Ann. soc. entomol. Fr. (n.s.), 2012, 48 (3–4) : 299-307 ARTICLE

Development, reproductive capacity and diet of the Mediterranean grasshopper *Arcyptera brevipennis vicheti* Harz 1975 (Orthoptera: Caelifera: Acrididae: Gomphocerinae)

Eva Schultner [1,4], Elodie Blanchet [2], Christine Pagès [2], Gerlind U. C. Lehmann [1,3] & Michel Lecoq [2]

[1] Department of Zoology, Free University Berlin, Königin-Luise-Strasse 1-3, 14195 Berlin, Germany
[2] CIRAD UPR Bioagresseurs: analyse et maîtrise du risque, Montpellier, F-34398 France
[3] Department of Biology, Humboldt Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany
[4] Department of Biosciences, University of Helsinki, Viikinkari 9, 00014 Helsinki, Finland

Abstract. *Arcyptera brevipennis vicheti* Harz 1975 (Orthoptera: Acrididae) is a rare grasshopper native to Mediterranean grassland habitats in the Languedoc-Roussillon region of southern France. Changes in land-use have modified these unique habitats, thus threatening the survival of *A. b. vicheti* populations. To improve the conservation of this species this study aimed to describe important aspects of its biology and ecology. Development of nymphs passed through five instars after hatching and was closely associated with the Mediterranean spring season. A prominent sexual size dimorphism is highlighted, but the larger females developed in the same number of instars as males. Hind femur length and number of antenna segments were useful characters when distinguishing between nymphal instars. All individuals were brachypterous, indicating that *A. b. vicheti* is unable to fly. Adult females laid 15 eggs on average and deposited no more than two egg pods in their lifetime. Grass debris made up 93% of faecal content of both sexes. Our results provide valuable information for the conservation of this highly endangered grasshopper species.

Résumé. Développement, capacité de reproduction et régime alimentaire du criquet méditerranéen. *Arcyptera brevipennis vicheti* Harz 1975 (Orthoptera : Caelifera : Acrididae : Gomphocerinae). *Arcyptera brevipennis vicheti* Harz 1975 (Orthoptera : Acrididae) est un criquet indigène rare des pelouses du Languedonc-Roussillon dans le sud de la France. Les changements dans l'aménagement du territoire ont modifié ces habitats uniques, menaçant ainsi la survie des populations d' *A. b. vicheti*. Afin d'améliorer la conservation de cette espèce, cette étude s'est donnée pour mission de décrire les grands aspects de sa biologie et de son écologie. Le développement des larves passe par 5 stades après l'éclosion et est étroitement associée avec le printemps méditerranéen. Un fort dimorphisme sexuel est mis en évidence mais les femelles de grande taille se développent avec le même nombre de stades larvaires que les mâles. La longueur du fémur postérieur et le nombre de segments des antennes sont des caractères utiles pour distinguer les stades larvaires. Tous les individus sont brachyptères, ce qui indique qu'*A. b. vicheti* est incapable de vol. Les femelles adultes pondent une moyenne de 15 oeufs et ne déposent pas plus de 2 oothèques durant leur vie. Les débris herbeux constituent jusqu'à 93% des contenus fécaux des deux sexes. Nos résultats fournissent des informations précieuses pour la conservation de cette espèce fortement menacée.

Keywords: Life history, sexual size dimorphism, conservation, grassland, Acrididae.

Modification and fragmentation of grassland habitats are major threats to insect diversity and especially the intensification of agricultural activities, combined with the abandonment of traditional, extensive land-use practices, are responsible for changes in grasslands and thus for the decline of numerous insect species (Samways 1994; Samways 2005). Although the importance of biodiversity in maintaining functioning ecosystems is well documented (Hooper *et al.* 2005), the biology of most insect species is still poorly understood and information on consequences of habitat fragmentation and modification are insufficient.

Grasshoppers are especially good models when it comes to studying interactions between insects and changing grassland habitats (Samways 1997). Ranging from highly mobile, generalist species to habitat specialists displaying low dispersion capacities, grasshoppers show a great diversity of life histories and ecological requirements (Uvarov 1966; 1977; Chapman & Joern 1990; Ingrisch & Köhler 1998). In addition, they are widely distributed and as primary consumers play a major role shaping grassland habitats and influencing ecosystem dynamics (Dempster 1963;

E-mail: eva.schultner@helsinki.fi, gerlind.lehmann@t-online.de, blanchet.elodie@gmail.com, christine.pages@cirad.fr, michel.lecoq@cirad.fr
Accepté le 19 avril 2012

Köhler 1988; Joern & Gaines 1990). Although many common species have been studied exhaustively due to their significance as agricultural pests (Anonymous 1982; Samways & Lockwood 1998), information on rare grasshoppers showing a high degree of ecological specialisation remains sparse (Maes *et al.* 2006; Hochkirch *et al.* 2008). This is unfortunate, as specialists are usually more sensitive to local changes in habitat and climate, and can therefore serve as indicators of the short-term effects of habitat modifications (Reinhardt *et al.* 2005).

Arcyptera brevipennis vicheti Harz 1975 (Orthoptera: Acrididae) is an extremely rare, univoltine grasshopper species found only in rocky grassland habitats of the French Mediterranean garrigue (Voisin 2003). The grasshopper diversity of these habitats is considerable, but strong declines in pasture grazing have been leading to the widespread modification of these grasslands and threatening many endemic species (Samways 2009). *A. b. vicheti*'s patchy distribution (Kruseman 1982; Monard 1986) suggests that this species has a narrow ecological niche. In this context, study of life histories has proven to be especially useful because it can give insight on important aspects of maturation, survival and reproduction (Roff 2002). More precisely, development and growth have been shown to be key factors in determining grasshopper ecology as they influence locomotion and dispersal abilities, fecundity, mating success and types of predators (Whitman 2008). As grasshoppers are hemi-metabolous insects, a first step in describing their development consists of determining the number and duration of development stages (instars) that individuals go through after hatching and up to the imaginal moult. It has been shown that the number of instars is variable among species, sexes and sometimes even individuals (Ingrisch 1998). Instar duration on the other hand seems influenced primarily by environmental factors like temperature and nutritional quality of food (Uvarov 1966; Joern & Gaines 1990; Danner & Joern 2004). These same factors may also influence nymphal growth characteristics, resulting in varying body size measurements according to development stage (Ingrisch 1998).

Regarding reproduction, female reproductive capacity is important when describing grasshopper biology, as it can be used to estimate population fecundity. Two factors determine reproductive potential in female grasshoppers: the number of eggs laid at one time (clutch size) and the number of clutches or egg pods laid by a single female in its lifetime (Richards & Waloff 1954; Uvarov 1966; 1977). While clutch size is limited by body size constraints, the maximum number of clutches per female can vary considerably between controlled and natural conditions (Köhler & Brodhun 1987; Kriegbaum 1997), indicating that environmental conditions and habitat characteristics strongly influence the reproductive potential of grasshopper populations.

Finally, food selection significantly determines grasshopper ecology, being closely linked to the ecological and physiological requirements and general behaviour of both young hoppers and adults (Muralirangan *et al.* 1997). Quality and nutritional value of food plants can affect survival, development rate and aspects of life history (Bernays & Simpson 1990; Raubenheimer & Simpson 2003; Berner *et al.* 2005). Diet varies greatly among species and both indirect assessment of diet in natural conditions and direct estimation based on food selection experiments in laboratory conditions have shown that nutritional regimes can range from monophagous to polyphagous, with a majority of species being polyphagous (Chapman 1990; Köhler 1998). Strict monophagy is assumed to be rare, and even potentially monophagous species will usually feed on other plants in no-choice experiments (Chapman & Sword 1997). However, most authors agree that true feeding preferences can only be determined by examining food plant use in natural conditions. As data on the diet of rare species in the field is sparse, the study of *A. b. vicheti* provides a unique opportunity to complement current knowledge.

The present paper aims to describe the biology and ecology of *Arcyptera brevipennis vicheti*, focusing on nymphal growth and development, female reproductive capacity and adult diet in natural conditions. The results will hopefully contribute to improving the conservation of this rare species.

Methods and Material

Studied species and laboratory conditions

A total of 60 female and 51 male nymphs were collected in rocky grassland habitats on the Causse d'Aumelas (03°38'54"E, 43°34'42"N) in the Hérault département of southern France in April 2008. This limestone plateau covers an area of about 220 km^2 and rises gradually from 70 m above sea level to reach its highest point at an altitude of 349 m.

The Causse d'Aumelas exhibits habitats typical to Mediterranean landscapes, with rocky grasslands interspersed with patches of dense garrigue schrubs like *Quercus coccifera* L., *Juniperus communis* L. and *Buxus sempervirens* L. Individuals were collected on one site representative of grassland habitats, characterised by a mosaic of bare ground, rock, sparse grassy vegetation and small patches of denser woody vegetation. *Brachypodium retusum* (Pers.) P. Beauv. clearly dominated, covering about 55% of the total surface area (data not shown). Other abundant plants included several *Bromus* species, *Thymus vulgaris* L. and *Phlomis lynchitis* L.

After collection, individuals were placed in separate cages (10 × 17 cm), which were labeled with the capture date and development stage at capture. Estimation of development stage was based primarily on body size and coloration as 1st instar hoppers are distinctively smaller than older nymphs (compare results). Both 1st and 2nd instar hoppers can additionally be distinguished by a prominent horizontal black line on the hind femur, which is lacking in older instars. Individuals were sexed using characteristics of external genitalia (Uvarov 1966). The studied laboratory population consisted of 55 first instars (23 males, 32 females), 36 second instars (20 males, 16 females) and 20 third instars (8 males, 12 females). Cages were distributed haphazardly and mixed regularly in a hermetic growth cell which was set at a L:D regimen of 16:8 with temperatures of 30 °C and 19 °C, respectively. Humidity was kept constant at 55%. The animals were fed with an assortment of plants (primarily grasses) collected near the facilities and freshly prepared every two days. Cages were checked for the presence of moults every day and development and growth parameters recorded within the same day once the integument had hardened.

Development and Growth

The number of instars and instar duration were measured separately for each individual by recording the number of development stages and the number of days between successive moults. As the first moult coincides with hatching and animals were collected in the field after hatching, development stages were recorded starting with the first mobile nymphs. Coloration of external genitalia, hind femurs and pronotal lateral carina was documented in each development stage.

Seven growth parameters were sampled per individual and instar: i) total body length from the tip of the vertex to the posterior tip of the abdomen ii) pronotum length measured along the central carina iii) hind femur length measured from tip to tip along the exterior of the femur iv) body weight recorded by weighing all individuals in a clean glass tube on a Precisa XB 160M scale with an accuracy of ±0.1 mg v) number of antenna segments counted starting with the first segment of the flagellum, excluding the caput vi) tegmina length recorded after axial rotation and measured from the starting point at the posterior end of the pronotum to the tips and vii) ratio of total body length to tegmen length calculated separately for each individual and development stage. All body size measurements were determined to the nearest 0.1 mm under a stereomicroscope fitted with an ocular micrometer.

Reproductive capacity

For egg-pod analysis, female and male *A. b. vicheti* were held in captivity in joint cages during spring 2007 under the same conditions used for determining hopper development. In total, females deposited 23 egg-pods, which were collected and stored until April 2008. Examination consisted of measuring length and diameter of egg-pods to the nearest millimeter using a standard ruler (±1 mm), recording the position of the eggs in the pod and counting the number of eggs per pod.

For ovarian dissection, a total of 58 females were collected on the Causse d'Aumelas on nine occasions in July 2008, placed in tubes marked with the date and brought back to the laboratory. Individuals were then transferred to large plastic cages, provided with an assortment of fresh plants (mainly grasses) and kept in a growth cell overnight. The following morning, females were killed using cyanide. Ovaries were removed and the number of ovarioles, clutch marks and resorption bodies counted in the left ovary of each female. The number of viable eggs produced by this ovary was calculated by subtracting the number of resorption bodies from the total number of ovarioles. Prior studies have shown that ovaries are symmetric in grasshopper species, and that egg development success in one ovary reflects that of the second ovary (Launois-Luong 1978). Therefore, by doubling the number of viable eggs in the left ovary, an estimation of the total number of eggs per clutch was attained. The percentage of functional ovarioles was then estimated based on the total number of eggs per clutch, divided by the total number of ovarioles. Finally, the total number of clutches per female was determined based on the number of clutch marks and/or resorption bodies per ovariole.

Diet in natural conditions

Adult diet was studied using a non-invasive technique of faecal content analysis (Köhler 1998). For collection of faecal pellets, 11 adult females and 9 males were captured randomly on the Causse d'Aumelas in June 2008 and placed in tubes marked with date and sex. The animals were kept until at least one faecal pellet had been produced. Individuals were then released and the faeces refrigerated until further analysis. Preceding analysis, faeces samples were immersed in 50% bleach solution for 5–10 minutes to destroy cell contents. Samples were then placed on filter paper and rinsed abundantly with water before being mounted on microscope slides. Slides were analysed visually (Leitz Biomed, magnification ×10) and faecal contents classified as belonging to either monocotyledonous or dicotyledonous plants based on size and shape of epidermis cells. Contents were then quantified by estimating proportions of both epidermis types. Four slides (2 females, 2 males) were analysed in detail by examining further epidermal characteristics (i.e. size and shape of trichomes, number and disposition of stomata) and comparing with a reference catalogue of typical Mediterranean grassland plants in the hope of identifying dominant species (Chara 1984).

Statistical analysis

Statistical analysis was conducted using the software package R 2.7.2 (R Development Core Team 2008). Morphometric differences, differences in instar duration and differences between the number of eggs found in egg-pods and calculated from ovarian dissection were analysed with one-way and two-way ANOVAs using instar and/or sex as explanatory variables for growth and development parameters and estimation method for reproductive capacity. Differences in ratios of tegmina length to total body length were analysed with a generalized linear model for binomially distributed data using instar and sex as explanatory variables. Tukey's HSD (95% family-wise confidence level) was used as a post-hoc test. In addition, Student's t-test for independent values was used to compare total development times of males and females and the proportion of monocot and dicot epidermis in male and female faeces. Finally, correlations between body size parameters were tested with Pearson's product-moment correlation coefficient.

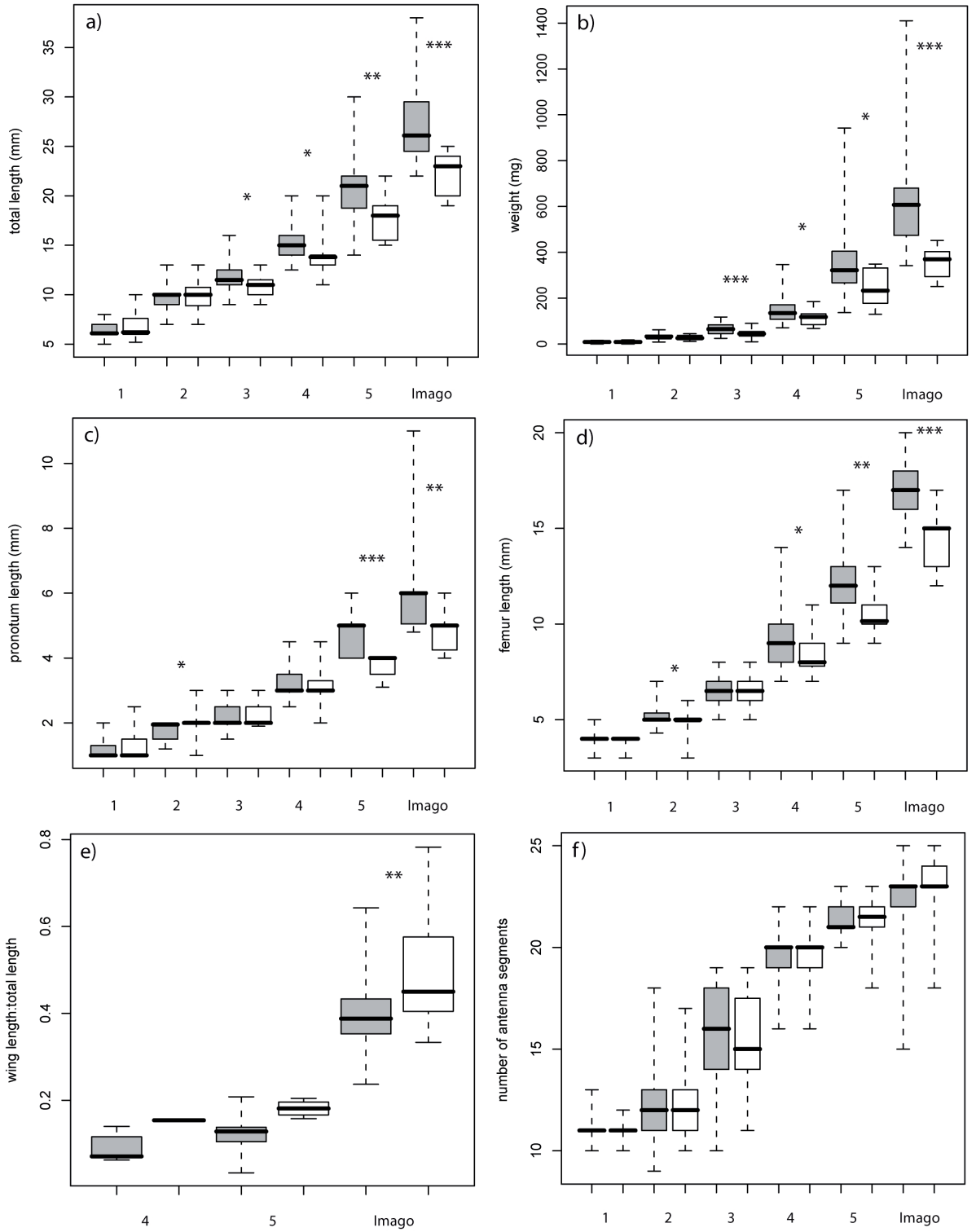

Figure 1
Boxplots of size measurements in *Arcyptera brevipennis vicheti* males (white boxes) and females (grey boxes), separated for instars. **a,** total length; **b,** weight; **c,** pronotum length; **d,** femur length; **e,** tegmina length : total length; **f,** number of antenna segments. Differences tested with two-way ANOVA (factors: sex/instar) and verified with Tukey's HSD for a-d and f. Differences tested with GLM for binomial data (factors: sex/instar) for e. (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Results

Development

Individuals of both sexes invariably passed through five nymphal development stages after hatching. First and 2nd instars moulted after about three days, while 3rd and 4th instar hoppers completed development after approximately four and five days, respectively. Development time was longest for 5th instar females, with a mean (± SD) of 5.9 ± 1.9 days. Whereas developmental duration differed between instars (two-way ANOVA, factor instar: $F_{4,187}$= 16.77, P < 0.001), it was independent of the sexes ($F_{1,187}$= 1.44, P = 0.221). The two males which reached adulthood did so after 20 and 22 days, respectively. The five females reached maturity after 19 to 25 days. As only seven individuals survived from the first moult to adulthood, mean total development times were estimated based on the sum of mean durations for each instar and sex, summarizing data of all individuals. On average, females developed in 21.4 days and males in 19.6 days.

Light brown color of lateral carina distinguished first instar hoppers from later development stages. All later instars were very similar in coloration: the initial dark brown band on the hind femur of 1st and 2nd instar hoppers became harder to distinguish as the rest of the body darkened in color. Lateral carina turned white in 2nd instar hoppers and the edges darkened; bright white carina with black edges were characteristic for all later instars. The tips of the dorsal and ventral ovipositor valves were beige in young female hoppers and began to darken in 3rd instars. In adult females, tips were dark brown. The male subgenital plate was beige with brown spots throughout development. The interior of the hind femurs turned a reddish-orange color in 5th instar hoppers whereas imagines had bright red femurs. The underside of the abdomen turned yellowish-green after the imaginal moult.

Growth

First instar hoppers measured 6–7 mm in total length, increasing steadily during the course of development to reach (mean ± SD) 27.2 ± 3.7 mm in adult females and 22.4 ± 2.1 mm in adult males (Fig. 1). Pronotum lengths ranged from 1.2 ± 0.3 mm in 1st instar females to 5.9 ± 1.2 mm in female adults. For males, pronotum lengths in 1st instars were similar to those measured for females (1.3 ± 0.5 mm) but differences became more pronounced with increasing development and pronotum lengths for adult males averaged only 4.9 ± 0.7 mm. The same was true for hind femur length and weight. While femur length averaged 4.1 ± 0.4 mm in 1st instar females and 3.9 ± 0.3 mm in 1st instar males, adult female femur lengths averaged 16.9 ± 1.5 mm versus only 14.5 ± 1.4 mm in adult males. Adult females weighed 620 ± 207 mg while adult males reached weights of 362 ± 61 mg. The heaviest female weighed 1418 mg while the heaviest male weighed 460 mg. A strong positive correlation between the three length measurements was found for females and males (total versus pronotum length: Females: R^2 = 0.94, n = 197; Males: R^2 = 0.91, n = 125; total versus femur length: Females: R^2 = 0.96, n = 197; Males: R^2 = 0.93, n = 125; femur versus pronotum length: Females: t = R^2 = 0.94, n = 197; Males: R^2 = 0.92, n = 125).

Differences between instars were highly significant for all body size parameters for females (one-way ANOVA: $F_{5,193\text{-}194}$ = 150.29–556.83, ($F_{2,44}$ = 64.63 for tegmina length), P < 0.001) and males (one-way ANOVA: $F_{5,119\text{-}121}$ = 127.10–405.39, ($F_{2,17}$ = 14.04 for tegmina length), P < 0.001). Total length, femur length and number of antenna segments separated all female instars. In contrast, significant differences in pronotum length and weight appeared only in older hoppers and imagines. Distinctions between male instars were slightly less pronounced. Only femur length differed significantly between all development stages while fourth and 5th instars and imagines differed in total length, pronotum length and weight.

The existence of a sexual size dimorphism was obvious, with females being larger in all tested parameters (except number of antenna segments and tegmina length) if corrected for the instar (Fig. 1).

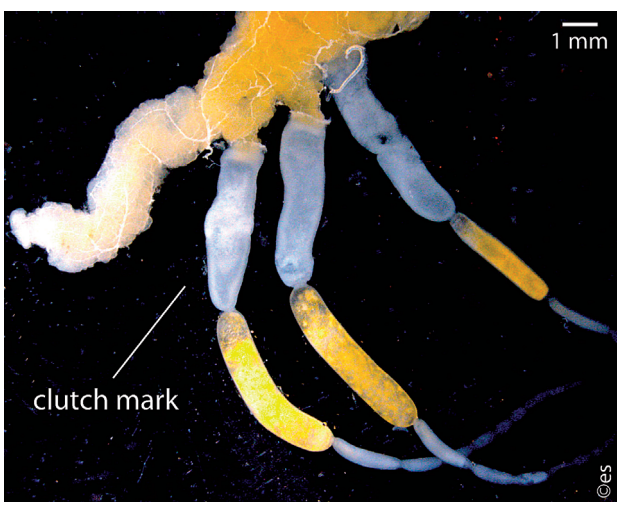

Figure 2
Three ovarioles with fresh translucent clutch marks at their base.

Differences based on the interaction of both nymphal stage and sex were highly significant for total length, pronotum length, femur length and weight (two-way ANOVA: $_{F5,193\text{-}194}$ = 9.63–13.94, P < 0.001). Instar and sex did not interact significantly for the number of antenna segments (two-way ANOVA, factors: sex/instar, $F_{5,313} = 0.18$, P = 0.97) or absolute tegmina length ($F_{2,61}$ = 0.061, P = 0.94). The ratio between tegmina length and total length was not significantly different between males and females (GLM for binomial data, factors: sex/instar, $F_{1,57} = 0.015$, P = 0.90).

Reproductive capacity

Egg-pods were slightly oval in shape and had concave lids that were lined with the secretions of the accessory glands exuded during oviposition. Eggs were arranged at a 45° angle to the length axis of the pod and filled out the bottom half. Length of egg-pods averaged 185 ± 19 mm, diameter averaged 98 ± 16 mm. Egg-pods contained a mean number of 15 ± 5 eggs, 53% of pods containing between 13 and 16 eggs. One of the studied eggpods contained an exceptionally high number of 36 eggs. Egg numbers in egg-pods corresponded well with the mean number of 18 ovarioles ±1 (9 per ovary) recorded for more than half (55%) of the dissected females. A further third of females had 16 ovarioles while 14 and 20 ovarioles were found in 2% and 12% of females respectively. Comparison of the results obtained from egg-pod examination and ovarian dissection showed that the number of eggs laid by females and the number of eggs found in pods did not differ (one-way ANOVA; $F_{1,50}$ = 0.46, P = 0.50). The maximum recorded number of clutches per lifetime was two per female, based on clutch marks at the base of ovarioles (Fig. 2). Of the 58 females dissected in the lab, 29 had not laid eggs at all, 16 had deposited one clutch and 13 had deposited two. Both first and second clutches contained 15.8 eggs on average, which resulted in a mean ovariole functionality of 90%. Although one third of females showed an ovariole functionality of 100% in first clutches, only 15% retained full ovariole functionality in second clutches.

Diet in natural conditions

All studied individuals fed mainly on monocotyledonous versus dicotyledonous plants (t-test: t = 43.75, n = 20, P < 0.001). Accordingly, monocot debris dominated faecal content (t-test, t = –1.46, n = 20, P = 0.082) in 92% of females and 94% of males. *Brachypodium retusum* (Pers.) P. Beauv. was nearly exclusively responsible for the high monocotyledonous plant faecal content: in the four samples analysed in detail, *B. retusum* epidermis constituted around 90% of the plant debris found.

Discussion

The number of instars in Caelifera is quite consistent, ranging between 4 and 9 stages. *A. b. vicheti* invariantly had five nymphal instars plus the adult stage after hatching. This is in concordance with findings in the close relative *A. microptera* Fisher-Waldheim 1833, which also has five post-hatching hopper instars, and Gomphocerinae grasshoppers in general, which have four, five or rarely six instars (Ramsay 1964; Ingrisch 1998).

Although males and females passed through an identical number of six development stages, females were always the larger sex. Such a sexual size dimorphism (SSD) has been linked to differences in the number of instars between the sexes – with larger females usually having one more instar than males (Hochkirch & Gröning 2008) or facultatively inserting an additional development stage to increase body size (Esperk *et al.* 2007). Differences in development time have been found to cause SSD in other arthropods (Wiklund & Forsberg 1991; Wedell 1992; Maklakov *et al.* 2004; Berner & Blanckenhorn 2006) but we did not find any significant variations in development time between male and female *A. b. vicheti*. However, this could have been linked to the small number of replicates, with only seven individuals surviving to adulthood, possibly due to inadequate rearing conditions. Nevertheless, a recent study found only weak positive relationships between SSD and development times in arthropods, and its authors suggest that growth rate differences are more important in determining SSD (Blanckenhorn *et al.* 2007). Observations in the laboratory showed that female *A. b. vicheti* usually consumed more food in less time than males. It is possible that the difference in appetite is reflected by growth rate and subsequently body size. However, the effect was not quantified and further studies are necessary to confirm this assumption.

Development time was coherent with findings on related species like *A. microptera*, which developed in 30 days under controlled conditions (Moritz 1915). Development times however are known to vary according to environmental conditions and temperature in particular (Uvarov 1977; Ingrisch 1998), and mean development time in *A. b. vicheti* actually doubled under natural conditions (E.Schultner, unpublished data). A further hint for the strong interaction between environmental conditions and the timing of *A. b. vicheti* development was the very early appearance of

this species in the field. Along with *A. microptera*, *A. b. vicheti* occurs earlier in the spring season than other univoltine Gomphocerinae species (Weidner 1969). This indicates that these two species have evolved to optimally exploit the duration of the spring season, with hatching occurring when spring rainfalls set in and ovipositing taking place before the ground has completely dried out. Hopper development also seems timed to allow reproduction to take place in early summer before preferred grass plants dessicate or lose nutritional value (Joern & Gaines 1990), which has been suggested to be a restrictive ecological feature in other mediterranean Orthoptera (Lehmann & Lehmann 2008, A. Guendouz-Benrima *et al.* 2011).

Differentiation of young hoppers based on body size measurements was not always possible because measures of size and weight often overlapped between successive nymphal stages. Distinguishing hopper instars generally became easier with advancing development as differences became more pronounced. The significant increases in pronotum length and weight occurring in later instars indicate that the final growth phase strongly determines adult body size. An easier way of distinguishing hopper instars than through body size measurements was pigmentation. Timing of changes in pigmentation of lateral carina, hind femur and abdomen underside was consistent for all individuals and almost no variation in color or intensity was observed.

The mean number of ovarioles and eggs per pod show a strong relationship between body size and number of ovarioles in grasshoppers in general (Whitman 2008; Ackman & Whitman 2008). For example, small grasshopper species with mature female body weights of 170–280 mg have 8–10 ovarioles (Richards & Waloff 1954; Joern & Gaines 1990). Larger species like *Stethophyma grossum* L. 1758 with body weights of 860 mg count a mean of 20 ovarioles. *A. b. vicheti* females with mature weights of 600 mg and 16–18 ovarioles fall well into these ranges. Furthermore, ovariole numbers in female *A. b. vicheti* were identical to those found for its close relative *A. microptera* (Ingrisch 1998).

Reproductive capacity of a population however is influenced by a number of other factors, such as length of the preoviposition period and number of females participating in reproduction. *A. b. vicheti* females underwent a preoviposition period of approximately 24 days while the subsequent reproductive period lasted about 21 days (data not shown). About 53% of females survived long enough in natural conditions to deposit one egg-pod and 37% deposited a second pod. The proportion of females participating in oviposition can be a strong indicator of the influence of environmental conditions on fecundity: for example, a study on seven sahelian grasshoppers found that the percentage of females participating in oviposition was high when conditions were favourable and dropped sharply when summer aridity caused vegetation to desiccate (Launois-Luong 1979). In *Chrotogonus senegalensis* Krauss 1877, participation dropped from 76% during favourable spring conditions to 17% during summer. Similarily, female *Locusta migratoria* L. 1758 in Madagascar showed participation levels varying rapidly from 0–100% within a few days, depending on rainfall (Lecoq 1975). Participation levels for *A. b. vicheti* fall into similar ranges as those found for sahelian grasshoppers and although most of these species have longer reproductive periods and lay more eggs per clutch than *A. b. vicheti*, the maximum number of eggs produced by 100 females is similar. This is because female *A. b. vicheti* have an unusually high percentage of functional ovaries (91 % versus only 72% in sahelian species). Data on *Omocestus rufipes* Zetterstedt 1821, indicate that high ovariole functionality is common in species whose life cycle is linked to a relatively short period of favourable conditions (Chara *et al*. 1986). *A. b. vicheti* females may therefore compensate the short three-week reproductive period and limited number of eggs per pod with their consistently high percentage of functional ovarioles to ensure an adequate production of progeny.

Adult *A. b. vicheti* specialise on grasses, a prominent feature in Gomphocerinae species (Capinera 1985; Chapman 1990; Picaud *et al.* 1999). The dominance of *B. retusum* debris in all of the closely studied samples suggest that *A. b. vicheti* is a specialised feeder, which would match evidence on monophagous grasshoppers that feed on a single grass species (Gangwere 1991; Muralirangan *et al.* 1997). However, it is possible that these findings simply correspond to the dominance of *B. retusum* within the plant communities of collecting sites rather than depict true feeding preferences (Chapman 1990). Nevertheless, our results imply that *A.b. vicheti* adults are highly dependent on *B. retusum* or grass species of similar nutritional value as their primary food source. The same could be true for earlier development stages, although diet of instars was not quantified in our study. However, second to fifth instars were most often found on grasses (data not shown), indicating that instars may share the dietary preferences of adults. Threats to grass populations are evident throughout the Mediterranean region, with declines in pasture grazing and similar extensive agricultural practices leading to increased colonization of open grassland patches through shrubs

and trees (Navarro *et al.* 2006; Jauregui *et al.* 2008). Without any management efforts (e.g. intensification of grazing, periodic clearing of shrubs/trees - through fire or manually) directed at the conservation of such grasslands, the long-term surival of *A. b. vicheti* populations is surely threatenend.

Adult body size in *A. b. vicheti* is relatively small when compared to economically important, gregarious grasshoppers like *Locusta migratoria* and *Schistocerca gregaria* Forskål 1775. Nevertheless, it is one of the largest Caelifera species found in calcerous grassland habitats of the Mediterranean and female body length surpasses that of common species *Chorthippus brunneus* Thunberg 1815, *C. vagans* Eversmann 1848 and *Calliptamus barbarus* Costa 1836 by several millimeters. The majority of smaller grasshoppers in these habitats however are capable of flight. Nowadays, *A. b. vicheti* is probably threatened by manifold factors, ensuing from its low mobility and high conspicuousness, combined with an ever-increasing modification of its habitats (Reinhardt *et al.* 2005). Especially the disappearance of open grasslands within the garrigue could have detrimental effects on this species' survival due to its apparent dependence on *Thero-Brachypodietea* communities for food. Furthermore, shrub colonization of grasslands may lead to modifications in microclimate, which have been shown to have detrimental effects on acridid populations during specific phases of life history like hatching and reproduction (Bieringer & Zulka 2003). In addition, increasing aridity caused by global climate change may lead to the desiccation of high-quality food plants earlier in the season and inhibit females from satisfying their nutritional needs and/or water requirements during the reproductive period (Bernays 1990; Bernays & Simpson 1990). However, rising temperatures have also been shown to increase development rates in Orthoptera and reaching maturity earlier in the season could allow females to continue to benefit from high quality food plants throughout reproduction (Whitman 1986; Kareiva *et al.* 1993; Walters & Hassall 2006). Overall, *A. b. vicheti* adult body size suggests a trade-off between the relatively short development times needed to survive the variable Mediterranean spring season and reach maturity before summer temperatures peak, and the optimal body sizes necessary for reproduction and dispersion (Whitman 2008).

Acknowledgments. We would like to thank Jean-Francois Duranton for his advice concerning field work and plant determination, My Hanh Luong-Skovmand for her help with ovarian dissection and Alex Franc for his support with data analysis. We are also grateful to Arne Lehmann for his critical comments on our manuscript. This study was made possible by the financial support of the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD) and the Conseil Regional of the Languedoc-Roussillon region.

References

Ackman O., Whitman D.W. 2008. Analysis of body size and fecundity in a grasshopper. *Journal of Orthoptera Research* **17**: 249-257.

Anonymous 1982. *The locust and grasshopper agricultural manual*. Center of Overseas Pest Research, London, 690 p.

Bernays E.A. 1990. Water regulation, p. 129-141 *in:* **Chapman R.F., Joern A. (eds.)**, *Biology of grasshoppers*. John Wiley and Sons, New York City.

Bernays E.A., Simpson S.J. 1990. Nutrition, p. 105-128 *in:* **Chapman R.F., Joern A. (eds.)**, *Biology of grasshoppers*. John Wiley and Sons, New York City.

Berner D., Blanckenhorn W.U. 2006. Grasshopper ontogeny in relation to time constraints: adaptive divergence and stasis. *Journal of Animal Ecology* **75**: 130-139.

Berner D., Blanckenhorn W.U., Korner C. 2005. Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. *Oikos* **111**: 525-533.

Bieringer G., Zulka K.P. 2003. Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. *Biodiversity and Conservation* **12**: 1481-1495.

Blanckenhorn W.U., Dixon A.F.G., Fairbairn D.J., Foellmer M.W., Gibert P., van der Linde K., Meier R., Nylin S., Pitnick S., Schoff C., Signorelli M., Teder T., Wiklund C. 2007. Proximate causes of Rensch's rule: Does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* **169**: 245-257.

Capinera J.L. 1985. Determination of host plant preferences of *Hemileuca oliviae* (Lepidoptera: Saturniidae), *Paropomala wyomingensis* (Orthoptera: Acrididae), and *Diapheromera veli* (Orthoptera: Phasmatidae) by choice test and crop analysis. *Journal of the Kansas Entomological Society* **58**: 465-471.

Chapman R.F. 1990. Food selection, p. 39-72 *in:* **Chapman R.F., Joern A. (eds.)**, *Biology of grasshoppers*. John Wiley and Sons, New York City.

Chapman R.F., Joern A. 1990. *Biology of Grasshoppers*. John Wiley and Sons, New York City, 563 p.

Chapman R.F., Sword G.A. 1997. Polyphagy in the Acridomorpha, p. 183-195 *in:* **Gangwere S.K., Muralirangan M.C., Muralirangan M. (eds.)**, *The Bionomics of Grasshoppers, Katydids and their Kin*. CAB International, Wallingford.

Chara B. 1984. *Régimes alimentaires et production des oeufs des acridiens dans la nature*. Thèse de doctorat, Université d'Aix Marseille III, Marseille, 48 p.

Chara B., Bigot L., Loisel R. 1986. Contribution à l'étude du régime alimentaire d'*Omocestus ventralis* Zetterstedt, 1821 (Orthoptera: Acrididae) dans les conditions naturelles. *Ecologia Mediterranea* **12**: 25-32.

Danner B.J., Joern A. 2004. Development, growth, and egg production of *Ageneotettix deorum* (Orthoptera : Acrididae) in response to spider predation risk and elevated resource quality. *Ecological Entomology* **29**: 1-11.

Dempster J.P. 1963. The population dynamics of grasshoppers and locusts. *Biological Reviews of the Cambridge Philosophical Society* **38**: 490-529.

Esperk T., Tammaru T., Nylin S. 2007. Intraspecific variability in number of nymphal instars in insects. *Journal of Economic Entomology* **100**: 627-645.

Gangwere S.K. 1991. Food habits and feeding behavior of locusts and grasshoppers, p. 1-56 *in:* **Vickery V.R. (ed.)**, *Field Guides to Locusts and Grasshoppers of the World*. Orthopterists' Society Field Guide, Sainte Anne de Bellevue, QC.

Guendouz-Benrima A., Doumandji Mitiche B., Petit D. 2011. Effects of weak climatic variations on assemblages and life cycles of Orthoptera in North Algeria. *Journal of Arid Environments* **75**: 416-423.

Hochkirch A., Gärtner A.C., Brandt T. 2008. Effects of forest-dune ecotone management on the endangered heath grasshopper, *Chorthippus vagans* (Orthoptera: Acrididae). *Bulletin of Entomological Research* **98**: 449-456.

Hochkirch A., Gröning J. 2008. Sexual size dimorphism in Orthoptera (*sens. str.*) - a review. *Journal of Orthoptera Research* **17**: 189-196.

Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setala H., Symstad A.J., Vandermeer J., Wardle D.A. 2005: Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**: 3-35.

Ingrisch S. 1998. Lebenszyklus und Phänologie, p. 51-114 *in:* **Ingrisch S., Köhler G. (eds.)**, *Die Heuschrecken Mitteleuropas*. Westarp Wissenschaften, Magdeburg.

Ingrisch S., Köhler G. 1998. *Die Heuschrecken Mitteleuropas*. Westarp Wissenschaften, Magdeburg, 460 p.

Jauregui B.M., Rosa-Garcia R., Garcia U., WallisDeVries M.F., Osoro K., Celaya, R. 2008. Effects of stocking density and breed of goats on vegetation and grasshopper occurrence in heathlands. *Agriculture Ecosystems & Environment* **123**: 219-224.

Joern A., Gaines S.B. 1990. Population dynamics and regulation in grasshoppers, p. 415-482 *in:* **Chapman R.F., Joern A. (eds.)**, *Biology of grasshoppers*. John Wiley and Sons, New York City.

Kareiva P.M., Kingsolver J.G., Huey R.B. 1993. *Biotic Interactions and Global Change. Sinauer Associates*. Sunderland, MA, 559 p.

Köhler G. 1988. Persistence and Formation of Grasshopper Associations (Orthoptera: Acrididae) in Central European Grassland Ecosystems. *Zoologische Jahrbücher* **115**: 303-327.

Köhler G. 1998. Nahrung, p. 148-186 *in:* **Ingrisch S., Köhler G. (eds.)**, *Die Heuschrecken Mitteleuropas*. Westarp Wissenschaften, Magdeburg.

Köhler G., Brodhun H.P. 1987. Untersuchungen zur Populationsdynamik zentraleuropäischer Feldheuschrecken (Orthoptera: Acrididae). *Zoologische Jahrbücher* **114**: 157-191.

Kriegbaum H. 1997. Grasshopper Reproductive Strategies Measured in the Field: a Trade-off Between Age at Maturity and Egg Production per Day. *Naturwissenschaften* **84**: 157-159.

Kruseman G. 1982. *Matériaux pour la faunistique des Orthoptères de France 2: les acridiens des Musées de Paris et d'Amsterdam*. Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam, Amsterdam, 133 p.

Launois-Luong M.H. 1978. Méthode pratique d'interprétation de l'état des ovaires des acridiens du Sahel. *Annales de Zoologie Ecologie Animale* **10**:569-587.

Launois-Luong M.H. 1979. Étude comparée de l'activité génésique de sept acridiens du Sahel dans des conditions éco-météorologiques semblables. *Annales de Zoologie Ecologie Animale* **11**: 209-226.

Lecoq M. 1975. *Les déplacements par vol du Criquet migrateur malgache en phase solitaire: leur importance sur la dynamique des populations et la grégarisation*. Ministère de la Coopération, Paris, 272 p.

Lehmann G.U.C., Lehmann A.W. 2008. Variation in Body Size among Populations of the Bushcricket *Poecilimon thessalicus* (Orthoptera: Phaneropteridae): An Ecological Adaptation? *Journal of Orthoptera Research* **17**: 165-169.

Maes D., Ghesquiere A., Logie M., Bonte D. 2006. Habitat Use and Mobility of Two Threatened Coastal Dune Insects: Implications for Conservation. *Journal of Insect Conservation* **10**: 105-115.

Maklakov A.A., Bilde T., Lubin Y. 2004: Sexual selection for increased male body size and protandry in a spider. *Animal Behavior* **68**: 1041-1048.

Monard A. 1986. *Étude bio-écologique des peuplements acridiens du Bas-Languedoc*. Thèse de doctorat, Université Pierre et Marie Curie, Paris, 543 p.

Moritz L.D. 1915. *Biological observations on Acrididae of the Turgai province*. Lyubitel Prirodui, St. Petersburg, 29 p. [In Russian].

Muralirangan M.C., Muralirangan M., Partho P.D. 1997. Feeding behaviour and host selection strategies in acridids, p.163-182 *in:* **Gangwere S.K., Muralirangan M.C., Muralirangan M. (eds.)**, *The Bionomics of Grasshoppers, Katydids and Their Kin*. CAB International, Wallingford.

Navarro T., Alados C.L., Cabezudo, B. 2006. Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *Journal of Arid Environments* **64:** 298-322.

Picaud F., Nanthieras C., Coudon I., Bellet A., Petit D. 1999. Gradation dans l'abandon de la graminivorie chez deux sous-espèces de *Chorthippus binotatus* (Acrididae: Gomphocerinae): approches descriptives et expérimentales. *Annales de la Société Entomologique de France (N.S.)* **35**: 238-241.

Ramsay G.W. 1964. Moult number in Orthoptera. *New Zealand Journal of Science* **7**: 644-666.

Raubenheimer D., Simpson S.J. 2003. Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. *Journal of Experimental Biology* **206**: 1669-1681.

Reinhardt K., Kohler G., Maas S., Detzel P. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography* **28**: 593-602.

Richards O.W., Waloff N. 1954. Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bulletin* **17**: 1-182.

Roff D.A. 2002. *Life History Evolution*. Sinauer Associates, Sunderland, MA, 527 p.

Samways M.J. 1994. *Insect Conservation Biology*. Chapman and Hall, London, 358 p.

Samways M.J. 1997. The Conservation Biology of Orthoptera, p. 481-496 *in:* **Gangwere S.K., Muralirangan M.C., Muralirangan M. (eds.)**, *The Bionomics of Grasshoppers, Katydids and their Kin*. CAB International, Wallingford.

Samways M.J. 2005. *Insect Diversity Conservation*. Cambridge University Press, Cambridge, 342 p.

Samways M.J. 2009. Insect population changes and conservation in the disturbed landscapes of mediterranean-type ecosystems, p. 313-331 *in:* **Rundel P.W. (ed.)**, *Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems*. Springer, New York.

Samways M.J., Lockwood J.A. 1998. Orthoptera conservation : pests and paradoxes. *Journal of Insect Conservation* **2**: 143-149.

Uvarov B.P. 1966. *Grasshoppers and locusts. A handbook of general acridology. Volume 1*. University Press, Cambridge, 475 p.

Uvarov B.P. 1977. *Grasshoppers and locusts. A handbook of general acridology. Volume 2*. Centre for Overseas Pest Research, London, 613 p.

Voisin, J.F. 2003. Atlas des Orthoptères (Insecta: Orthoptera) et des Mantides (Insecta: Mantodea) de France. *Patrimoines naturels* **60**: 1-104.

Walters R.J., Hassall M. 2006. The temperature-size rule in ectotherms: may a general explanation exist after all? *American Naturalist* **167**: 510-523.

Wedell N. 1992. Protandry and mate assessment in the Wartbiter *Decticus verrucivorus* (Orthoptera: Tettigoniidae). *Behavioral Ecology and Sociobiology* **31**: 301-308.

Weidner H. 1969. Beobachtungen wandernder Feldheuschrecken auf hoher See. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* **42**: 118-121.

Whitman D.W. 1986. Developmental thermal requirements for the grasshopper *Taeniopoda eques* (Orthoptera: Acrididae). *Annals of the Entomological Society of America* **79**: 711-714.

Whitman D.W. 2008. The significance of body size in the Orthoptera: a review. *Journal of Orthoptera Research* **17**: 117-134.

Wiklund C., Forsberg J. 1991. Sexual size dimorphism in relation to female polygamy and protandry in butterflies - A comparative study of Swedish Pieridae and Satyridae. *Oikos* **60**: 373-381.