

Somatic and population adaptations of *Polysarcus denticauda* (Orthoptera) in extreme altitudes

Peter Kaňuch & Anton Krištín

Kaňuch, P. & Krištín, A. 2009: Somatic and population adaptations of *Polysarcus denticauda* (Orthoptera) in extreme altitudes. — Entomol. Fennica 20: 207–214.

Altitudinal preferences, somatic and population adaptations in different ecological conditions were analysed in flightless bush-cricket species *Polysarcus denticauda* (Charpentier, 1825). Altitudinal analysis was performed in GIS software (more than 60 sites in Slovakia, Central Europe). Seasonal occurrence and population density were recorded in selected sites. To compare differences, absolute values of measurements (length of body, hind femur and tibia, cerci and weight) and Body Condition Index were taken from males. Study species prefers mesophilous montane up to alpine meadows in higher elevations (over 600 m a.s.l.). The development started over one month earlier in lowlands and populations reached several fold higher density there. Males from lowlands had body parameters significantly bigger apart from cerci. Cerci were significantly longer in males from mountains. However, males of the same size were significantly heavier in higher altitudes. In conclusion, refuges of montane meadows ecosystem support species survival nowadays.

P. Kaňuch, A. Krištín, Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, SK-960 53 Zvolen, Slovakia; E-mail: kristin@savzv.sk

P. Kaňuch, Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden; E-mail: kanuch@netopiere.sk

Received 29 July 2008, accepted 23 October 2008

1. Introduction

During evolution, some animal species survived in habitats of various altitudes and reconstruction of their origin is difficult today. A possible key to answer this question can be the ecological and morphological adaptations at various altitudes (Blackburn *et al.* 1999, Hodkinson 2005). Generally by “Bergmann’s rule”, there is an assumption that at higher altitudes individuals of species are bigger (Atkinson & Sibly 1997). However, literature exists that cite many examples to support or disprove this rule (for a review see Blackburn *et al.* 1999). The response of invertebrate species to different environments experienced along alti-

tudinal gradients is diverse and often contradictory. Some aspects of insect ecology show a positive or negative reaction to altitudinal changes (Hodkinson 2005). There are many examples of various taxonomic and ecological invertebrate groups, e.g. butterflies (Hawkins & DeVries 1996), grasshoppers (Berner *et al.* 2004, Berner & Blanckenhorn 2006, Bidau & Marti 2007), beetles (Smith *et al.* 2000), land snails (Hausdorf 2003), etc.

There are hypotheses that such responses may serve as analogues for climate warming effects occurring at a particular fixed altitude or latitude over time. Hodkinson (2005) reviewed factors that individually and collectively influenced the

morphology, behaviour, ecophysiology, growth and development, survival, reproduction, abundance, and spatial distribution of insect species and communities in different altitudes. Reactions can be direct, with insect characteristics or performance responding to changing environmental parameters (e.g. Roff 1990, Joyce *et al.* 2004), or they can be indirect and mediated through the insect's interaction with other organisms (the host plant in the case of herbivorous insects, competitor species, parasitoids, predators and pathogens; e.g. Smith & Donahue 1991, Bird & Hodgkinson 1999).

For the study of animal life strategies along elevational gradients, less mobile and well-distributed species are appropriate (Hausdorf 2003, Joyce *et al.* 2004). In our study we used model, flightless species of bush-cricket *Polysarcus denticauda* (Charpentier, 1825; Orthoptera: Tettigoniidae) which occurs in various, often even extreme altitudes in its area of distribution (Harz 1969, Thorens & Nadig 1997, Detzel 1998). Questions about the species' existence in extreme altitudinal conditions and its possible adaptations in different environments motivated us i) to analyse altitudinal distribution in Central Europe (Slovakia) with the aim to identify altitudinal (habitat) preferences and ii) to identify somatic and population adaptations in different ecological conditions of extreme altitudes.

2. Material and methods

2.1. Study species

Polysarcus denticauda is one of the biggest short-wing species of European bush-crickets (Harz 1969). It is unable to fly, awkward in jumping, therefore restricted in its spreading in to new areas. Body length can reach 47 mm, weight 6 g. This obligatory herbivorous species occurs in meadow habitats and in a wide range of altitudes from lowlands up to 2,300 m a.s.l. (Harz 1969, Detzel 1998). In spite of that, more studies consider it as orophilous species, thus associated with mountain meadows (Frivaldszky 1867, Detzel 1998, Ingrisch & Köhler 1998, Maas *et al.* 2002). However, mass (outbreak) occurrence was observed in lowlands in the past; e.g. in Hungary

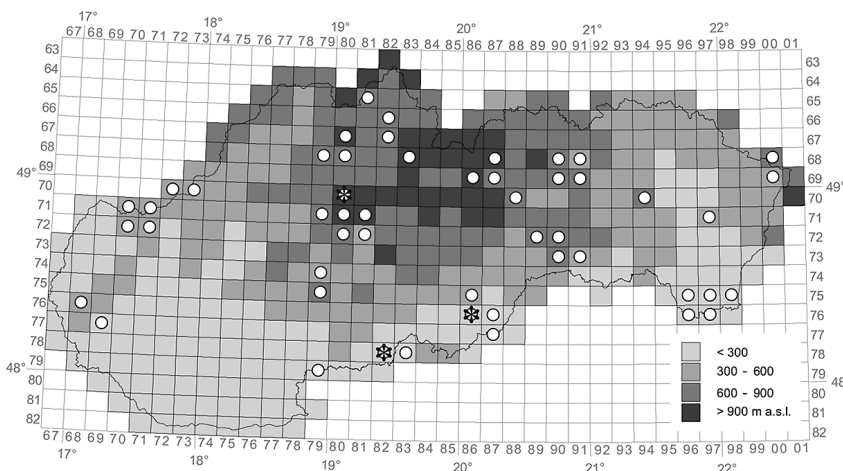
(Nagy 1983), Austria (Berg & Zuna-Kratky 1997), Slovenia (Us 1992) and Slovakia (Gulička 1954). Its origin is unclear; often Pontic or Ponto-Mediterranean origin is mentioned and current occurrence is restricted to Europe (Detzel 1998, Ingrisch & Köhler 1998). In a lot of European countries it is endangered by the intensification of agriculture (destruction of meadows). Thus in lowlands and Western Europe, populations are quite isolated (Detzel 1998).

2.2. Data collection and analysis

Data about species distribution in selected area of Slovakia were obtained from more than 60 sites. Historical (since 19th cent.; Frivaldszky 1867) and recently published (since 1954) and own data since 1994–2007 were collated (Krištín *et al.* 2008). Altitudinal analysis was performed in mapping squares DFS (Slovak Fauna Databank). Mean altitude of each from 430 squares (ca. 11 × 12 km) in the area of Slovakia (ca. 50,000 km²) was computed using values of contour lines (gauge was 10 m) crossing a square in software ArcView GIS 3.2 (Fig. 1). Area was divided into four altitudinal levels (< 300 m a.s.l. = 35% of the area, 300–600 = 33%, 600–900 = 24%, and > 900 = 8%). On the base of positive recorded species occurrence in mapping squares, possible trend of altitude preference was tested using simple regression.

Populations from extreme locations (lowland and montane) within Slovakia were selected for the analysis of differences in population characteristics of the species (Fig. 1). During a long-term survey of species distribution in 1996–2007, seasonal occurrence of developmental stadiums and sexes (n = 17 lowland, 8 montane sites) and population density (n = 2 sites, each with 10 plots in size 100 m² from lowland and montane sites, respectively) were recorded. Population density was surveyed acoustically by the number of singing males at the peak season (10–14 days after hatching of imagos) and all males were checked individually by catching and releasing them after census. Standard and similar sampling conditions (sunny and warm weather, 24–26 °C around midday) ensured comparable data without effect of temperature on insect activity (according to Niel-

Fig. 1. Distribution of *Polysarcus denticauda* in mapping squares DFS in Slovakia (white circles; detailed data set is presented in Krištín *et al.* 2008), categorised in four altitudinal levels (the level presents average altitude of the square). Sampling sites LOW (two from lowland) and MON (one from mountains) are shown with asterisk.



sen 1971). Abundance estimation of simultaneously singing males was performed on mentioned plots during three-hourly visits of 3–4 field workers. Differences in population abundance between lowland and montane populations were tested using non-parametric Mann-Whitney *U*-test.

Biometric analysis was performed on the sample of two lowland populations (LOW = Peťov and Bakta, Juhoslovenská kotlina Basin, 48° 06' 12"–48° 23' 54" N, 19° 28' 58"–20° 05' 27" E, mesophilous hay meadows, S–SE aspect, slope < 10°, 160–280 m a.s.l., 9.1 °C average annual temperature) and one montane population (MON = Križna, Veľká Fatra Mts., 48° 53' 12" N, 19° 02' 33" E, mesophilous mountain hay meadows, W–SW aspect, slope 10–40°, 1,400–1,500 m a.s.l., 2.6 °C average annual temperature, Fig. 1). Lowland sites are 90 and 95 km away as the crow flies from the montane population. Independence between montane and lowland populations was defined by accompanying orthopteran species composition. Altogether, 79% of species occurred exclusively on lowland or montane sites ($n = 38$ species). Montane community characterised species as *Metrioptera brachyptera* (Linnaeus, 1761), *Miramella alpina* (Kollar, 1833), *Podisma pedestris* (Linnaeus, 1758), *Pseudopodisma nagyii* Galvagni et Fontana, 1996, *Arcyptera fusca* (Pallas, 1773) and lowland *Leptophyes albiovittata* (Kollar, 1833), *Phaneroptera falcata* (Poda, 1761), *Conocephalus fuscus* (Fabricius, 1793), *Ruspolia nitidula* (Scopoli, 1786),

Oecanthus pellucens (Scopoli, 1763), respectively.

Bush-cricket was collected and measured at the time of peak imago activity ($n_{\text{LOW}} = 28$, $n_{\text{MON}} = 32$ males and $n_{\text{LOW}} = 21$, $n_{\text{MON}} = 1$ females). Immediately after measurements, individuals were released at the site of capture. Biometric data represent: length of body, hind right femur and tibia, right cercus (Fig. 2; ovipositor in females) and weight. Females occurred in both sites but for biometric analysis were not used, because we did not determine stage of eggs development (which modify body length and weight). All males used for analysis were singing, i.e. spermatophore de-

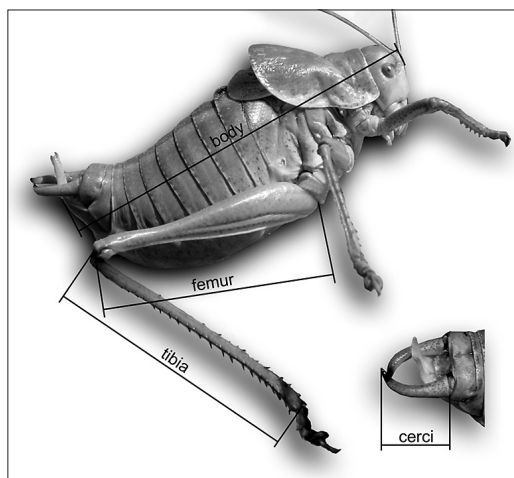


Fig. 2. Measurements of *P. denticauda* males used in this study.

velopment (weight) was in the equal pre-copulation phase (Loher & Dambach 1989). The hand measurement of live individuals was performed by the same author and digital calliper (accuracy ± 0.03 mm).

Body weight was determined by pocket digital scale (accuracy ± 0.1 g). Since absolute weight also increases with body size, for determination of relative fitness we used Body Condition Index (BCI). For our purpose it was slightly modified (see Ransome 1995) and calculated as mean of partial indices (i.e. body mass (g)/ selected measurement (mm), multiplied by average value of selected measurement in population). Our modification took into account four length measurements which should avoid the overestimation of one measurement.

Differences in all body measurements between two types of populations were tested using non-parametric Mann-Whitney *U*-test.

3. Results

3.1. Altitudinal preferences

Mean altitude of species occurrence (median \pm 95% CI) in the study area was 610 ± 4 m a.s.l. ($n = 50$ sites). The highest altitude recording of the species was 1,630 m a.s.l. On the basis of analysis of altitudinal distribution it is apparent that the species prefers higher elevations (over 600 m a.s.l., Fig. 3). The number of mapping squares decreases with their increasing mean altitude in Slovakia. However, the percentage of positive squares ($n = 51$) significantly increased with altitude. The highest percentage was in the highest level (over 900 m a.s.l., $R^2 = 0.018$, ANOVA $F_{(1,428)} = 7.994$, $p = 0.005$). In these elevations, the species occurs in mesophilous montane up to alpine meadows above tree line and in isolated forest meadows with traditionally long-term mow and pasture management. Except for mountain areas, the species occurs also in lowlands and basins (from 120 up to 300 m a.s.l., Fig. 1). Similarly, the species occurred in mesophilous meadows. Lowland meadows, neighbouring or surrounded by arable land, sometimes also with wetlands, were always located in areas of less intensive agriculture.

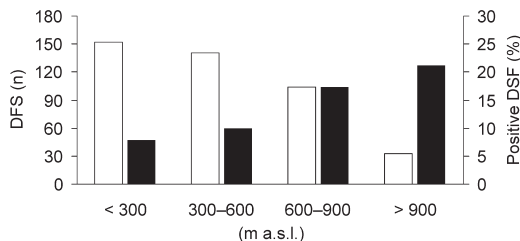


Fig. 3. Number of mapping squares DFS (white columns, see Fig. 1) and percentage of positive squares with occurrence of *P. denticauda* (black columns) in four altitudinal levels in Slovakia.

3.2. Seasonal occurrence and population density

Regarding seasonal occurrence, the development of males and females started over one month earlier in lowland populations. Male imagos in sites with low elevation had already occurred by the end of May (26 May – 15 July) and females in early June (6 June – 25 July, $n = 17$ localities). In comparison, the occurrence of adult males was not found until the beginning of July (3 July – 20 August) and females in mid-July (15 July – 24 August, $n = 8$ localities) in montane sites. Populations reached six fold higher density in lower altitudes (Mann-Whitney *U*-test; $Z = 5.410$, $p = 0.000$). Median (Min–Max) density of singing males was 12 (9–24)/ 100 m² ($n = 20$ plots) in

Table 1. Descriptive statistic of *Polysarcus denticauda* males ($n = 60$) and females ($n = 22$) in Slovakia (measurements were taken as shown in Fig. 2).

Measurement	Mean \pm SD	Min–Max
<i>Males</i>		
Body (mm)	34.9 \pm 1.5	31.2–38.2
Hind femur (mm)	23.3 \pm 1.9	19.9–27.2
Hind tibia (mm)	24.0 \pm 2.2	20.2–28.6
Cerci (mm)	6.1 \pm 0.4	5.2–7.1
Weight (g)	3.1 \pm 0.3	2.4–3.7
<i>Females</i>		
Body (mm)	41.7 \pm 2.9	36.3–48.3
Hind femur (mm)	26.7 \pm 1.1	22.3–27.9
Hind tibia (mm)	28.6 \pm 1.6	22.8–30.6
Ovipositor (mm)	21.1 \pm 0.7	19.6–22.3
Weight (g)	5.1 \pm 0.5	4.1–5.9

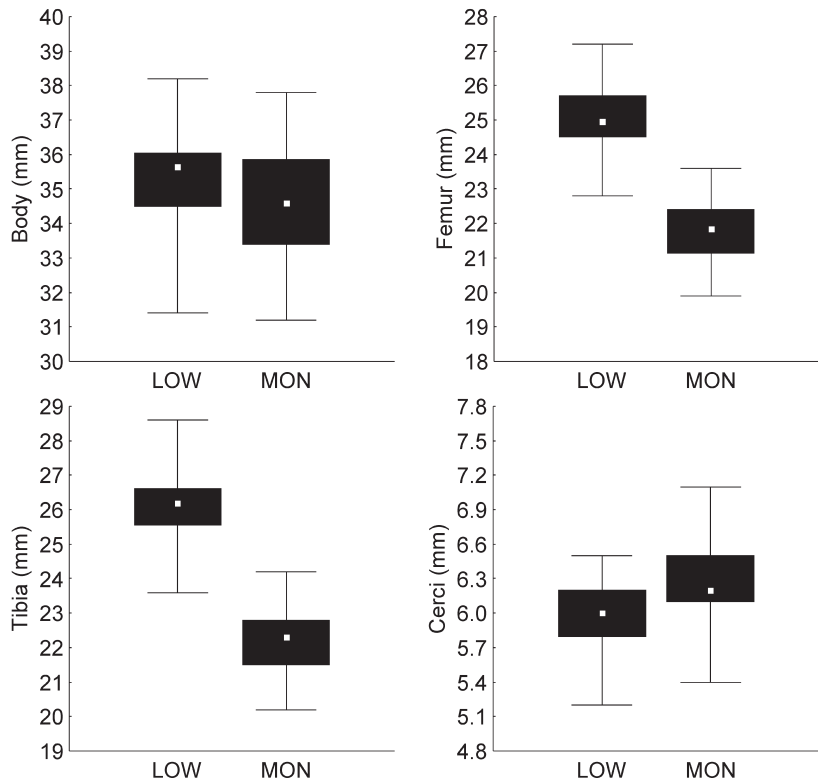


Fig. 4. Comparison of measurements (body length, hind femur and tibia, cerci) of males from lowland ($n_{LOW} = 28$) and montane ($n_{MON} = 32$) elevations (middle point = median, box = percentiles 25–75%, whiskers = min–max range).

lowlands. In contrast, we found only 2 (1–8) males/ 100 m² ($n = 20$ plots) in montane meadows.

3.3. Body size variation

In conditions of Central Europe, males of *P. denticauda* reached mean (\pm SD) body length 34.9 ± 1.5 mm and weight 3.1 ± 0.3 g, and females 41.7 ± 2.9 mm and 5.1 ± 0.5 g, respectively (Table 1). When comparing absolute values of measurements, males from lower elevations had body parameters significantly bigger (Mann-Whitney *U*-test; body – $Z = 2.159$, $p = 0.031$; femur – $Z = 6.572$, $p < 0.001$; tibia – $Z = 6.594$, $p < 0.001$), apart from cerci ($n_{LOW} = 28$, $n_{MON} = 32$ males; Fig. 4). Cerci were significantly longer in males from montane population ($Z = -3.215$, $p = 0.001$). No difference was found in absolute weight in comparison of lowland and montane individuals. It resulted in the determination of relative size of males which illustrated individual fitness. Considering body weight to body size (in BCI) we

found that males of the same size would be significantly heavier in higher altitudes (Mann-Whitney *U*-test; $Z = -4.282$, $p < 0.0001$, Fig. 5).

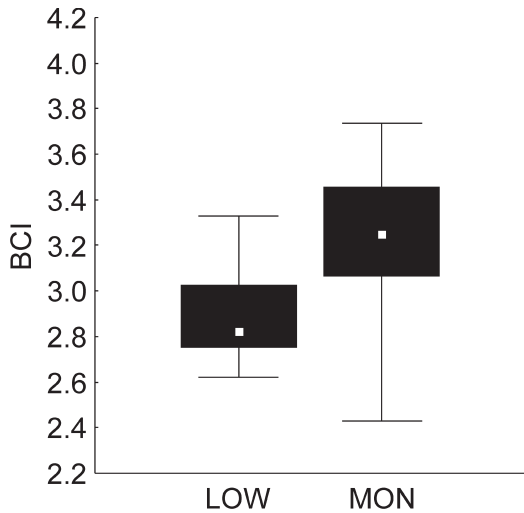


Fig. 5. Comparison of Body Condition Index of males from lowland ($n_{LOW} = 28$) and montane ($n_{MON} = 32$) elevations (middle point = median, box = percentiles 25–75%, whiskers = min–max range).

4. Discussion

Similar to other invertebrates, questions about altitude (habitat) preferences and origin of model species remain open (cf. Nagy 1960, Detzel 1998). Historical data show the species' occurrence to be equal in mountain as well as in lowland regions (Frivaldszky 1867, Horváth 1890, Gulička 1954, Detzel 1998, Holuša *et al.* 2007) and so its distribution in some of these regions is certainly not invasive. However, nowadays, *P. denticauda* in particular mainly occurs in mountain mesophilous meadows in Europe (Maas *et al.* 2002); in lowlands, it survives only in the most preserved natural meadow habitats (e.g. Hortobágy – Nagy 1983, Neusiedler See – Berg & Zuna-Kratky 1997).

Many studies analysed adaptative mechanisms of invertebrates to various elevations. At high altitude, grasshoppers *Omocestus viridulus* (Linnaeus, 1758) evolved faster development and the correlated change in body size led to an altitudinal size cline mediating a trade-off with female fecundity (Berner & Blanckenhorn 2006). It is generally accepted, that individuals are smaller in bigger population density (also because there is less food and space). As a consequence, abundance is constrained by energy availability (Blackburn & Gaston 1999) and diurnal course of activity (Nielsen 1971). Such a pattern also appears in grasshoppers tending to outbreaks (e.g. *Doclostaurus maroccanus* (Thunberg, 1815) – Nagy 1995). Similarly, during rare outbreaks in *P. denticauda* (up to 20 ind./ m²), individuals which have migratory behaviour have a smaller body size and darker coloration (Harz 1969, Detzel 1998). That phenomenon appeared only in lowlands in conditions of Central Europe. However, it has not been observed for at least the last 55 years (cf. Gulička 1954, Detzel 1998). In our study we found that in lower altitudes males had bigger density, ontogenetic development of both sexes started earlier and males reached bigger absolute body size (Fig. 4). In total, biometric parameters of montane or lowland males and females (Table 1) fit averages found in the species area of distribution (Harz 1969).

Thus Bergmann's rule was not confirmed in our study. The South American grasshopper *Dichroplus vittatus* Bruner, 1900 also followed

the converse to Bergmann's rule latitudinally but not altitudinally where no significant trends were observed. For males, variability of body size increased with latitude but not with altitude (Bidau & Marti 2007). Likewise, there is no significant correlation between body size of land snail species and altitude in the Alps although a negative correlation of body size and altitude is frequent within species (Hausdorf 2003). Even in montane beetles of the genus *Nicrophorus*, individuals were always greater at the lower elevations and the results indicate that both life-history strategies and developmental processes may be involved in the elevational variation (Smith *et al.* 2000). In support of Bergmann's rule is the finding of increasing body size with increasing altitude and decreasing temperature with the mountain cricket *Hemideina maori* (Pictet et Saussure, 1891) in New Zealand (Joyce *et al.* 2004). Chown & Klok (2003) tested the hypothesis by comparing intraspecific altitudinal body size clines in a monophyletic group of weevils (Coleoptera) from two regions that differ substantially in seasonality. On a relatively aseasonal island, body size increases with altitude, whereas on the more seasonal island the opposite was found. In Tenebrionidae (Coleoptera) from Israel it was found that body size was not correlated with altitude in three species, while four species demonstrated changes in body size with altitude. Three species decreased their body size along the altitudinal gradient, whereas one demonstrated the opposite trend (Krasnov *et al.* 1996).

For indirect calculation of individual fitness, there exists the suitable and easy tool of BCI (Ransome 1995), which was used in our study. Although in lower altitudes our bush-cricket were absolutely bigger (suitable microclimate for development), we can conclude that in higher elevations individuals survive with higher fitness (Fig. 5). It is known that length of bush-cricket cerci (used to facilitate copulation) correlates with males' mating success (Ritz & Sakaluk 2002, Vahed 2002). We suggest that our montane males are sexually more efficient. Moreover, preference for heavier males may reflect a female's preference for a larger spermatophore and therefore a greater direct benefit (Lehmann & Lehmann 2008). In conclusion, *P. denticauda* seems to be originally a lowland species, which

corroborates the data about outbreaks from low altitudes in the past (Gulička 1954, Harz 1969, Detzel 1998). However, on the base of present distributional patterns, somatic and population adaptations, refuges of montane meadow ecosystems support species' survival nowadays. This habitat is where core populations of the species are distributed today (Pyrenees, Alps, and Carpathians).

Acknowledgements. We would like to thank Vladimíra Fabriciusová, Peter Tuček, Marek Veľký, Martin Sáróssy and Branislav Kršiak for assistance in field work, and Sally Phillips for language improvement. Anonymous referees are acknowledged for comments and criticism of the previous version of the manuscript. This work was funded by VEGA Grant Agency (Nos. 2/0130/08, 2/0110/09).

References

- Atkinson, D. & Sibly, R. M. 1997: Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. — *Trends in Ecology and Evolution* 12: 235–239.
- Berg, H.-M. & Zuna-Kratky, T. 1997: Heuschrecken und Fangschrecken. Eine Rote Liste der in der Niederösterreich gefährdeten Arten. — NÖ Landesregierung, Wien. 112 pp.
- 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., Korner, C. & Blanckenhorn, W. U. 2004: Grasshopper populations across 2000 m of altitude: is there life history adaptation? — *Ecography* 27: 733–740.
- Bidau, C. J. & Marti, D. A. 2007: *Dichroplus vittatus* (Orthoptera: Acrididae) follows the converse to Bergmann's rule although male morphological variability increases with latitude. — *Bulletin of Entomological Research* 97: 69–79.
- Bird, J. M. & Hodkinson, I. D. 1999: Species at the edge of their range: The significance of the thermal environment for the distribution of congeneric *Craspedolepta* species (Sternorrhyncha: Psylloidea) living on *Epilobium angustifolium* (Onagraceae). — *European Journal of Entomology* 23: 1–8.
- Blackburn, T. M. & Gaston, K. J. 1999: The relationship between animal abundance and body size: A review of the mechanisms. — *Advanced Ecology Research* 28: 181–210.
- Blackburn, T. M., Gaston, K. J. & Loder, N. 1999: Geographic gradients in body size: a clarification of Bergmann's rule. — *Diversity and Distributions* 5: 165–174.
- Chown, S. L. & Klok, C. J. 2003: Altitudinal body size clines: latitudinal effects associated with changing seasonality. — *Ecography* 26: 445–455.
- Detzel, P. 1998: Die Heuschrecken Baden-Württembergs. — Verlag Eugen Ulmer, Stuttgart. 580 pp.
- Frivaldszky, J. 1867: A magyarországi egyenesröpök magánrajza (Monographia Orthopterorum Hungariae). — Egenberger Ferdinand Magyar Akadémia Könyvtárusnál, Pest. 201 pp. [In Hungarian.]
- Gulička, J. 1954: Beitrag zur Kenntnis der Verbreitung einiger Orthopteren und Dermapteren in der Slowakei. — *Biologia, Bratislava* 9: 617–630. [In Slovak with German abstract.]
- Harz, K. 1969: Die Orthopteren Europas. Vol. I. — Verlag Dr. W. Junk B. V., Den Haag. 749 pp.
- Hausdorf, B. 2003: Latitudinal and altitudinal body size variation among north-west European land snail species. — *Global Ecology and Biogeography* 12: 389–394.
- Hawkins, B. A. & DeVries, P. J. 1996: Altitudinal gradients in the body sizes of Costa Rican butterflies. — *Acta Oecologica* 17: 185–194.
- Hodkinson, I. D. 2005: Terrestrial insects along elevation gradients: species and community responses to altitude. — *Biological Reviews* 80: 489–513.
- Holuša, J., Kočárek, P. & Marhoul, P. 2007: Occurrence of the bush-cricket *Polysarcus denticauda* (Ensifera: Tettigoniidae) in the Czech Republic. — *Práce a studie Muzea Beskyd* 19: 254–255. [In Czech with English abstract.]
- Horváth, G. 1890: *Orphanía denticauda* Charp. — *Természettudományi Közlöny* 22: 444–445. [In Hungarian.]
- Ingrisch, S. & Köhler, G. 1998: Die Heuschrecken Mitteleuropas. Die Neue Brehm Bücherei 629. — Westarp Wissenschaften, Magdeburg. 460 pp.
- Joyce, S. J., Jamieson, I. G. & Barker, R. 2004: Survival of adult mountain stone weta *Hemideina maori* (Orthoptera: Anostomatidae) along an altitude gradient as determined by mark-recapture. — *New Zealand Journal of Ecology* 28: 55–61.
- Krasnov, B., Ward, D. & Shenbrot, G. 1996: Body size and leg length variation in several species of darkling beetles (Coleoptera: Tenebrionidae) along a rainfall and altitudinal gradient in the Negev Desert (Israel). — *Journal of Arid Environment* 34: 477–489.
- Krištín, A., Kaňuch, P., Fabriciusová, V. & Balla, M. 2008: On distribution and ecology of the bush-cricket *Polysarcus denticauda* (Orthoptera, Tettigoniidae) in Slovakia. — *Polish Journal of Entomology* 77 (In press.).
- Lehmann, G. U. C. & Lehmann, A. W. 2008: Bushcricket song as a clue for spermatophore size? — *Behavioral Ecology and Sociobiology* 62: 569–578.
- Loher, W. & Dambach, M. 1989: Reproductive behavior. — In: Huber, F., Moore, T. E. & Loher, W. (eds.), *Cricket behavior and neurobiology*: 43–82. Cornell University Press, Ithaca. 565 pp.
- Maas, S., Detzel, P. & Staudt, A. 2002: Gefährdungsanalyse der Heuschrecken Deutschlands. Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte. — Bun-

- desamt für Naturschutz, Bonn-Bad Godesberg. 401 pp.
- Nagy, B. 1960: Vertikale Grenzen des Vorkommens der Sägeschrecke (*Saga pedo* Pall.) in Ungarn. — *Folia Entomologica Hungarica* (S. N.) 13: 251–252.
- Nagy, B. 1983: A survey of the Orthoptera fauna of the Hortobágy National Park. — In: Mahunka, S. (ed.), *The Fauna of the Hortobágy National Park II*: 81–117. Akadémiai Kiadó, Budapest. 489 pp.
- Nagy, B. 1995: Are locust outbreaks a real danger in the Carpathian Basin in the near future? — *Journal of Orthoptera Research* 4: 143–146.
- Nielsen, E. T. 1971: Stridulatory activity of *Eugaster* (Orthoptera, Ensifera). — *Entomologia Experimentalis et Applicata* 14: 234–244.
- Ransome, R. D. 1995: Earlier breeding shortens life in female greater horseshoe bats. — *Philosophical Transactions of the Royal Society of London B* 350: 153–161.
- Ritz, M. S. & Sakaluk, S. K. 2002: The role of the male's cerci in copulation and mate guarding in decorated crickets (*Gryllodes sigillatus*). — *Journal of Zoology, London* 257: 519–523.
- Roff, D. A. 1990: The evolution flightlessness in insects. — *Ecological Monographs* 60: 389–422.
- Smith, W. K. & Donahue, R. A. 1991: Simulated influence of altitude on photosynthetic CO₂ uptake potential in plants. — *Plant Cell and Environment* 14: 133–136.
- Smith, R. J., Hines, A., Richmond, S., Merrick, M., Drew, A. & Fargo, R. 2000: Altitudinal variation in body size and population density of *Nicrophorus investigator* (Coleoptera: Silphidae). — *Environmental Entomology* 29: 290–298.
- Thorens, P. & Nadig, A. 1997: Atlas de distribution des Orthopteres de Suisse. Documenta faunistica helvetiae 16. — Centre suisse de cartographie de la faune, Neuchâtel. 236 pp.
- Us, P. A. 1992: Fauna of Orthopteroidea in Slovenija. — Slovenska akademija znanosti i umetnosti, Ljubljana. 314 pp. [In Slovenian.]
- Vahed, K. 2002: Coercive copulation in the alpine bush-cricket *Anonconotus alpinus* Yersin (Tettigoniidae: Tettigoniinae: Platycleidini). — *Ethology* 108: 1065–1075.