

## Patch choice in a grasshopper – an individually based field approach (Caelifera: Gomphocerinae)

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### Summary

As part of conservation efforts, the patch choice of the Meadow grasshopper, *Chorthippus parallelus* (Zetterstedt), was studied on an isolated Dutch heath of about 0.3 ha. The mean population size was around 220 individuals with a median adult lifetime of 10–11 days and maxima of at least one month. Throughout the study period (July, August) nymphs and adults used the same patches. Marked adults, released at four points some distance from the population's distribution sites, moved in two weeks from their releasing points to the nearest distribution site. These sites correlated with the highest potential sunshine hours. There were considerable differences in the vegetation structure between the preferred sites. During the night the grasshoppers rested on 15 out of 27 plant species available, mainly proportional to their dominance. No clear relationship was found between resting height and the ambient microsite temperature or humidity.

### Zusammenfassung

Auf einer Heidefläche von ca. 0,3 ha im Veluwe-Gebiet (Niederlande) wurde die Mikrohabitatwahl des Gemeinen Grashüpfers, *Chorthippus parallelus* (Zetterstedt), untersucht. Die Populationsgröße betrug ca. 220 Individuen, die mittlere adulte Lebensdauer 10–11 Tage mit Maxima von mindestens einem Monat. Während der Untersuchungsperiode (Juli, August) nutzten Larven und Imagines dieselben Habitatflecken. Markierte Imagines, die an vier Stellen etwas abseits der sonst bevorzugten Zentren ausgesetzt wurden, bewegten sich im Laufe von zwei Wochen wieder zum jeweils benachbarten Zentrum. Diese Stellen korrelierten mit der höchsten potenziellen Sonnenscheindauer auf der Heidefläche. Die bevorzugten Habitatflecken unterschieden sich erheblich in ihrer Vegetationsstruktur. Des Nachts ruhten die Grashüpfer an insgesamt 15 von 27 verfügbaren Pflanzenarten, zumeist proportional ihrer Dominanz. Es ergab sich keine klare Beziehung zwischen der Aufenthaltshöhe an der Pflanze und der Temperatur und Luftfeuchte in unmittelbarer Umgebung.

### Introduction

The success of conservation efforts in insects depends mainly on knowing the species' habitat requirements, which are multifactorial and dynamic with interactions mainly among components of the microclimate, vegetation structure, and the biology of the species (COLLINS & THOMAS 1991). In Orthoptera, since many decades habitat preferences have been studied descriptively in numerous faunistic and ecological surveys (for the Netherlands especially since LENSINK 1963,

and later summarized in KLEUKERS et al. 1997). It was JOERN (1982), who introduced the detailed method of structure analysis of grasshoppers in arid grassland of Texas by observing the individuals in the vegetation structure and microhabitat. According to this, the species do not inhabit microhabitats at random and use only a restricted range of them. To manage grasshopper populations for conservation this range should be known, considering that some species show ontogenetic changes in their preferences (LENSINK 1963, ATKINSON & BEGON 1988, CHERRILL & BROWN 1992).

Recent conservation ecology focuses on the problem of habitat fragmentation and its influence on population viability (e.g. SETTELE et al. 1996, BEISSINGER & MCCULLOUGH 2002, for grasshoppers KÖHLER 1999). In the Netherlands, in 1992 a survey of grasshoppers of heath land fragments was performed showing that only half of the species found on the heath lands also occurs in the relatively small and more or less isolated fragments. The Meadow grasshopper, *Chorthippus parallelus*, occurred in about three-quarters of the fragments (MABELIS et al. 1994). A subsequent dispersal study showed that individuals of a heath land population stay in their home area with few maximum lifetime dispersal ranges of about 60 m (OPITZ et al. 1998). It was argued that besides dispersal the habitat choice of this species is decisive for persisting in most of the Dutch heath lands.

We therefore elucidated the patch choice of the Meadow grasshopper (*C. parallelus*) within a structured habitat (heath land) by mapping the spatial distribution of juveniles and adults over their life time. In parallel, marked adult grasshoppers were released away from their preferred habitat patches in order to follow their subsequent movement, preferred host-plants and microsites on these plants. Over the study period we correlated local abundances with microhabitat parameters to detect local preferences.

## Materials and methods

### Species

For this study, we used the Meadow grasshopper, *Chorthippus parallelus* (Zetterstedt), a widespread and common species throughout Europe (HARZ 1975), distributed from rather wet to more xerothermic habitats from the plains to subalpine regions. In the Netherlands, it occurs in southern and eastern districts, inhabiting all kinds of relatively moist grassland, heaths, and dunes (KLEUKERS et al. 1997). It feeds mainly on several species of grasses, but it is also reported to feed on some herbs. The egg-pods contain 8–10 eggs and are laid separately in the upper soil layer. One female produces about 20–50 eggs, depending on how long it lives (INGRISCH & KÖHLER 1998).

### Study site

The study was performed on the Veluwe (near Arnhem, 6°E and 52°N, about 40 m above s.l.) consisting of a mosaic of heath lands, grasslands, and woodlands (MABELIS et al. 1994). Here several local populations of *C. parallelus* live in heath land habitats, and in grass verges along forest paths and roads. Our study site was near Schaarsbergen, a typical, but small heath land of about 100 x 20 (–40) m (3.000 m<sup>2</sup>) with a patchy distribution of rather different vegetation types

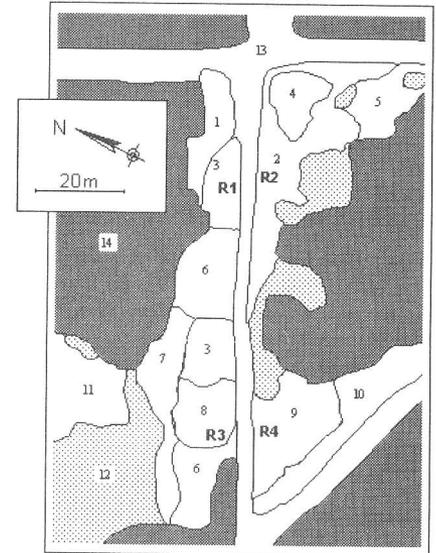
surrounded by open woodlands and crossed by a forest path (Fig. 1). The trees of the surrounding woodland differed in height and density and provided shady areas, changing during the day and the season. So the potential sunshine hours within the habitat patches differed gradually due to variable shading (see Fig. 3b - from early August to early September).

The open study site was divided into 116 squares of 25 m<sup>2</sup> (5 x 5 m) each, and their corners were marked with reflective sticks allowing an individual grasshopper's position to be mapped precisely (< 1 m), even during nocturnal counts. The grasshopper distribution was investigated for each square on 24 days from 6 July till 4 September 1996.

On the study site the vegetation was mapped by estimating the percentage species cover in each square. Altogether 27 plant species were structurally dominant. Including the edges, this resulted in 14 structurally different vegetation patches, where one of the following plant species dominated: *Rubus fruticosus*, *Deschampsia flexuosa*, *Carex arenaria*, *Festuca rubra*, *Calluna vulgaris* and *Cladonia furcata* (Fig. 1).

Fig. 1: Study plot divided into different vegetation patches:

- 1: open soil, sporadically *Deschampsia flexuosa*, *Carex arenaria*;
  - 2: short vegetation (due to rabbit grazing), dominated by *Festuca rubra*; *Juncus effusus*, *Luzula luzuloides*, *Rhytidadelphus squarrosus* common;
  - 3: vegetation dominated by *Cladonia furcata*, partly by *D. flexuosa*, *C. arenaria*, *Calluna vulgaris*;
  - 4: bush vegetation (*Sambucus nigra*, *Rosa canina*, *Rubus fruticosus*);
  - 5: vegetation dominated by *Glechoma hederacea* and *F. rubra*;
  - 6: vegetation dominated by *C. arenaria*; *L. luzuloides*, *Hypericum perforatum*, *C. furcata* common;
  - 7: vegetation dominated by *R. fruticosus*, *G. hederacea*, *Scleropodium purum*, *F. rubra*;
  - 8: vegetation dominated by *S. purum*, *C. furcata*, partly *C. vulgaris*, *R. fruticosus*;
  - 9: vegetation dominated by *D. flexuosa*, sporadically *Molinia caerulea*;
  - 10: open soil covered with leaves, sporadically *D. flexuosa*;
  - 11: vegetation dominated by *G. hederacea*, *Urtica dioica*, sparsely *R. fruticosus*;
  - 12: vegetation dominated by *R. fruticosus*;
  - 13: open soil, partly short grass vegetation;
  - 14: woodland dominated by *Pinus* or *Betula*, *D. flexuosa* dominant in herb layer;
- R1–R4: - releasing points of marked grasshoppers.



### Distribution of grasshoppers

The heath land population of *C. parallelus* was studied over two months from 6 July till 4 September 1996 (S.O.) including both the nymphs (L3/4) and the phenological peak of the adult grasshoppers as the most active stage. Nine daylight surveys were carried out in 4–7-day intervals by line transects (KLINGELHÖFER & KÖHLER 2000), passing all squares of 5 x 5 m in the same sequence and frequency. The numbers of nymphs and adults observed in each square and day were counted separately. As no other similar species were present, juveniles could be unambiguously identified. To represent the spatial distributions spectral diagrams of Corel-Chart Version 4 were used.

Furthermore, a mark-release experiment was conducted. From 29–31 July, from the study site 120 adult *C. parallelus* were marked a few days after their final moult, by gluing small, numbered plastic discs (to number queen bees - Honig Müngersdorff, Köln) dorsally on the pronotum. Additionally, small (5 x 1.5 mm) pieces of reflective tape (Scotchlite High Gain 7610 - Fa. 3M Germany GmbH, Neuss) were fixed on their hind tibiae. This enabled resight rates of 83% during nocturnal checks (22–24 p.m.) with a head-lamp, and individuals were visible at a distance of about 50 m.

At each of four points within different vegetation patches, 15 females and 15 males were released immediately after marking (Fig. 1, R1–R4), resulting in a total of 120 marked adults. These release points were chosen at different distances from the main distribution sites of the unmarked individuals. Throughout the whole study period, the squares were surveyed at night at 1–3-day intervals resulting in a total of 818 resights. The average population size (adults) was estimated, using the Lincoln-index (KREBS 1999), considering four control days in August (1, 5, 9, 16) and one in September (4).

The initial movements of marked adults were studied by comparing directions and intensities of movement between the four released groups on the first two days after releasing. We used the circular statistic programme Oriana 1.0 (KOVACH 1994) where distances between two resight points of an individual (the first is that at release) are converted into vectors. These vectors then correspond to the distance and direction the grasshoppers moved (Fig. 5).

### Patch characteristics

To estimate the potential sunshine hours in early August, mid-August and early September a horizonscope (Fa. Tageslichttechnik, Stuttgart, Germany) was used for each square (5 x 5 m) of the study site. With this simple instrument the effect of shading (by shrubs and trees) on the potential sunshine hours at the observation point can be estimated (MÜHLENBERG 1993). The relation of the potential sunshine hours on grasshopper abundance in the squares was examined by Spearman rank correlation.

Furthermore, the daily weather data (6.7. – 4.9.96) from the stations De Bilt (about 45 km distant; means of temperature, relative humidity and sunshine) and Deelen (about 6 km distant; rainfall) were used.

Because no active grasshoppers were found during the night surveys, the plants on which individual grasshoppers rested were noted for each patch, representing

the last choice of each day. On the three plant species most frequently occupied, 258 individual resting heights above ground level were measured with a folding rule, and temperature and relative humidity at the resting sites with a recorder (RHT 200 ebro). Differences between males and females in the frequencies of the occupied plant species were compared by the chi-square-test.

## Results

### Population size and adult lifetime

The estimated numbers of adults at the study site in August and at the beginning of September amounted to 196, 230, 206, 242, and 214 individuals. According to this, the average population size of *C. parallelus* was around 220 individuals, which corresponds to a density of about seven individuals per 100 m<sup>2</sup>. Thus, approximately 55% of the adults were marked.

Due to mortality, the number of resights decreased from 352 in the first 6-day interval at the beginning of August, to 28 in the last interval in early September. The median adult lifetime was 10 days (females) and 11 days (males), but 20% of the marked individuals of both sexes survived for at least one month.

### Distribution pattern

With respect to unmarked nymphs, in July two main distribution sites and a few scattered localities were found (Fig. 2). In about 40% of the squares no *C. parallelus* could be found. By the end of July the density of nymphs decreased first in

the central part of the study site, due to earlier adult moulting. In the southwestern edge of the study site adults occurred at least six days later (Fig. 2, 26.07).

Throughout August the distribution of unmarked adults (based on observations of five days) showed a similar pattern to that of the nymphs one month before (Fig. 3a). The numbers of unmarked individuals from line transects in the clusters of nymphs (in July) and adults (in August) were highly correlated (Spearman's  $r = 0.453$ ,  $P < 0.001$ ).

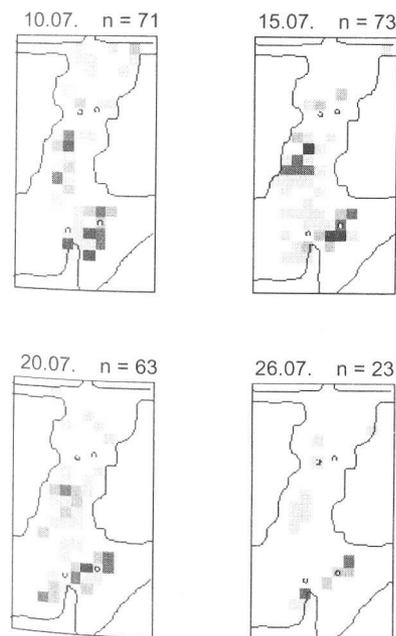


Fig. 2: Distribution pattern of juvenile *C. parallelus* on four days in July; releasing points of marked grasshoppers.

The dispersion of marked adults was determined in the initial days by the four releasing points with R1 and R2 distinctly away from the nearest distribution cluster of unmarked adults (compare Fig. 4 and 3a). Within two weeks of relocation, the marked grasshoppers shifted north, especially in R1 and R2. Later in August, the surroundings of the releasing points stayed completely free of marked individuals, which resulted in a similar distribution pattern as in the unmarked individuals (Fig. 3a and 4). Patterns of unmarked and marked individuals in comparable time intervals were highly significantly correlated (Table 1).

In detail, the relocation can be shown by comparing the initial movements of marked adults after releasing among the four groups (Fig. 5). For R1 and R2 much greater distances of group movement have been calculated compared to R3 and R4, corresponding inversely proportional with distances to the nearest cluster of natural dispersion. The strongest preference for a movement direction existed for R2 resulting in a vectoral concentration of 0.67 (Table 2).

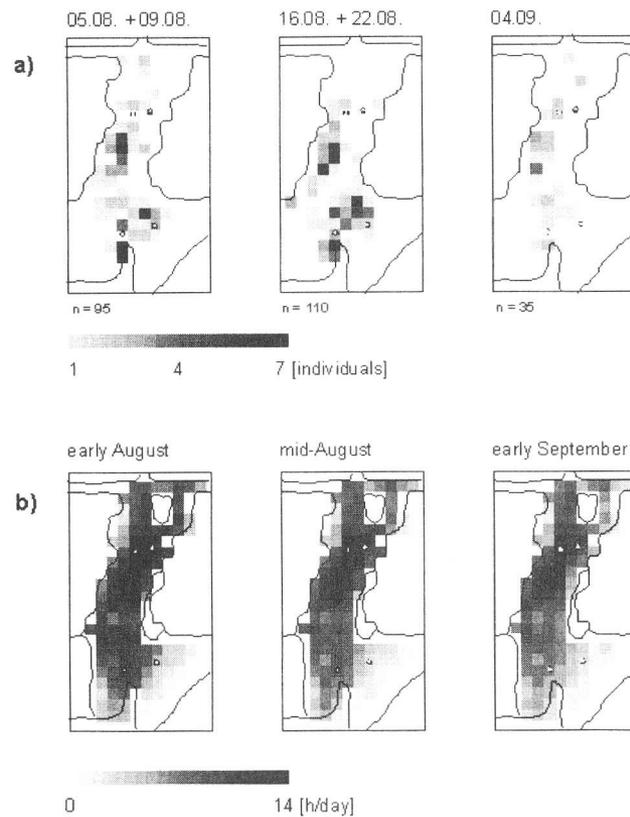


Fig. 3:  
a) Distribution pattern of nonmarked adults of *C. parallelus* in August, based on data from five daylight surveys in relation to b) changing pattern of potential sunshine hours during August; circles are the releasing points of marked grasshoppers.

Table 1: Correlation coefficients (Spearman's  $r$ ) between spatial distribution pattern of marked and nonmarked adults of *Chorthippus parallelus*; \*\*\*  $p < 0.001$ .

		Pattern of unmarked adults		
		05.08. + 09.08.	16.08. + 22.08.	04.09.
Pattern of marked adults	05.08. – 10.08.	0.60 ***		
	17.08. – 22.08.		0.54 ***	
	29.08. – 02.09.			0.42 ***

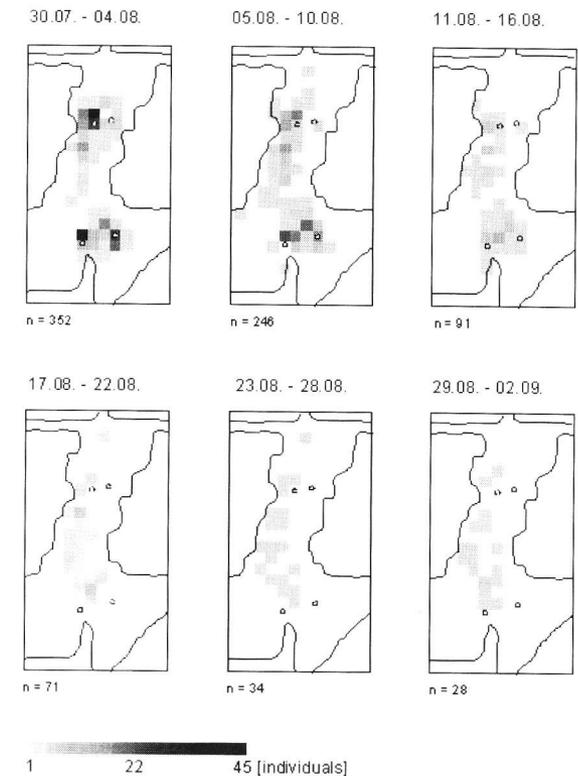


Fig. 4:  
Distribution pattern of marked adults of *C. parallelus* in August divided into six-day intervals.

Table 2: Statistical parameters (programme Oriana 1.0) to initial movements of marked adults of *Chorthippus parallelus* within the first two days after releasing. Every released group has been examined separately.

	group 1	group 2	group 3	group 4
number of refound individuals n	20	22	24	25
total distance moved [m]	197	196	110	110
angle of the mean vector $\mu$	219°	256°	269°	158°
concentration around $\mu$	0.33	0.67	0.38	0.30
95% confidence interval for $\mu$	202°–235°	248°–263°	249°–288°	133°–183°

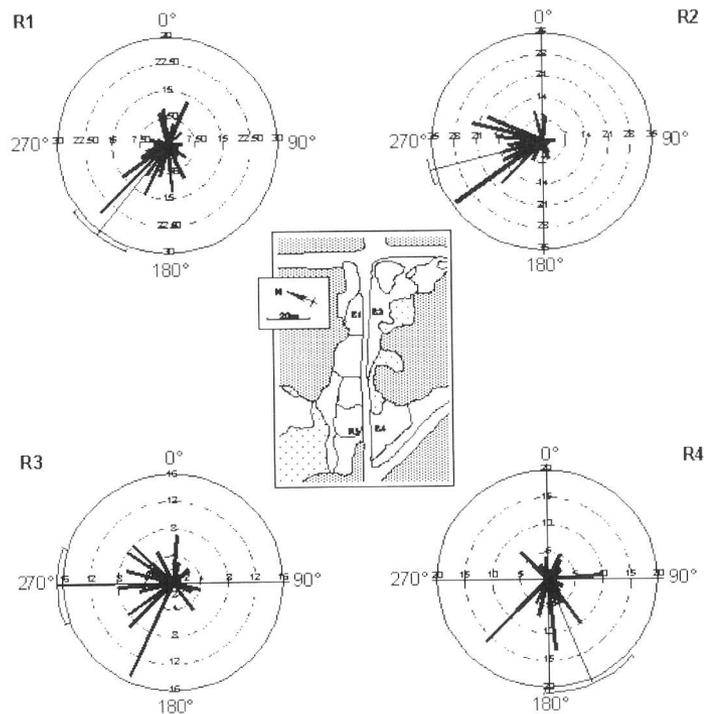


Fig. 5: Initial movements of marked *C. parallelus* adults within the first two days after releasing. Circular histograms show movement directions and total distances from releasing points R1 - R4. For statistical parameters see Table 2.

### Patch choice

The abundances of both unmarked and marked grasshoppers correlate significantly positive to the corresponding potential sunshine hours in these squares (Table 3). Regarding the choice of vegetation patches, both sexes preferred four vegetation patches that differed considerably in their vegetation composition; with either *Deschampsia flexuosa*, *Carex arenaria*, or *Rubus fruticosus* being dominant. In 6 out of 14 structurally differing patches no *C. parallelus* was detected (compare Fig. 6a and Fig. 1).

Table 3: Correlation coefficients (Spearman's  $r$ ) between spatial distributions of marked and unmarked adults of *Chorthippus parallelus* and sun influx pattern of the study plot; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

		n	Sun influx pattern		
			early August	mid-August	early September
spatial distribution of unmarked grasshoppers	05.08. + 09.08.	95	0.33 ***		
	16.08. + 22.08.	110		0.20 *	
	04.09.	35			0.36 ***
spatial distributions of marked grasshoppers	30.07. - 04.08.	352	0.34 ***		
	05.08. - 10.08.	246	0.34 ***		
	11.08. - 16.08.	91	0.25 **	0.21 *	
	17.08. - 22.08.	71		0.34 ***	
	23.08. - 28.08.	34		0.31 ***	0.32 ***
	29.08. - 02.09.	28			0.24 **

The dominant plants of the preferred patches also contained most of the marked grasshoppers during the night surveys, so 47% of the observations were made on *Deschampsia* and *Carex*, but still 25% on *Rubus*. Altogether 15 out of 27 plant species found on the plot and several unidentified foliage, dead branches or stems were used by *C. parallelus*. The dominant plant species of vegetation patches 6 (*C. arenaria*) and 9 (*D. flexuosa*) were also used mostly for resting, but this was not the case for the dominant plant species of patches 3 (*D. flexuosa*) and 8 (*R. fruticosus*) (Fig. 6b). Furthermore, males and females seem to differ in their preference for a plant species for resting ( $\chi^2 = 13.2$ ;  $P = 0.04$ ).

The maximum resting height amounted to 0.56 m in males and 0.44 m in females. On *Rubus*, males stayed higher than females (Mann-Whitney U-test:  $z = -3.96$ ,  $P < 0.001$ ). This preference was not observed in the lower growing grass species *D. flexuosa* ( $z = -0.85$ ,  $P = 0.393$ ), and *C. arenaria* ( $z = -1.78$ ,  $P = 0.075$ ; Fig. 7). There was no clear relationship between resting height at night and ambient temperature and humidity at the resting sites. Spearman's Rank correlation analyses gave different results for the three plant species involved (Table 4).

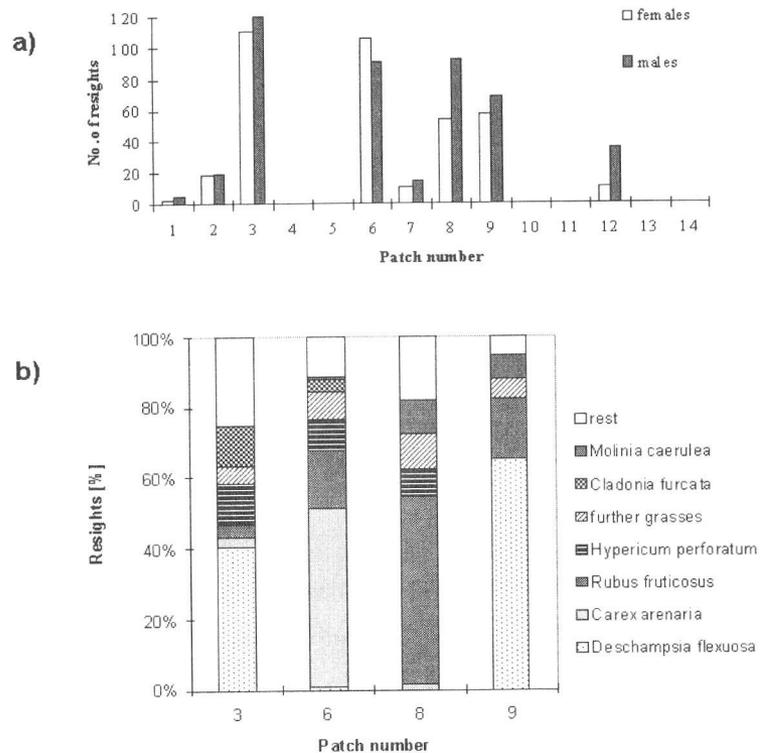


Fig. 6: Patch selection of marked *C. parallelus* adults.  
 a) Total numbers of resights per patch,  
 b) percentage of plant species where marked grasshoppers have been found on night surveys within the four most occupied patches.

Table 4: Correlation coefficients (Spearman's *r*) between heights above the ground where marked adults of *C. parallelus* have been reobserved and ambient temperature and moisture data measured close to the grasshoppers. n.s. = not significant; \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ .

	<i>Carex arenaria</i>	<i>Deschampsia flexuosa</i>	<i>Rubus fruticosus</i>
Sample size	52	113	93
Ambient temperature	n.s.	0.36 ***	n.s.
Relative humidity	0.25 *	-0.20 *□	0.41 ***

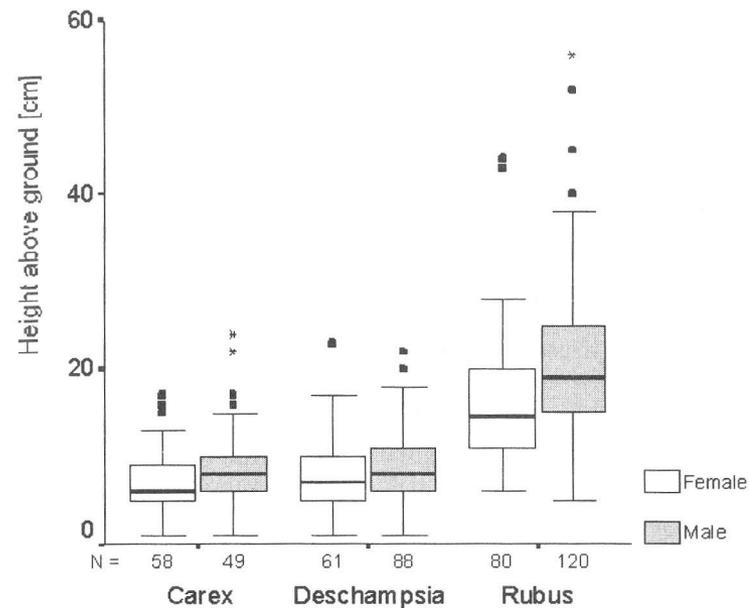


Fig. 7: Heights above ground of resting marked *C. parallelus* adults at night for three of the most occupied plant species (N = number of observations).

## Discussion

Species conservation decisions are increasingly made on the basis of habitat models, derived from detailed studies of populations (KLEYER et al. 1999/2000, SCHRÖDER 2000). In Orthoptera, in contrast to long-standing experience in general species' habitat requests, only few studies, beginning with JOERN (1982), deal with detailed microsite use by individuals (e.g. LANGMAACK & SCHRADER 1997). By combining distribution surveys with mark-release technique our results in *C. parallelus* show nearly the same distribution pattern in nymphs as in adults, confirming that the preferred patches agree with the oviposition sites of female grasshoppers. For conservation efforts it means that no patch change from juveniles to adults needs to be taken into account. This relative simple habitat use is maybe the reason why *C. parallelus* belongs to the most widespread grasshoppers in Dutch heath lands and elsewhere. Studies on other Orthoptera species show that preferences may differ between juvenile instars and adults, as investigated already by LENSINK (1963) in intensive studies on *Chorthippus biguttulus*, *C. albomarginatus*, and *Myrmeleotettix maculatus* in dune habitats of the former isle of Voorne in the southern Netherlands. This was also confirmed on sand dunes in England, where *C. brunneus* and *M. maculatus* became less aggregated during nymphal dispersal, but the adults re-aggregated to an extend (ATKINSON & BEGON 1988). Most of the first instar larvae of *Bryodemella tuberculata*,

living on dealpine riverbanks, settled more or less regularly in patches of low vegetation, whereas adults were distributed irregularly and also on overgrown patches (REICH 1991). In the wart-biter, *Decticus verrucivorus*, the first instars are associated with short, sparse turf, whereas older stages shifted into dense grass tussocks (CHERRILL & BROWN 1992). Using mark-release technique it was found that the adult bush-cricket *Platycleis albopunctata* moved from the end of July to mid-October in the direction of patches with a more open vegetation cover (WALTER 1994). With this technique, also changes of preferred habitat patches over the adult lifetime were detected in *Stenobothrus lineatus* (SAMIETZ 1996) and *Gomphocerippus rufus* (OPITZ & KÖHLER 1998).

For patch choice in detail, microclimate and vegetation structure indicated as most important (for Central European Orthoptera summarized by INGRISCH & KÖHLER 1998). Our experiment with *C. parallelus* shows that the potentially most sunny patches over the season are preferred, both in the distribution patterns and in the mark-release experiment, where a considerable individual movement to these patches occurred. The consequence for conservation is that isolated heath lands fragments will be effectively smaller for several grasshopper species than their total area indicates. Furthermore, our results suggest patch choice in grasshoppers as a primarily two-step process with a preference of microclimate (sunny sites) at first. So we observed in *C. parallelus* that in occasionally shaded habitats the individuals prefer primarily the sunniest patches without considering special vegetation structures. In contrast, in open habitats with very high insolation throughout the day, the individuals select distinct vegetation structures with obviously distinct microclimatic properties. In *Stenobothrus lineatus*, a positive correlation between the abundance of adults and the coverage of the grass *Bromus erectus* was found, in accordance with microclimatic differences between the structure of a *Bromus* vegetation and other structural units (SAMIETZ 1996, SAMIETZ et al. 1996). This may be due to behavioural thermoregulation (SAMIETZ & KÖHLER 1998) as well as to selection of egg-laying sites suitable for embryonic development (WINGERDEN et al. 1992). On Dutch heath lands the density of *Stenobothrus stigmaticus* correlated negatively with the structural density of the grass *Deschampsia flexuosa*, measured by light extinction. This may also be caused by the lower temperatures in the dense vegetation, resulting in a delayed embryonic development and larval hatch (WINGERDEN & BONGERS 1989).

The vegetation not only modifies microclimate, but for grasshoppers it provides also host plants as food and resting sites. The last are scarcely studied elements of individual patch choice in grasshoppers (SÄNGER 1977, MARTI 1989). In *C. parallelus*, we obtained information about nocturnal resting sites, which are rather stable perhaps over the whole night, because we have never seen walking individuals during night checks. It should be expected that the grass-feeding *C. parallelus* prefers *Deschampsia* and *Carex* which are known food-plants (reviewed in INGRISCH & KÖHLER 1998). However, *C. parallelus* on the heath land did not favour distinct host plants as overnight resting sites and, in consequence, resting plants need not be food-plants.

The choice of distinct resting heights at night could be explained differently. Resting heights might result from the grasshopper remaining at a particular place on a

plant, either at random, or because it searches microclimatically favourable places, or because it selects resting sites that have low predation risk at night. Random decision is suggested by the broad individual variability in resting heights compared to the spectrum of heights available. Perhaps it is influenced also by the less stable leaves and flower stems of the grasses comparing with the robust shoots of *Rubus*, where the adult grasshoppers can climb higher. Microhabitat choice can be excluded however as no clear relationships to temperature and humidity could be detected. We are unable to exclude the third possibility since no information about nocturnal predators (Lycosidae, Carabidae, Formicidae) were available. But the fact that in few cases only small fragments of marked grasshoppers could be found, shows a rapid destruction of dead individuals by a considerable predatory potential on a meadow (KÖHLER et al. 2002 - for dry calcareous grassland).

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## References

- ATKINSON, D. & M. BEGON (1988): Changes in grasshopper distribution and abundance at sites in the North Merseyside sand dunes. – *Naturalist* 113: 3–19.
- BEISSINGER, S.R. & D.R. McCULLOUGH (eds.) (2002): *Population Viability Analysis*. – University of Chicago Press, Chicago.
- CHERRILL, A.J. & V.K. BROWN (1992): Ontogenetic changes in the micro-habitat preferences of *Decticus verrucivorus* (Orthoptera: Tettigoniidae) at the edge of its range. – *Ecography* 15: 37–44.
- COLLINS, N.M. & J.A. THOMAS (eds.) (1991): *The Conservation of Insects and Their Habitats*. – Academic Press, London.
- HARZ, K. (1975): *Die Orthopteren Europas II. (Unterord. Caelifera)*. – Dr. W. Junk B.V., The Hague.
- INGRISCH, S. & G. KÖHLER (1998): *Die Heuschrecken Mitteleuropas*. – Westarp Wissenschaften, Magdeburg.
- JOERN, A. (1982): Vegetation structure and microhabitat selection in grasshoppers. – *South-western Naturalist* 27 (2): 197–210.
- KLEUKERS, R., NIEUKERKEN, E. VAN, ODÉ, B., WILLEMSE, L. & W. VAN WINGERDEN (1997): *De sprinkhanen en krekels van Nederland (Orthoptera)*. – Nationaal Natuurhistorisch Museum / European Invertebrate Survey, Leiden, Nederlande.
- KLEYER, M., KRATZ, R., LUTZE, G. & B. SCHRÖDER (1999/2000): *Habitatmodelle für Tierarten: Entwicklung, Methoden und Perspektiven für die Anwendung*. – *Zeitschrift für Ökologie und Naturschutz* 8: 177–194.
- KLINGELHÖFER, J. & G. KÖHLER (2000): Wie schätzt man die Populationsgröße bei Feldheuschrecken (Caelifera: Acrididae)? – Ein Beitrag zur Populationsgefährdungsanalyse. – *Beiträge zur Ökologie, Jena* 4 (2): 91–117.
- KÖHLER, G. (1999): *Ökologische Grundlagen von Aussterbeprozessen – Fallstudien an Heuschrecken (Caelifera et Ensifera)*. – Laurenti, Bochum.
- KÖHLER, G., HAHN, S., REINHARDT, K., WAGNER, G. & M. RITZ (2002): Was geschieht mit toten Heuschrecken auf Magerrasen? Ein Freilandexperiment. – *Articulata* 17 (2): 33–49.
- KOVACH, W.L. (1994): *Oriana for Windows version 1.0: User's Manual*. – Kovach Computing Services, Pentraeth, Wales, U.K.
- KREBS, C.J. (1999): *Ecological Methodology*, 2nd ed. – Menlo Park, California.
- LANGMAACK, M. & G. SCHRADER (1997): Microhabitat analysis of three fen-grassland grasshopper species (Acrididae: Gomphocerinae). – *Entomologia Generalis* 22 (1): 45–55.
- LENSINK, B.M. (1963): Distributional ecology of some Acrididae (Orthoptera) in the dunes of Voorne, Netherlands. – *Tijdschrift voor Entomologie* 106: 357–443.
- MABELIS, A., GRIFFIOEN, R., SCHRÖDER, R.J.H. & W.K.R.E. VAN WINGERDEN (1994): Grasshoppers in heathland fragments surrounded by woodland. – *Proceedings of Experimental and Applied Entomology, N.E.V. Amsterdam* 5: 115–121.
- MARTI, T. (1989): *Heuschrecken und Landschaft. Ein exemplarischer Einblick in Theorie und Praxis goetheanistischer Naturwissenschaft*. – P. Haupt, Bern & Stuttgart.
- MÜHLENBERG, M. (1993): *Freilandökologie*, 3. überarb. Aufl. – Quelle & Meyer, Wiesbaden.
- OPITZ, S. & G. KÖHLER (1998): Wie nutzen Feldheuschrecken (Caelifera: Gomphocerinae) ihr Habitat? – *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* 11: 619–622.
- OPITZ, S., KÖHLER, G. & A. MABELIS (1998): Local movement of the grasshopper *Chorthippus parallelus* (Zett.). – *Proceedings of Experimental and Applied Entomology, N.E.V. Amsterdam* 9: 53–58.
- REICH, M. (1991): *Struktur und Dynamik einer Population von Bryodemata tuberculata (Fabricius, 1775) (Saltatoria, Acrididae)*. – Ph. D. Thesis, Ulm University, Ulm, Germany.
- SÄNGER, K. (1977): Über die Beziehungen zwischen Heuschrecken (Orthoptera: Saltatoria) und der Raumstruktur ihrer Habitate. – *Zoologische Jahrbücher für Systematik und Ökologie* 104: 433–488.
- SAMIETZ, J. (1996): Zur Mikrohabitatnutzung einer Heuschreckenart in Halbtrockenrasen: *Stenobothrus lineatus* (Panzer)(Insecta: Caelifera). – *Verhandlungen der Gesellschaft für Ökologie* 26: 569–573.
- SAMIETZ, J., BERGER, U. & G. KÖHLER (1996): A population vulnerability analysis of the stripe-winged grasshopper, *Stenobothrus lineatus* (Caelifera: Acrididae). – In: SETTELE, J., MARGULES, C.R., POSCHLOD, P. & K. HENLE (eds.): *Species Survival in Fragmented Landscapes*. – Kluwer Academic Publisher, Dordrecht et al.: 299–311.
- SAMIETZ, J. & G. KÖHLER (1998): The impact of behavioural thermoregulation on reproductive rates in a grasshopper. In: BAUMGÄRTNER, J., BRANDMAYR, P. & B.F.J. MANLY (eds.): *Population and Community Ecology for Insect Management and Conservation*. – Balkema, Rotterdam & Brookfield: 63–73.
- SCHRÖDER, B. (2000): *Zwischen Naturschutz und Theoretischer Ökologie: Modelle zur Habitat-eignung und räumlichen Populationsdynamik für Heuschrecken im Niedermoor*. – Ph. D. Thesis, Technische Universität Braunschweig.
- SETTELE, J., MARGULES, C.R., POSCHLOD, P. & K. HENLE (eds.) (1996): *Species Survival in Fragmented Landscapes*. – Kluwer Academic Publisher, Dordrecht et al.
- WALTER, R. (1994): Zur Mobilität und zum Habitat von *Platycleis albopunctata* (Goeze 1778). – *Articulata* 9 (1): 1–23.
- WINGERDEN, W.K.R.E. VAN & W. BONGERS (1989): De verspreiding van *Stenobothrus stigmaticus* (Rambur) 1839 (Orthoptera, Acrididae) in relatie tot de vegetatiestructuur van *Deschampsia flexuosa* bij begrazing. – *Nieuwsbrief Saltabel, Leiden* 2: 20–27.
- WINGERDEN, W.K.R.E. VAN, MUSTERS, J.C.M., CANNEMEIJER, F. & W. BONGERS (1992): Simulation of hatching dates in three *Chorthippus* species (Orthoptera: Acrididae) in unfertilized and lightly fertilized grasslands. – *Proceedings of Experimental and Applied Entomology, Amsterdam* 3: 86–93.