



INTERSEXUAL DIFFERENCES IN BODY TRAITS IN SELECTED COCKROACH SPECIES*

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Abstract

In cockroaches sexual dimorphism in body size is common and all patterns are exhibited, however female size bias predominates. The aim of present study was to evaluate intersexual differences in body dimensions and weight in 12 cockroach species: *Blaberus craniifer* Burmeister, *Blaberus discoidalis* Serville, *Blaberus boliviensis* Princis, *Eublaberus posticus* (Erichson), *Eublaberus distantii* (Kirby), *Archimandrita tessellata* Rehn, *Blaptica dubia* (Serville), *Panchlora nivea* (L.), *Nauphoeta cinerea* (Olivier), *Phoetalia pallida* (Brunner von Wattenwyl), *Shelfordella lateralis* (Walker) and *Periplaneta americana* (L.). Fifty male and 50 female adults of each species were weighted and their body length, length and width of pronotum and lengths of antennae and tegmina were measured. In all species female-biased sexual size dimorphism was present: females were significantly heavier and their pronota were longer and wider. Also females body length had higher values in 10 out of 12 species. In other two species intersexual differences in body length appeared to be insignificant. On the other hand, male antennae were significantly longer in majority of studied species, with exception of *P. nivea*, *P. pallida* and *N. cinerea*. Thus, in majority of studied species, males had longer antennae in spite of their smaller sizes.

Introduction

Cockroaches inhabit various natural and anthropogenic habitats. Most species of cockroaches dwell in the tropical or subtropical areas (HUTCHINS et al. 2003). They make up to 24% of the today's tropical forests

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canopies biomass (BASSET 2001). On the other hand, dozens of species of cockroaches are able to adapt to live in human-changed environment.

In the natural environment cockroaches are important organisms as detritivores (NALEPA et al. 2001, SCHEU and SETALA 2002). They feed on dead vegetation, animals and excrements (ROTH and WILLIS 1957), thereby maintaining a balance in the ecosystem. They may be the part of the food chain as nourishment for insectivorous plants, other insects, amphibians, reptiles and mammals (BOROSSUT 1983).

Many cockroach species are able to colonize different environments. In addition to their natural environments as forests, grassland and caves, they are perfectly adapted to anthropogenic environments. In most cases, man is responsible for spreading cockroaches to new environments (ROTH and WILLIS 1960).

Most people perceive cockroaches as negative figures in the world of insects. It is partly justified because they carry pathogens, parasites, etc. They also cause damage or contaminate food. However, only some species of this group can be threat to humans. People take actions to control species considered as pests such as *Periplaneta americana*, *Blatta orientalis*, *Blatta germanica* and *Nauphoeta cinerea* (HILL 2002). Despite many concerns, cockroaches are increasingly selected as model animals in many studies and projects (HUBER et al. 1990). The studies on cockroaches are focused on morphology, physiology, behaviour, evolution and pathogen transmission (BELL 1981). These insects are characterized by easy adaptation to new condition, fast growth, high fertility, vitality and are omnivorous (SCHAL et al. 1984).

The above mentioned facts increase interest in cockroaches in many areas, they are used as feed for exotic animals and kept as pets.

Characteristics that are relevant to determine sexual dimorphism can be the size, shape and colour of particular body parts such as the head (antennae, composed eyes), thorax (pronotum, hindwings, forewings, tegmina, legs) or abdomen (tergum, sternum, subgenital plate, styli, cerci) (BELL et al. 2007). Measurement of body length used in research sometimes depends on wings presence. Some authors measure body length from top of the head to the end of abdomen, while others measures from the beginning of the pronotum to the end of the wings. Sexual dimorphism in body size (sexual size dimorphism – SSD) is common in cockroaches and all patterns exist, but female size bias predominates (BELL et al. 2007). Depending on which sex is larger, it is defined as female-biased sexual size dimorphism (female-biased SSD) or male-biased sexual size dimorphism (male-biased SSD) (BLANCKENHORN et al. 2009). Females of cockroaches often are heavier, and have larger abdomen, sometimes incubate ootheca

and acquire a greater weight in preparation for pregnancy. It is worth to notice that adult body mass largely depends on diet and availability of food during larval development.

Although cockroaches attract interest of scientists and one can find very good sources of knowledge of this insect group (e.g. BELL et al. 2007), there is lack of biometric data of some (many?) species, even popular ones. DJERNÆS et al. (2020) provided (as electronic supplement files) tables with body and pronotum lengths of males and females of many Blaberoidea species, but antennae and tegmina lengths were not given (only information if males and females of a given species are apterous, brachypterous or macropterous).

The aim of this study was to create a biometric data of 12 species. Greater attention was directed to these parts of the cockroaches body, which are particularly significant in recognising their sex. Measurements of specific body parts of insects were made to determinate whether sexual dimorphism of these species was observed. The study was performed on twelve species of cockroaches. Within the family Blaberidae there have been selected: *Blaberus craniifer* Burmeister, *Blaberus discoidalis* Serville, *Blaberus boliviensis* Princis, *Eublaberus posticus* (Erichson), *Eublaberus distanti* (Kirby), *Archimandrita tessellata* Rehn, *Blaptica dubia* (Serville), *Panchlora nivea* (L.), *Nauphoeta cinerea* (Olivier) and *Phoetalia pallida* (Brunner von Wattenwyl). The other two species belong to the Blattidae family: *Shelfordella lateralis* (Walker) and *Periplaneta americana* (L.).

Species were selected based on their availability and usefulness for the experiment. Moreover, species such as *P. americana*, *N. cinerea*, *B. discoidalis* and *S. lateralis* gained attention among scientist and breeders. They are considered as model insects for experiments and research (HUBER et al. 1990).

Materials and Methods

Twelve species of cockroaches: *Blaberus craniifer*, *Blaberus boliviensis*, *Blaberus discoidalis*, *Eublaberus distanti*, *Eublaberus posticus*, *Archimandrita tessellata*, *Blaptica dubia*, *Panchlora nivea*, *Phoetalia pallida*, *Nauphoeta cinerea*, *Shelfordella lateralis* and *Periplaneta americana* were studied. Fifty males and females from each species were selected for measurement. After a last moulting, imago forms were separated from the rest of the group, to exclude the possibility of fertilization, food consumption or possible injuries caused by other individuals, and in order to standardize measurements.

All above mentioned species were kept in incubator with a daily cycle: 12 hours of light at temperature of 28°C and 12 hours of dark at temperature of 24°C. They were kept in plastic containers (dimensions: 35cm x 30cm x 15cm) with upper ventilation, water was added to containers (spraying). Coconut fibers were used as a litter, carton egg trays were provided as harborages for some species (*Nauphotea cinerea*, *Blaptica dubia*, *Phoetalia pallida*, *Shelfordella lateralis*, *Periplaneta americana*). All species were fed with the same food: fruits, vegetables (mainly apples and carrots) and dog food. Cockroaches were caught every three days and measured on the same day or the day after exoskeleton hardened. Individuals' sex was determined by subgenital plate size measurement or (in *B. dubia* and *S. lateralis*) wings presence. Only adults without external damages or deformities (e.g. lost leg or antennae) were included in our study.

The following measurement were made:

- length of antennae, measured from the scape to the end of flagellum;
- length and width of pronotum, measured at the most extended part;
- tegmina length, measured from the end of pronotum to the end of tegmina;
- body length, measured from the head beginning to the end of abdomen. This method of measuring body length was used due wing reduction in some of studied animals;
- body weight.

All measurements were performed by the same person (A.P.) using the same grasp involving hold on to the sides of cockroach's body, so that there was no increase or decrease of the abdomen. With this grasp insects were able to freely maintain the abdomen. Electronic calliper (Swiss Precision Instruments) and electronic weighing scales (Diamond model 100) were used. ANOVA was performed to asses potential intersexual differences.

Results

All means and standard deviations of taken measurements are presented in Table 1.

Out of 12 selected cockroach species, *Archmandrita tessellata* was the largest and the heaviest. *Panchlora nivea* have the smallest males and *Phoetalia pallida* have the smallest females.

It was also shown that statistically significantly larger (body length) in majority of species were females. Additionally, females always had longer and wider pronotum, and were heavier. We stated that tegmina were significantly longer in females of seven studied species, but in five studied

species males had longer tegmina (females of *B. dubia* and *S. lateralis* have reduced wings). On the other hand, males usually have longer antennae but in three small species females had significantly longer antennae. Most of differences were statistically significant, only body length differences in *Blaptica dubia* and *Periplaneta americana* were not significant (Tables 1, 2).

Table 1

Body dimensions and weight of males and females: means and (SD).

Fifty males and 50 females of every species were measured

Species	Traits											
	Body length [mm]		Pronotum width [mm]		Pronotum length [mm]		Antennae length [mm]		Tegmina length [mm]		Body weight [g]	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	F
<i>B. craniifer</i>	45.63 (2.64)	49.11* (2.66)	16.48 (0.70)	18.81* (0.75)	11.84 (0.44)	13.19* (0.61)	32.96 (2.61)	30.34* (3.40)	45.48 (1.66)	48.07* (1.88)	2.49 (0.41)	3.63* (0.52)
<i>B. discoidalis</i>	40.26 (2.53)	44.33* (2.69)	15.23 (0.70)	17.17* (0.79)	10.51 (0.39)	11.47* (0.46)	25.11 (2.41)	23.66* (2.21)	35.14 (1.54)	35.81* (1.60)	1.78 (0.21)	2.83* (0.34)
<i>B. boliviensis</i>	39.42 (2.67)	42.30* (1.96)	15.17 (0.58)	16.57* (0.63)	10.43 (0.41)	11.27* (0.36)	25.55 (2.17)	24.40* (1.37)	35.28 (1.21)	34.30* (1.67)	1.80 (0.17)	2.68* (0.26)
<i>E. posticus</i>	42.22 (3.16)	46.39* (3.18)	16.25 (1.09)	17.56* (0.89)	11.55 (0.67)	12.34* (0.52)	30.07 (2.63)	28.16* (1.71)	35.37 (1.75)	38.89* (1.76)	2.70 (0.53)	3.86* (0.76)
<i>E. distanti</i>	44.83 (3.46)	46.83* (2.27)	16.50 (0.81)	17.00* (0.72)	11.68 (0.61)	11.92* (0.58)	26.17 (1.89)	23.78* (1.82)	38.02 (1.40)	40.70* (1.38)	3.83 (0.54)	4.68* (0.57)
<i>A. tessellata</i>	54.30 (3.08)	57.98* (2.03)	24.20 (0.90)	26.94* (0.95)	15.08 (0.52)	16.36* (0.55)	34.22 (2.35)	28.84* (2.54)	50.60 (2.09)	47.08* (1.90)	4.80 (0.62)	7.21* (0.75)
<i>B. dubia</i>	34.08 (1.84)	33.92 (2.19)	12.26 (0.52)	14.87* (0.69)	8.70 (0.42)	9.64* (0.41)	19.98 (2.32)	17.58* (2.23)	32.44 (1.08)	10.01* (0.88)	1.27 (0.17)	1.74* (0.26)
<i>P. nivea</i>	12.90 (0.90)	18.74* (1.45)	4.58 (0.33)	6.60* (0.59)	3.69 (0.38)	5.08* (0.36)	11.07 (0.93)	12.94* (1.17)	14.53 (0.85)	20.17* (1.03)	0.08 (0.02)	0.25* (0.05)
<i>N. cinerea</i>	23.44 (1.89)	25.73* (1.48)	7.72 (0.38)	8.30* (0.44)	5.44 (0.26)	5.82* (0.34)	19.87 (1.44)	20.75* (1.18)	16.82 (0.69)	19.67* (0.96)	0.44 (0.05)	0.56* (0.07)
<i>P. pallida</i>	15.55 (0.80)	18.63* (0.93)	4.99 (0.23)	6.07* (0.26)	3.22 (0.25)	3.89* (0.23)	11.73 (0.87)	12.49* (0.93)	13.58 (0.52)	15.57* (0.61)	0.13 (0.01)	0.24* (0.03)
<i>S. lateralis</i>	21.48 (1.32)	22.98* (1.27)	6.18 (0.32)	7.53* (0.39)	4.85 (0.39)	5.72* (0.34)	24.96 (3.91)	21.62* (2.51)	21.97 (1.34)	5.62* (0.45)	0.28 (0.04)	0.45* (0.08)
<i>P. americana</i>	30.82 (1.68)	29.86 (3.56)	9.11 (0.46)	9.61* (0.57)	7.33 (0.37)	7.67* (0.36)	47.13 (4.37)	42.26* (4.32)	30.26 (1.71)	25.75* (1.77)	0.87 (0.11)	0.94* (0.20)

* Significantly different between males and females (ANOVA, $P < 0.05$)

Table 2

Comparison of biometrical traits between sexes (F-female biased, M-male biased)

Species	Body length	Pronotum width	Pronotum length	Antennae length	Tegmina length	Body weight
<i>B. craniifer</i>	F*	F*	F*	M*	F*	F*
<i>B. discoidalis</i>	F*	F*	F*	M*	F*	F*
<i>B. boliviensis</i>	F*	F*	F*	M*	M*	F*
<i>E. posticus</i>	F*	F*	F*	M*	F*	F*
<i>E. distanti</i>	F*	F*	F*	M*	F*	F*
<i>A. tessellata</i>	F*	F*	F*	M*	M*	F*
<i>B. dubia</i>	M	F*	F*	M*	M*	F*
<i>P. nivea</i>	F*	F*	F*	F*	F*	F*
<i>N. cinerea</i>	F*	F*	F*	F*	F*	F*
<i>P. pallida</i>	F*	F*	F*	F*	F*	F*
<i>S. lateralis</i>	F*	F*	F*	M*	M*	F*
<i>P. americana</i>	M	F*	F*	M*	M*	F*

*difference significant at p level <0.05), letter indicates sex with bigger value of the trait

Discussion

We selected cockroaches which represent two families (Blaberidae and Blattidae) in this study. These species were chosen due to their availability and ease to perform biometric measurements.

Occurrence, reduction or absence of certain body parts or their size may indicate the utilisation of adaptation to environmental conditions (MULLINS and COCHRAN 1987). Pronotum has many functions e.g. digging and substrate penetration (SIMPSON et al. 1986) or attacking intruder (SEELINGER and SEELINGER 1983). Using pronotum in establishing hierarchy was observed on males of *Blaberus craniifer* and *Nauphoeta posticus* (EWING 1967, 1972). Bigger pronotum is advantageous during foraging, defending or establishing position in hierarchy. However, it seems that statistically greater pronotum of females in all species in this study may result simply from the overall greater weight and length. Body length was insignificantly greater in males of *B. dubia* and *P. americana* only. In all investigated species females were more massive, since they invest more energy to prepare for reproduction.

“Like many animals active in low-light conditions, cockroaches often use tactile cues to avoid obstacles and guide their locomotion” (BELL et al. 2007). Longer antennae allow better environment investigation and faster reactivity. This is particularly important in the case of males seeking for

adult females to mate (e.g. SCHALLER 1978). In this study we showed that most cockroach antennae are statistically longer in males with exception of three small species (*P. pallida*, *N. cinerea*, *P. nivea*) in which females have longer antennae.

DJERNÆS et al. (2020) stated that “Body size in cockroaches ranges from 2.5 mm to 78 mm”. Average size and average weight of individuals vary, especially between genders. Males mature earlier than females (ESPERK et al. 2007). Females reach more massive body by more moulting, but this fact also depend on environmental factors (MULLINS and COCHRAN 1987). Development of cockroaches depends on many different factors which influence the SSD such as temperature and humidity. Moreover, cockroaches in groups grow faster and reach more body weight (WOODHEAD and PAULSON 1983), but excessive high density had opposite effect (GOUDEY-PIERRIERE et al. 1992). Damage of the antennae, legs or other body parts slow down development (TANAKA et al. 1987). Cockroaches take care of their offspring, which gives nymphs opportunity to develop faster due to avoidance of predatory attack and creates the best conditions for development during first days of life (PARK and CHOE 2003).

Data presented in this paper confirmed those reported in previous studies on body weight and length of *Blaberus craniifer* (CLARK and TRIBLEHORN 2014, CHOATE 2003, GERE 1985). Also data collected from measurements of *Periplaneta americana* (CLARK and TRIBLEHORN 2014, ROTH 2003) did not differ from our results. However, DAY (1950) reported a higher body mass for individuals that had no possibilities to get food or produce ootheca. Body length of *Nauphoeta cinerea* presented by BELL (1981) and ROTH (2003), *Panchlora nivea* given by DJERNÆS et al. (2020, after Hebard 1919) and *Eublaberus distanti* reported by OONINCX and DIERENFELD (2012) are comparable with our results. BELL et al. (2007) have written that; “A male *Archimandrita tessellata* measured by Gurney (1959) stretched to 85 mm”, whereas in our study maximum body length of *A. tessellata* (female!) was 61.9 mm. On the other hand, DJERNÆS et al. (2020) reported body length values of *A. tessellata* very similar to those presented here (average for females: 57.01 mm; in our study: 57.98 mm). In case of *Eublaberus posticus* DJERNÆS et al. (2020) also reported that values of body and pronotum length are higher in females, but absolute values given there are lower than in our study (e.g. average female body length 34.1 mm; in our study: 46.39 mm). These differences can probably be explained with the fact that authors mentioned above measured dead, dried specimens. DJERNÆS et al. (2020, after Hebard 1917) showed higher absolute values of body and pronotum length of *Phoetalia pallida* than stated in this paper, but they also stated higher values in females like

in our study (e.g. average male and female body length: 16.25 mm and 19.25 mm; in our study respectively: 15.55 mm and 18.63 mm). Our results on *Blaptica dubia* are in agreement with results given by POJASEK (2013): male antennae are longer, females are heavier, female pronotum is significantly longer and wider, but males body length is insignificantly longer. On the other hand, DJERNÆS et al. (2020, after HEBARD 1921) reported that not only females pronotum is longer, but also females body length is bigger (average male and female body length: 32.2 mm and 32.96 mm) – contrary to our result (average male and female body length: 34.08 mm and 32.92 mm).

To the best of authors' knowledge, no report about any measurements has been found for species such as *Blaberus boliviensis*, *Blaberus discoidalis* and *Shelfordella lateralis* so far.

Among insects, SSD is highly influenced by the environmental factors (TEDER and TAMMARU 2005) and further development. Female-biased SSD predominates in cockroaches (BELL et al. 2007) and also is common in invertebrates in general (FAIRBAIRN 2007), e.g. Acrididae (BIDAU et al. 2013), which was also confirmed in this study.

We conclude that sexual dimorphism is present among all of the studied species. Although *Blaptica dubia* and *Shelfordella lateralis* sexual dimorphism is easy to determine (because wings of females are reduced), it has been firmly confirmed in the measurements. Traits such as body weight, pronotum length and width indicate clearly female-biased SSD in all studied species, whereas males of majority of studied species had longer antennae.

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References

- BASSET Y. 2001. *Invertebrates in the canopy of tropical rain forests. How much do we really know?* Plant Ecol., 153: 87–107.
- BELL W.J. 1981. *The laboratory cockroach*. Chapman and Hall, London.
- BELL W.J., ROTH M.L., NALEPA C.A. 2007. *Cockroaches: ecology, behaviour and natural history*. The Johns Hopkins University Press, Baltimore.
- BIDAU C.J., MARTÍ D.A., CASTILLO E.R. 2013. *Rensch's rule is not verified in melanopline grasshopper (Acrididae)*. J. Insect. Biodivers., 1(12): 1–14.
- BLANCKENHORN W.U. 2009. *Causes and consequences of phenotypic plasticity in body size: the case of the yellow dung fly Scathophaga stercoraria (Diptera: Scathophagidae)*. In: *Phenotypic plasticity of insects: Mechanisms and consequences*. Eds. D. Whitman, T.N. Ananthakrishnan. CT: Science Publishers, Enfield, pp. 369–422.
- BOROŠUT R. 1983. *Allomonal secretions in cockroaches*. J. Chem. Ecol., 9(1): 143–158.
- CHOATE P. M. 2003. *Key for the Identification of the Cockroaches fauna (Insecta: Blattodea) of Florida*. Department of Entomology and Nematology, University of Florida, Gainesville.

- CLARK A.J., TRIBLEHORN J.D. 2014. *Mechanical properties of the cuticles of three cockroach species that differ in their wind-evoked escape behaviour*. Peer J., 2:e501.
- DAY M.F. 1950. *The histology of a very large insect, Macropanesthia rhinoceros Sauss. (Blattidae)*. Aust. J. Sci. Res. B, 3: 61–75.
- DJERNÆS M., VARADINOVÁ Z., KOTYK M., EULITZ U., KLASS K.-D. 2020. *Phylogeny and life history evolution of Blaberoidea (Blattodea)*. Arthropod Syst., 78: 29–67.
- ESPERK T., TAMMARU T., NYLIN S. 2007. *Achieving high sexual size dimorphism in insects females add instars*. Ecol. Entomol., 32(3): 243–256.
- EWING L.S. 1967. *Fighting and death from stress in a cockroach*. Science, 155: 1035–1036.
- EWING L.S. 1972. *Hierarchy and its relation to territory in the cockroach Nauphoeta cinerea*. Behaviour, 42: 152–174.
- FAIRBAIRN D.J. 2007. *Introduction: the enigma of sexual size dimorphism*. In: *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*. Eds. D.J. Fairbairn, W.U. Blanckenhorn, T. Székely. Oxford University Press, New York, pp. 1–10.
- GERE G. 1985. *Examination of the growth of Blaberus craniifer Burm. (Blattodea)*. Opusc. Zool. Budapest, 19–20: 63–68.
- GOUDEY-PIERRIERE F., BARRETEAU H., JACQUOT C., GAYRAL P., PERRIERE C., BROUSSE-GAURY P. 1992. *Influence of crowding on biogenic amine levels in the nervous system of the female cockroach Blaberus craniifer Burm. (Dictyoptera: Blaberidae)*. Comp. Biochem. Physiol. C Comp. Pharmacol., 103(1): 215–220.
- HILL D.S. 2002. *Pests of Stored Foodstuffs and Their Control*. Kluwer, Academic Publishers, New York.
- HUBER I., MASLER E.P., RAO B.R. 1990. *Cockroaches as models for neurobiology: applications in biomedical research*, vol. 1–2, CRC Press, Boca Raton.
- HUTCHINS M., EVANS A., GARRISON R.W., SCHLAGER N. 2003. *Grzimek's Animal Life Encyclopaedia, 2nd edition. Vol.3. Insects*. Gale Group, Farmington Hills.
- MULLINS D.E., COCHRAN D.G. 1987. *Nutritional ecology of cockroaches*. In: *Nutritional ecology of insects, mites, spiders and related invertebrates*. Eds. F.J. Slansky, J.G. Rodriguez. John Wiley & Sons, New York, pp. 885–902.
- NALEPA C.A., BIGNELL D.E., BANDI C. 2001. *Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera*. Insectes Soc., 48(3): 194–201.
- OONINCX D.G.A.B., DIERENFELD E.S. 2012. *An investigation into the chemical composition of alternative invertebrate prey*. Zoo Biol., 31(1): 40–54.
- PARK Y., CHOE J. 2003. *Effects of parental care on offspring growth in the Korean wood-feeding cockroach, Cryptocercus kyebangensis*. J. Ethol., 21(2): 71–77.
- POJASEK A. 2013 *Biometria trzech gatunków karaczanów Blaptica dubia, Nauphoeta cinerea, Blaberus craniifer*. [Biometry of three cockroach species Blaptica dubia, Nauphoeta cinerea, Blaberus craniifer]. Unpublished Engineering Thesis, Poznań University of Life Sciences, Poznań (In Polish).
- ROTH L.M. 2003. *Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria: Blaberidae)*. Orient. Insects, 3(1): 1–186.
- ROTH L.M., WILLIS E.R. 1957. *The medical and veterinary importance of cockroaches*. Smithsonian Misc. Collect., 134: 147.
- ROTH L.M., WILLIS E.R. 1960. *The biotic associations of cockroaches*. The Lord Baltimore Press, Baltimore.
- SCHAL C., GAUTIER J.Y., BELL W.J. 1984. *Behavioural ecology of cockroaches*. Biol. Rev., 59: 161–271.
- SCHALLER D. 1978. *Antennal sensory system of Periplaneta americana L.* Cell Tiss. Res., 191: 121–139.
- SCHEU S., SETALA H. 2002. *Multitrophic interactions in decomposer food webs*. In: *Multitrophic Level Interactions*. Eds. T. Tscharnkte, B. Hawkins B. Cambridge University Press, Cambridge, pp. 223–264.
- SEELINGER G., SEELINGER U. 1983. *On the social organization, alarm and fighting in the primitive cockroach Cryptocercus punctulatus*. Z. Tierpsychol., 61: 315–333.

- SIMPSON B.S., RITZMANN R.E., POLLACK A.J. 1986. *A comparison of escape behaviors of the cockroaches *Blaberus craniifer* and *Periplaneta americana**. *J. Neurobiol.*, 17: 405–419.
- TANAKA K., OHTAKE-HASHIGUCHI M., OGAWA E. 1987. *Repeated regeneration of the German cockroach legs*. *Growth*, 51: 282–300.
- TEDER T., TAMMARU T. 2005. *Sexual size dimorphism within species increases with body size in insects*. *Oikos*, 108: 321–334.
- WOODHEAD A.P., PAULSON C.R. 1983. *Larval development of *Diploptera punctata* reared alone and in groups*. *J. Insect Physiol.*, 29: 665–668.