



## ECOLOGY, BEHAVIOR AND BIONOMICS

### Body Size, Symmetry and Courtship Behavior of *Dysdercus maurus* Distant (Hemiptera: Pyrrhocoridae)

AS JORGE, C LOMÔNACO

Programa de Pós-graduação em Ecologia e Conservação dos Recursos Naturais, Instituto de Biologia, Univ Federal de Uberlândia, Uberlândia, MG, Brasil

#### Keywords

Coercive copula, cotton-stainer, fluctuating asymmetry, mate choice

#### Correspondence

CECÍLIA LOMÔNACO, Instituto de Biologia, Univ Federal de Uberlândia, 38.400-902, Uberlândia, MG, Brasil, [lomonaco@ufu.br](mailto:lomonaco@ufu.br)

Edited by Angelo Pallini – UFV

Received 02 April 2010 and accepted 27 August 2010

#### Abstract

This study analyses the role of body size and symmetry in the sexual selection and courtship behavior of *Dysdercus maurus* Distant. Sexual conflicts signaled by coercive mating, female resistance, and pre-copulation fights illustrate the mating system. Male-female struggles were observed in all mating attempts. Females tried to reject males by pushing or running and even by vigorously shaking their bodies, in attempts to dislodge the male from their dorsum. In spite of sexual conflicts during courtship, females actively chose their mates based on morphological and behavioral traits. Larger males with more symmetrical tibiae and longer tarsi that are better copula imposers were more successful in sexual competition. Evidence is presented that sexual conflict and female mate choice should not be mutually excluded.

#### Introduction

Body size is one of the most important quantitative trait that is subject to continuing evolution (Borgia 1979). It strongly affects fitness and it is also constantly being affected by environmental factors (Schmidt-Nielsen 1984). Typically, sexual selection is thought to influence male body size in the context of female choice and/or male-male competition (Dugatkin & Godin 1998). Large body size often increases pairing success in many organisms (Emlen & Oring 1977, Searcy 1982) and female choice for large males is common among insects (Choe & Crespi 1997).

Another body characteristic related to sexual selection is the fluctuating asymmetry (FA), which is defined as small random deviations of perfect trait symmetry in organisms showing bilateral symmetry (Parsons 1990). If the expression of a bilateral trait is produced by the same genome, then any asymmetry between the sides is a consequence of modifications in the normal development

program that may be caused by both environmental and genetic causes (Markow 1995). Consequently, FA could be a good indicator of individual developmental stability and fitness, and females of many species have been described as choosing more symmetrical males as mates (Moller & Pomiankowski 1993, Moller & Swadle 1997), including female insects (Santos 2001).

Sexual selection based on body size is widespread, and the female choice criteria may greatly differ from one species to another (Halliday 1993). Some female insects, for example, have been described as preferring symmetrical (Santos 2001, Beck & Pruett 2002) or vigorous (Shuker *et al* 2002) males for mating.

In order to increase their reproductive success, males tend to compete for female attention, sometimes developing a coercive copula behavior. This kind of behavior is based on the female reluctance to accept a particular male, consequently promoting sexual conflicts between genders (Gavrilets *et al* 2001, Arnqvist & Rowe 2002).

*Dysdercus maurus* Distant, the “cotton-stainer”, is a very important agricultural pest in tropical regions (Brisolla *et al* 1992). This species is responsible for losses of seed weight, seed oil content and for several cotton ball damages produced by bacterial and fungal opportunistic attacks in many Malvaceae species (Almeida *et al* 1986). According to Nóbrega (1989), this insect displays an elaborated courtship behavior, initiated by the male attempting to laterally approach the female and touching her body with his antennae. The female may reject the male by running away or may allow copulation after numerous courting positions. The male assumes the final copulation posture, positioning itself in a diametrically opposite direction in relation to the female body (tail-tail insertion). During copula, which may last three days, females may continue to feed (Siddiqi 1988, Almeida 1994). The copula does not limit both male and female to move, eat, drink and even excrete. Females will lay eggs shortly after disengagement. Pressured by intra-sexual selection, the long period of engagement is probably related to the male strategy to avoid sperm competition (Alcock 1994).

This study investigates and analyses the role of body size and symmetry in the sexual selection of *D. maurus*, and describes some aspects of the sexual conflict established during courtship behavior in this species. The tested hypothesis is that these insect females actively choose their reproductive partners based not only on courtship behavior, but also by considering male body traits.

## Material and Methods

### Sample individuals

Insect pairs in copula ( $n = 90$ ) and non-paired males ( $n = 50$ ) and females ( $n = 50$ ) of *D. maurus* were collected on cotton balls of plants cultivated at the Experimental Garden of the Instituto de Agronomia da Universidade Federal de Uberlândia, Minas Gerais (18°57'S, 48°12'W). The insects were captured manually from January to April, 2007, and maintained in glass bottles. While being removed from the plants, care was taken in order to avoid disengagement of the pairs. Subsequently, after completion of observations in the laboratory, all individuals were sacrificed and preserved in 70% ethanol.

### Behavioral observations

The collected non-paired males and females were kept in plastic arenas containing wet sand as a substrate. Insects were fed daily with fresh cotton balls and the arenas were covered with nylon fabric. The study focused on two kinds of behavior: courtship activities and male competitive conducts. The courtship and copula

performance were observed considering 50 couples randomly formed (one male and one female placed in a 441 cm<sup>3</sup> arena). Individual male's competitive behavior was observed in arenas (5,400 cm<sup>3</sup>) where 10 males and 10 females were uniformly allocated, keeping 250 cm<sup>3</sup> for each individual. Observation periods of one hour were undertaken, resulting in 30h of observations for each kind of behavior (total of 60h). Complementary field observations were also periodically carried out at the Experimental Garden.

### Morphometric and biomass measurements

Pairs of antennae, and of anterior and posterior legs were taken from the collected individuals and mounted on microscope slides and a cover slip. The slides were placed in a 10x magnifying stereomicroscope and the images were scanned. The computer program Adobe Photoshop® version 6.0 (Adobe 2000) was then used to obtain measurements of the length of the following traits: first foretarsus segment (T1), foretibia (FT) hindtibia (HT); and 3<sup>o</sup> (A3) and 4<sup>o</sup> (A4) antennae segments. Measurements of bilateral traits were obtained for both sides to evaluate FA. In order to verify accuracy, each trait was measured three times in a subsample of 15 individuals. Insects that were preserved in 70% ethanol were previously dried in an absorbent paper before being weighted on analytical scales.

### Statistical analyses

A correlation matrix of the original characters measured on the insect's right side was obtained using Pearson's correlation test indexes. The significant correlated characters were then used for a Principal Component Analysis (PCA) in order to reduce the multidimensionality of the data, obtaining an index of general body size (Manly 1994).

FA was calculated as the mean difference between the right (R) and the left (L) sides, i.e.  $FA = [(\sum |R - L|) / n]$  (Palmer & Strobeck 1986). A two-factor analysis of variance (ANOVA) was used to determine whether the between-sides variation was significantly larger than the measurement error (Woods *et al* 1998, Perfectti & Camacho 1999). According to Palmer & Strobeck (1986), it is necessary to distinguish FA from other kinds of asymmetry. A t-test was performed to verify whether the means of the signed right minus left distribution were not significantly different from zero, in order to discard the occurrence of directional asymmetry. Antisymmetry was tested by departures of the right-left frequency distribution from normality using Kolmogorov-Smirnov test. Size dependence of FA was tested for each sample by regressing the unsigned absolute difference of the right minus left measurements on trait size.

The normality of the data distribution was subsequently

verified by using the Lilliefors test. Then, the data were submitted to a “t” test in order to confirm whether there were significant differences in size, FA, weight and original morphometric measurements between paired and non-paired males (Zar 1984). The average ratio between male and female sizes was also calculated. All statistical procedures were performed using computer software package Systat® for Windows®, version 9.0 (Systat 2000).

## Results

### Courtship activities

The total of 234 mating attempts (male/female) and 17 successful matings were observed. In all cases, the behavior was initiated by the males, and all males tried to copulate with the first female found, even when several males and females were placed in the same arena. The male initiates the courtship behavior by touching the female’s body with the antennae, and then tries to mount her. Assuming a perpendicular position, the male touches the ventral portion of the female’s body with its antennae. Whilst mounted, the male everts the edeagus and rotates his body 90° in order to be in a parallel position in relation to the female’s body. The male then inserts the edeagus in the female’s genital cavity and dismounts the female’s dorsum, performing an 180° rotation, such that the two insects now face diametrically opposite directions.

During all observed encounters females tried to reject males. Their reactions against male courtship attempts varied from pushing and running to vigorously shaking their body, trying to dismount the male from their dorsum. During the male attempts to introduce the edeagus into the female’s genital cavity, she responded by touching her ventral body surface onto the floor in order to protect her genital cavities, using her legs and dorsum as shields. Immediately after the insertion of the edeagus, the female stopped reacting against the male and accepted the engagement. As a result of the female resistance to the male mating attempts, many females were left upside down, but even in this position, the male continued to attempt to introduce its edeagus into the female’s genital opening.

We did not observe any contest (fights) between males for female access (intrasexual selection). Fights between males were only observed in situations in which one male tried to copulate with another male. Apparently, the sexual gender is not immediately recognized by males, since numerous courtship behaviors were observed between males when they meet each other for the first time inside the arena. In some of these cases, the courtship ended without aggressions, but sometimes the

courted male pushed and tried to jump away from the other male. In addition, copula attempts with a female involving more than one male were also observed. In this case, the exclusion of one male simply occurred as the result of the impossibility of both individuals to mount the same female simultaneously, and no direct antagonistic actions between the contestant males were observed. Male copulation attempts involving paired-females were also observed, but these attempts never succeeded in separating the previous formed couples.

### Size differences between paired and non-paired males

The right side measurements of all morphological traits were correlated among themselves ( $P < 0.05$ ), excepting the length of the foretarsus segment, which was excluded from further analysis. The PCA analysis revealed that all coefficients of the first main component were positive, which indicates that the multivariate index of size had been adequately elaborated (Table 1). About 72.1% of the total morphometric variation corresponded to size variation (first main component), and the remaining 29.9% was attributed to shape distortion (the other main component). The multivariate index of size, the original trait measurements and the male’s weight had normal distributions according to the Kolmogorov-Smirnov test ( $P > 0.05$ ). The t test did not indicate any significant differences in the size index ( $t_{(45)} = -0.811$ ,  $P = 0.422$ ), FT ( $t_{(45)} = 0.209$ ,  $P = 0.835$ ), HT ( $t_{(45)} = -0.233$ ,  $P = 0.817$ ), A3 ( $t_{(45)} = -1.554$ ,  $P = 0.127$ ) nor A4 ( $t_{(45)} = -1.392$ ,  $P < 0.171$ ) between paired and non-paired males. On the other hand, significant differences were detected for T1 ( $t_{(45)} = -5.320$ ,  $P < 0.001$ ) and weight ( $t_{(77)} = 4.501$ ,  $P < 0.001$ ) between paired and non-paired males. Thus, *D. maurus* paired-males tend to have larger biomass (40.0 mg  $\pm$  1.00 and longer foretarsus segments (12.0 mm  $\pm$  0.25 than non-paired males (30.0 mg  $\pm$  1.00 and 11.1 mm  $\pm$  0.42, respectively).

Table 1 First two principal components extracted from the phenotypic correlation matrix of four morphological characters measured in the right side body of *Dysdercus maurus*.

Morphometric measurements (length)	First component	Second component
Foretibia	0.904	0.282
Hindtibia	0.876	0.330
3 <sup>o</sup> antennae segment	0.879	-0.072
4 <sup>o</sup> antennae segment	0.670	-0.718
Explained variance	2.805	0.708
% of the total explained variance	70.120	17.711

### Choice of symmetrical males

The measurement error of FA was negligible for all traits, as indicated by the highly significant side x individual effect on two-way ANOVA ( $F_{(14,60)} = 3051.915$ ,  $P < 0.001$  for T1;  $F_{(14,60)} = 345.980$ ,  $P < 0.001$  for FT;  $F_{(14,60)} = 449.571$ ,  $P < 0.001$  for HT;  $F_{(14,60)} = 6559.869$ ,  $P < 0.001$  for A3, and  $F_{(14,60)} = 189.592$ ,  $P < 0.001$  for the A4). All FA distributions were normal, and no evidence of antisymmetry was found. The asymmetry in all traits fluctuated around a mean zero. No correlation between size and FA was observed, except for the first foretarsus segment, which was then corrected (Table 2). The t test indicated that the successfully paired males have more symmetrical hindtibia segments ( $0.9 \text{ mm} \pm 0.12$ ) than non-paired males ( $1.4 \text{ mm} \pm 0.22$ ) ( $t_{(50)} = -2.054$ ,  $P = 0.045$ ), but no evidence of FA differences were found for the other traits analyzed ( $t_{(50)} = 0.726$ ,  $P = 0.472$  for T1;  $t_{(50)} = -0.906$ ,  $P = 0.062$  for FT;  $t_{(50)} = 1.185$ ,  $P = 0.068$  for A3, and  $t_{(50)} = -1.865$ ,  $P = 0.242$  for A4).

## Discussion

### Sexual behavior

Sexual conflicts signaled by coercive mating, female resistance, and pre-copulation fights between sexes are characteristic of the mating system developed by *D. maurus*. Forced copulation has been used as a typical example of conflict of interests between males and females, and demonstrates sexual coercion, already described for some groups of insects and arachnids (Allen & Simmons 1996, Peretti & Willemart 2007). Sexual coercion is a form of sexual antagonistic coevolution that predicts male-female struggles for controlling a reproductive event (Arnqvist & Rowe 2002, Chapman *et al* 2003), as seen in *D. maurus* courtship behavior.

The long period of copula in *D. maurus*, which increases the predation risk and makes foraging more difficult, may be a plausible reason for female reluctance,

since coercive copula is usually associated with high reproductive costs that reduce any aspect of survivorship success (Gavrilets *et al* 2001, Moore *et al* 2001, Stutt & Siva-Jothy 2001, Arnqvist & Rowe 2002).

Nevertheless, if this kind of intersexual selection tends to favor more manipulative males that are better copula-imposers, it is also an indirect indicative of male's fitness and vigor (Cordero & Eberhard 2003). Consequently, Eberhard (2002) considers that female resistance behavior during courtship does not necessarily imply forced copulation, but persuasion, because such behavior may function instead as a test in order to favor some males over others, or to induce the male to give up. As such, female defenses against coercive copula may be alternatively interpreted as an indirect way of male selection (Cordero & Eberhard 2003). Consequently, although receiving no direct benefits for having a confrontational behavior during courtship, females would be indirectly benefitted by producing good manipulative offspring (Kirkpatrick 1982, Price *et al* 1993, Iwasa & Pomiankowski 1999, Day 2000, Gavrilets *et al* 2001).

Sexual selection based on female choice results in any behavioral or physiological mechanism that makes a particular male more successful as a sexual mate (Kirkpatrick & Ryan 1991, Andersson 1994). Although sexual conflict and female choice are different hypotheses explaining the function and the evolution of sexual traits involved in mating, they are not necessarily mutually exclusive (Thornhill 1981, Peretti & Willemart 2007). In fact, Allen & Simmons (1996) and Peretti & Willemart (2007) presented evidence that sexual coercion and selective female choice may occur simultaneously.

### Selected males

Heavy *D. maurus* males possessing longer foretarsus segments tend to reproduce more successfully, probably because of their enhanced ability to enforce copulation. The advantages of these characteristics for coercive copula may be related to the ability of such males to subdue females

Table 2 Data distribution analysis, using one sample t test and Kolmogorov-Smirnov normality test applied to size differences between sides of the morphological traits of *Dysdercus maurus*. Pearson's correlation matrix between the fluctuating asymmetries and the right trait sizes (T1 = first foretarsus segment, FT = foretibia, HT = hindtibia; A3 = 3<sup>o</sup> antennae segment, A4 = 4<sup>o</sup> antennae segment).

Trait	n	One sample t test		Kolmogorov-Smirnov test		Pearson's correlation	
		t	P	D <sub>max</sub>	P	r	P
FT	94	0.112	0.911	0.060	0.506	-0.007	0.946
T1	97	-1.807	0.074	0.082	0.107	-0.312	0.002
HT	94	1.019	0.311	0.075	0.197	-0.142	0.173
A4	92	0.832	0.408	0.057	0.607	-0.150	0.154
A3	94	1.967	0.052	0.074	0.215	0.006	0.952

during the courtship behavior in spite of their reluctance. Additionally, larger males are probably better to spatially exclude their competitor when a female is being harassed by another male.

The absence of any observed difference in size between paired and non-paired males, in spite of the significant evidence of biomass differences between them, was probably due to the use of body appendices as the original variables for the estimation of the size index, instead of the use of measurements made on the body itself.

The success of larger males during sexual selection and the selection for larger females, which are usually more fecund, are the two main evolutionary forces favoring the increase of body size in several species (Honek 1993, Andersson 1994). Numerous studies have already registered the influence of body size in the results of aggressive combats between insect males (O'Neill 1983, Goldsmith 1987, O'Neill *et al* 1989, Rasmussen 1994). Sexual size dimorphism, as seen in *D. maurus*, with females being larger than males, is common in the majority of insects and it is referred to as female-biased size dimorphism (Andersson 1994). This pattern is most frequently attributed to fecundity selection, since egg or offspring size strongly increases with body size (Honek 1993).

Nevertheless, sexual selection can also favor smaller males through greater agility during courtship displays (Andersson & Norberg 1981, McLachlan 1987), faster development (Singer 1982, Bulmer 1983), higher searching capabilities for females (Fagerström & Wiklund 1982) or even due the female preference for smaller males (Petrie 1983, Steele & Partridge 1988).

Our previous observations (Jorge & Lomônaco 2009) indicated that female choice for a particular male is also based on her own size, which is a result of a trade-off between the negative influence of large partner size in female fecundity and the advantages of large male size for offspring fitness (Oliveira *et al* 2003). Although larger males may have the advantage of being better manipulators, they do not benefit the female's movements and foraging activities during the copulation period, which can be extended for up to three days, when the couple assumes the diametrically opposite direction posture. If females fail to conduct necessary feeding and defensive movements during the copula, the survivorship of their offspring may be at risk.

Females of *D. maurus* also choose males with more symmetrical hindtibiae. Symmetry may be related to female choice because it reflects an animal's ability to cope with the sum of the challenges during its growing period and, thus, it is a potential benefit or fitness indicator (Moller & Pomiankowski 1993). Additionally, symmetry may confer an advantage for males in maintaining themselves on the female's dorsum. Some

studies support the idea that low FA is linked to enhanced fitness when a structure having a mechanical significance is under selection. For example, *Sepsis cynipsea* (L.) females tends to copulate with males possessing more symmetrical foretibiae because of their better competitive ability to grip the female's wing bases and thereby remain on the female dorsum during the guarding period (Allen & Simmons 1996).

In conclusion, *D. maurus* females choose larger males with more symmetrical tibiae and longer tarsus that are better copula imposers. Evidence is presented that sexual conflict and female mate choice should not be mutually excluded.

### Acknowledgments

This project was partially supported by CAPES, which provided a scholarship to A S Jorge. We thank Dr Peter Gibs for English revision and FAPEMIG for publishing support.

### References

- Adobe Photoshop (2000) Adobe Systems Incorporated. San Jose, Adobe<sup>®</sup>.
- Alcock J (1994) Post insemination associations between males and females - the mate-guarding hypothesis. *Annu Rev Entomol* 39: 1-21.
- Allen GR, Simmons LW (1996) Coercive mating, fluctuating asymmetry and male success in the dung fly *Sepsis cynipsea*. *Anim Behav* 52: 737-741.
- Almeida AAD (1994) Structure of the reproductive system and mating behaviour of *Dysdercus fasciatus* Signoret, 1861 (Hemiptera, Pyrrhocoridae). *Rev Bras Entomol* 38: 595-598.
- Almeida JR, Xerez R, Jurberg J (1986) Comportamento de acasalamento de *Dysdercus maurus* Distant, 1901 (Hemiptera, Pyrrhocoridae). *An Soc Entomol Brasil* 15: 161-167.
- Andersson M (1994) Sexual selection. Princeton, Princeton University Press, 336p.
- Andersson M, Norberg RA (1981) The evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol J Linn Soc* 15: 105-130.
- Arnqvist G, Rowe L (2002) Antagonistic coevolution between the sexes in a group of insects. *Nature* 415: 787-789.
- Beck ML, Pruett JS (2002) Fluctuating asymmetry, sexual selection, and survivorship in male dark-winged damselflies. *Ethology* 108: 779-791.
- Borgia G (1979) Sexual selection and the evolution of mating systems, p.19-80. In Blum SM, Blum NA (eds) Sexual selection and reproductive competition in insects. New York Academic Press, 647p.

- Brisolla AD, Bergmann EC, Imenes SDL (1992) Aspectos biológicos de *Dysdercus peruvianus* Guérin-Ménéville, 1831, em condições de laboratório. *Arq Inst Biol* 59: 19-22.
- Bulmer MG (1983) Models for the evolution of protandry in insects. *Theor Popul Biol* 23: 314-322.
- Chapman T, Arnqvist G, Bangham J, Rowe L (2003) Sexual conflict. *Trends Ecol Evol* 8: 41-47.
- Choe JC, Crespi BJ (1997) Mating systems in insects and arachnids. Cambridge, Cambridge University Press, 387p.
- Cordero C, Eberhard G (2003) Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J Evol Biol* 16: 1-16.
- Day T (2000) Sexual selection and the evolution of costly female preferences: spatial effects. *Evolution* 54: 715-730.
- Dugatkin LA, Godin JJ (1998) How females choose their mates. *Sci Am* 4: 46-51.
- Eberhard WG (2002) Female resistance or screening? Male force vs. selective female cooperation in intromission in sepsid flies and other insects. *Rev Biol Trop* 50: 485-505.
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and mating systems. *Science* 197: 215-223.
- Fagerström T, Wiklund C (1982) Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. *Oecologia* 52: 164-166.
- Gavrilets S, Arnqvist G, Friberg U (2001) The evolution of female mate choice by sexual conflict. *Proc R. Soc Lond B Biol Sci* 268: 531-539.
- Goldsmith SK (1987) The mating system and alternative reproductive behaviors of *Dendrobias mandibularis* (Coleoptera: Cerambycidae). *Behav Ecol Sociobiol* 20: 111-115.
- Halliday T (1993) Sexual selection and mating systems, p.264-306. In Skelton, P (ed) *Evolution, a biological and palaeontological approach*. Milton Keynes, The Open University, 1064p.
- Honek A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66: 483-492.
- Iwasa Y, Pomiankowski A (1999) Good parent and good gene models of handicap evolution. *J Theor Biol* 200: 97-109.
- Jorge AS, Lomônaco C (2009) Size and partner choice in *Dysdercus maurus* Distant (Hemiptera: Pyrrhocoridae). *J Insect Behav* 22: 148-152.
- Kirkpatrick M (1982) Sexual selection and the evolution of female choice. *Evolution* 36: 1-12.
- Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350: 33-38.
- Manly BFJ (1994) *Multivariate statistical methods*. London, Chapman & Hall, 215p.
- Markow TA (1995) Evolutionary ecology and developmental instability. *Annu Rev Entomol* 40: 105-120.
- McLachlan A (1987) Male mating success in Diptera: advantages of small size. *Oikos* 48: 11-14.
- Moller AP, Pomiankowski A (1993) Fluctuating asymmetry and sexual selection. *Genetica* 89: 267-279.
- Moller AP, Swadle JP (1997) *Asymmetry, developmental stability and evolution*. Oxford, Oxford University Press, 304p.
- Moore AJ, Gowaty PA, Wallin WG, Moore PJ (2001) Sexual conflict and the evolution of female mate choice and male social dominance. *Proc R Soc Lond B Biol Sci* 268: 517-523.
- Nóbrega AMI (1989) Reprodução e longevidade de *Dysdercus maurus* Distant, 1901 (Hemiptera: Pyrrhocoridae). *An Soc Entomol Brasil* 18: 109-118.
- Oliveira I, Zanuncio JC, Serrão JE, Pereira JMM (2003) Reproductive potential of the predator *Suputius cincticeps* (Heteroptera: Pentatomidae) affected by female body weight. *Acta Sci* 25: 49-53.
- O'Neill KM (1983) The significance of body size in territorial interactions of male beeswolves (Hymenoptera: Sphacidae, *Philanthus*). *Anim Behav* 31: 404-411.
- O'Neill KM, Evans HE, O'Neill RP (1989) Phenotypic correlations of mating success in the sand wasp *Bembecinus quinquespinosus* (Hymenoptera: Aphecidae). *Can J Zool* 67: 2557-2568.
- Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurements, analysis, patterns. *Annu Rev Ecol Syst* 17: 391-421.
- Parsons PA (1990) Fluctuating asymmetry: an epigenetic measure of stress. *Biol Rev* 65: 131-145.
- Perfectti F, Camacho JP (1999) Analysis of genotypic differences in developmental stability in *Annona cherimola*. *Evolution* 53: 1396-1405.
- Peretti AV, Willemart RH (2007) Sexual coercion does not exclude luring behavior in the camel-spider *Oltacola chacoensis* (Arachnida, Solifugae, Ammotrechidae). *J Ethol* 25: 29-39.
- Petrie M (1983) Female moorhens compete for small, fat males. *Science* 220: 413-415.
- Price T, Schuluter D, Heckman NE (1993) Sexual selection when the female directly benefits. *Biol J Linn Soc* 48: 187-211.
- Rasmussen JL (1994) The influence of horn and body size on the reproductive behavior of the harned rainbow scarab beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). *J Insect Behav* 7: 67-82.
- Santos M (2001) Fluctuating asymmetry is nongenetically related to mating success in *Drosophila buzzatii*. *Evolution* 55: 2248-2256.
- Schmidt-Nielsen K (1984) *Scaling: Why is animal size so important?* Cambridge, Cambridge University Press, 241p.
- Searcy WA (1982) The evolutionary effects of mate selection. *Annu Rev Ecol Syst* 13: 57-85.
- Shuker D, Bateson N, Breitsprecher H, ODonovan R, Taylor H, Barnard C, Behnke J, Coilins S, Gilbert F (2002) Mating behavior, sexual selection, and copulatory courtship in a promiscuous beetle. *J Insect Behav* 15: 617-631.

- Siddiqi JI (1988) Behavioral responses of the male *Dysdercus cingulatus* Fabr. (Hemiptera: Pyrrhocoridae) towards the female sex pheromone. *Indian J Entomol* 50: 276-278.
- Singer MC (1982) Sexual selection for small size in male butterflies. *Am Nat* 119: 440-443.
- Steele RH, Partridge L (1988) A courtship advantage for small males in *Drosophila subobscura*. *Anim Behav* 36: 1190-1197.
- Stutt AD, Siva-Jothy MT (2001) Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius*. *Proc Natl Acad Sci U S A* 98: 5683-5687.
- Systat (2000) Systat for windows statistics, version 9.0. Chicago, SPSS Inc.
- Thornhill R (1981) *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive effort. *Annu Rev Ecol Syst* 12: 355-386.
- Woods RE, Hercus MJ, Hoffmann AA (1998) Estimating the heritability of fluctuating asymmetry in field *Drosophila*. *Evolution* 52: 816-824.
- Zar JH (1984) *Biostatistical analysis*. New Jersey, Prentice Hall, 718p.
-