour of the bare soil might also increase heat absorption and warming of these microsites (cf. Stoutjesdijk & Barkman, 1992).

Besides a favourable microclimate, a sufficient amount of food plays a crucial role in the selection of an oviposition site by butterflies (Fartmann & Hermann, 2006; García-Barros & Fartmann, 2009). For some species it is documented that females preferentially oviposit on large and luxuriant growing host plants (Porter, 1992; Ellis, 2003; Küer & Fartmann, 2005). Partly, this seems to be also true for *P. malvae*. According to Krämer et al. (2012) the selection of an oviposition site by *P. malvae* in central European calcareous grasslands reflects a trade-off between a suitable microclimate and the availability of sufficient food for the caterpillars. They observed that

warm microclimatic conditions were especially associated with small-growing *P. tabernaemontani* plants occurring on shallow soils with a high proportion of bare ground and short turf. However, the risk of these host plants desiccating and, hence, the danger of offspring loss was high. In contrast, the second most important host plant, *A. eupatoria*, grew in less extreme conditions and is a larger plant. The oviposition sites on molehills in our study combined both essential requirements for the successful larval development of *P. malvae*. Of all the molehills searched those with pre-adult stages of *P. malvae* had the highest host plant cover. Besides a sufficient amount of food, which may also be provided by other plants of *A. eupatoria* in the surrounding vegetation, molehills offer warm microclimatic conditions but with a low risk of desiccation of the host plant due to the deep soils.

In conclusion, molehills are important larval habitats for *P. malvae* in calcareous grasslands on deep soils. At these sites succession is rapid and there is little bare ground, even when they are managed (Ellenberg & Leuschner, 2010). In contrast to the other known breeding sites in calcareous grasslands (cf. Krämer et al., 2012), molehills with a high cover of host plants, especially *A. eupatoria*, have the essential requirements for the successful larval development of *P. malvae*: (i) sufficient food during the larval period and (ii) warm microclimatic conditions.

**ACKNOWLEDGEMENTS.** We are very grateful to J. Böhmi-chen, L. Holtmann, C. Höppner and N. Raude for support during field work. Moreover, we would like to thank G. Hermann for valuable comments on an earlier version of the manuscript.

## REFERENCES

- BATES D., MAECHLER M. & DAI B. 2008: *lme4: Linear Mixed Effects Models Using S4 Classes. R Package Version 0.999375-28*. Available from: <http://lme4.r-forge.r-project.org/>.

- CANALS R.-M. & SEBASTIÀ M.-T. 2000: Soil nutrient fluxes and vegetation changes on molehills. — *J. Veg. Sci.* **11**: 23–30.
- DAVIDSON A.D. & LIGHTFOOD D.C. 2007: Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. — *Ecography* **30**: 515–525.
- EBERT G. & RENNWALD E. 1991: *Die Schmetterlinge Baden-Württembergs. Band 1, Tagfalter I.* Eugen Ulmer, Stuttgart, 552 pp.
- ELLENBERG H. & LEUSCHNER C. 2010: *Vegetation Mitteleuropas mit den Alpen. 6th ed.* Eugen Ulmer, Stuttgart, 1357 pp.
- ELLIS S. 2003: Habitat quality and management for the northern brown argus butterfly *Aricia artaxerxes* (Lepidoptera: Lycaenidae) in North East England. — *Biol. Conserv.* **113**: 285–294.
- FARTMANN T. 2004: Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales. Biozöologie von Tagfaltern und Widderchen in einer alten Hudelandchaft. — *Abh. Westf. Mus. Naturk.* **66**: 1–256.
- FARTMANN T. 2006: Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. — *Ann. Zool. Fenn.* **43**: 335–347.
- FARTMANN T. & HERMANN G. 2006: Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa – von den Anfängen bis heute. In Fartmann T. & Hermann G. (eds): Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. — *Abh. Westf. Mus. Naturk.* **68**: 11–57.
- FLEISCHER K., STREITBERGER M. & FARTMANN T. 2013: The importance of disturbance for the conservation of a low-competitive herb in mesotrophic grasslands. — *Biologia* **68**: 398–403.
- GARCÍA-BARROS E. & FARTMANN T. 2009: Butterfly oviposition: sites, behaviour and modes. In Settele J., Shreeve T.G., Konvicka M. & van Dyck H. (eds): *Ecology of Butterflies in Europe*. Cambridge University Press, Cambridge, pp. 29–42.
- GRÖNING J., KRAUSE S. & HOCHKIRSCH A. 2007: Habitat preferences of an endangered insect species, Cepero's groundhopper (*Tetrix ceperoi*). — *Ecol. Res.* **22**: 767–773.
- JACQUEMART A.-L., CHAMPLUVIER D. & DE SLOOVER J. 2003: A test of mowing and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. — *Wetlands* **23**: 376–385.
- JENTSCH A. 2007: The challenge to restore processes in face of nonlinear dynamics – on the crucial role of disturbance regimes. — *Restor. Ecol.* **15**: 334–339.
- JONES C.G., LAWTON J.H. & SHACHAK M. 1994: Organisms as ecosystem engineers. — *Oikos* **69**: 373–386.
- KING T.J. 1977: The plant ecology of ant-hills in calcareous grasslands. I Patterns of species in relation to ant-hills in southern England. — *J. Ecol.* **65**: 235–256.
- KRÄMER B., KÄMPF I., ENDERLE J., PONIATOWSKI D. & FARTMANN T. 2012: Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. — *J. Insect Conserv.* **16**: 857–865.
- KÜER A. & FARTMANN T. 2005: Prominent shoots are preferred: microhabitat preferences of *Maculinea alcon* ([Denis & Schiffermüller], 1775) in Northern Germany. — *Nota Lepid.* **27**: 309–319.
- MCCUNE B. & KEON D. 2002: Equations for potential annual direct incident radiation and heat load. — *J. Veg. Sci.* **13**: 603–606.
- MÜLLER-WILLE W. 1981: *Westfalen. Landschaftliche Ordnung und Bindung eines Landes. 2. Auflage.* Aschendorffsche Verlagsbuchhandlung, Münster, 411 pp.
- ÖDMAN A.M., SCHNOOR T.K., RIPA J. & OLSSON P.A. 2012: Soil disturbance as a restoration measure in dry sandy grasslands. — *Biodivers. Conserv.* **21**: 1921–1935.
- PICKETT S.T.A. & WHITE P.S. 1985: *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, 472 pp.
- PORTER K. 1992: Eggs and egg-laying. In Dennis R.L.H. (ed.): *The Ecology of Butterflies in Britain*. Oxford University Press, Oxford, pp. 46–72.
- REICHMAN O.J. 2007: The influence of pocket gophers on the biotic and abiotic environment. In Begall S., Burda H. & Schleich C.E. (eds): *Subterranean Rodents. News from Underground*. Springer, Berlin, Heidelberg, pp. 271–286.
- REINHARDT R. & BOLZ R. 2011: Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands. — *Natursch. Biol. Vielfalt.* **70**: 167–194.
- ROY D.B. & THOMAS J.A. 2003: Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. — *Oecologia* **134**: 439–444.
- SALZ A. & FARTMANN T. 2009: Coastal dunes as important strongholds for the survival of the rare Niobe fritillary (*Argynnis niobe*). — *J. Insect Conserv.* **13**: 643–654.
- SASAKI T. & YOSHIHARA Y. 2013: Local-scale disturbance by Siberian marmots has little influence on regional plant richness in a Mongolian grassland. — *Plant Ecol.* **214**: 29–34.
- SEIFAN M., TIELBÖRGER K., SCHLOZ-MURER D. & SEIFAN T. 2010: Contribution of molehill disturbances to grassland community composition along a productivity gradient. — *Acta Oecol.* **36**: 569–577.
- SETTELE J., FELDMANN R. & REINHARDT R. (eds) 1999: *Die Tagfalter Deutschlands*. Eugen Ulmer, Stuttgart, 452 pp.
- SIMKIN S.M. & MICHENER W.K. 2004: Mound microclimate, nutrients and seedling survival. — *Am. Midl. Nat.* **152**: 12–24.
- STOUTJESDIJK P. & BARKMAN J.J. 1992: *Microclimate Vegetation and Fauna*. Opulus Press, Uppsala, 216 pp.
- THOMAS J.A. 1991: Rare species conservation: case studies of European butterflies. In Spellerberg I.F., Goldsmith F.B. & Morris M.G. (eds): *The Scientific Management of Temperate Communities for Conservation*. Blackwell Scientific, Oxford, pp. 149–197.
- TOCKNER K. & STANFORD J.A. 2002: Riverine flood plains: present state and future trends. — *Environ. Conserv.* **29**: 308–330.
- TSCHÖPE O. & TIELBÖRGER K. 2010: The role of successional stage and small-scale disturbance for establishment of pioneer grass *Corynephorus canescens*. — *Appl. Veg. Sci.* **13**: 326–335.
- WAGNER W. 2006: Die Gattung *Pyrgus* in Mitteleuropa und ihre Ökologie – Larvalhabitate, Nährpflanzen und Entwicklungszyklen. In Fartmann T. & Hermann G. (eds): Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa. — *Abh. Westf. Mus. Naturk.* **68**: 83–122.
- WALKER L.R. 2011: Integration of the study of natural and anthropogenic disturbances using severity gradients. — *Austral Ecol.* **36**: 916–922.
- WALKER L.R. 2012: *The Biology of Disturbed Habitats*. Oxford University Press, Oxford, 319 pp.
- WARREN S.D. & BÜTTNER R. 2008: Active military training areas as refugia for disturbance-dependent endangered insects. — *J. Insect Conserv.* **12**: 671–676.
- WEISS S.B., MURPHY D.D. & WHITE R.R. 1988: Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. — *Ecology* **69**: 1486–1496.

- WHITE P.S. & JENTSCH A. 2004: Disturbance, succession and community assembly in terrestrial plant communities. In Temperton V.M., Hobbs R.J., Nuttle T. & Halle S. (eds): *Assembly Rules in Restoration Ecology – Bridging the Gap between Theory and Practice*. Island Press, Washington, D.C., pp. 341–366.
- WÜNSCH Y., SCHIRMEL J. & FARTMANN T. 2012: Conservation management of coastal dunes for Orthoptera has to consider oviposition and nymphal preferences. — *J. Insect Conserv.* **16**: 501–510.
- YOSHIHARA Y., OHKURO T., BUUVEIBAATAR B., UNDARMAA J. & TAKEUCHI K. 2010: Pollinators are attracted to mounds created by burrowing animals (marmots) in a Mongolian grassland. — *J. Arid Environ.* **74**: 159–163.
- ZAITLIN B. & HAYASHI M. 2012: Interactions between soil biota and the effects of geomorphological features. — *Geomorphology* **157/158**: 142–152.
- ZHANG Y., ZHANG Z. & LIU J. 2003: Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. — *Mamm. Rev.* **33**: 284–294.

Received March 5, 2013; revised and accepted May 2, 2013