

BEHAVIOURAL ELEMENTS INFLUENCING MATING SUCCESS OF *SYMMORPHUS ALLOBROGUS* (HYMENOPTERA: EUMENINAE)

Anna BUDRIENĖ, Eduardas BUDRYS

Institute of Ecology of Vilnius University, Akademijos 2, LT-08412 Vilnius-21, Lithuania. E-mail: anna@ekoi.lt, ebudrys@ekoi.lt

Abstract. Elements of the predatory wasp *Symmorphus allobrogus* mating behaviour are described, their influence on mating success is assessed based on laboratory observations. The analysis revealed that in the premounting phase activities of males, abdomen extension and substrate antennation, in particular, play a decisive role in predetermining mating success. In the precopulatory phase, activities of both sexes are nearly equal in importance. Struggle of female individuals negatively affects mating success, while their shaking increases the likelihood of copulation. Antennation and stroking of the abdomen are the most important elements of male behaviour, stimulating copulation. In the copulatory phase of mating visible activities of males have little influence on the duration of copulation, whilst shaking and struggle of females induce an earlier termination of it.

Key words: mating behaviour, mating success, predatory wasp, *Symmorphus allobrogus*, Eumeninae, Vespidae

INTRODUCTION

The behaviour of animals before, during and after copulation has recently experienced a renaissance of interest. Studies of mating behaviour provide explanations for the diversity and evolution of mating systems (Emlen & Oring 1977; Thornhill & Alcock 1983; Arnqvist & Nilsson 2000), patterns of mate guarding and sperm competition (Parker 1970; Alcock 1994), adaptations of copulatory mechanisms in groups of closely relative species (Boake & Hoikkala 1995; Markow *et al.* 1996; Eberhard 2001; Boughman 2002; Miller 2003), or even can give a taxonomic tool for species diagnosis in Hymenoptera (Abeelluck & Walter 1997).

The likelihood of copulation is the result of various interacting factors, including the female reproductive status (Ringo 1996; Sauter & Brown 2001; Wedell *et al.* 2002), male courtship behaviour (Jachmann & van den Assem 1996; McClintock & Uetz 1996) and male choice (Van Dongen *et al.* 1998; Bonduriansky 2001; Reinhold *et al.* 2002), female responses to courtship and female choice (Thornhill 1983; Qvarnström & Forsgren 1998; Edvardsson & Arnqvist 2000), as well as mutual mate choice (Cunningham & Birkhead 1998).

The reproductive behaviour of aculeate Hymenoptera is the product of selection for the ability of males to compete with one another for access to females and to locate sites in which to search or wait for potential mates

(Alcock 1978; Batra 1978; Cowan 1991). Within Eumeninae, male mating behaviour is associated with spatial distribution and mating frequency of females (Smith & Alcock 1980). Females of most species are monandrous, therefore males are under selection pressure to be the first in reaching the virgin female, and they use combinations of visual, tactile and olfactory cues (Alcock *et al.* 1978; Eickwort & Ginsberg 1980; Shimron & Hefetz 1985). Within the order Hymenoptera, factors favouring male choosiness are not clear (Bonduriansky 2001). In Vespidae, the evidence of the use of male pheromones to attract females is lacking, whilst female close-range or contact pheromones that may be involved in the recognition of conspecifics have been found in some species (Ayasse *et al.* 2001). In laboratory conditions the main phases of sexual behaviour and mating behavioural elements of various Eumeninae species may differ considerably (Cowan 1986; Budrienė 2001), providing ethological characters for evolutionary comparisons. However, to authors' knowledge, the effect of eumenine wasp behavioural elements on their mating success has not been studied in detail yet.

The objectives of the present study were as follows: (1) to establish and describe mating behavioural elements of *Symmorphus allobrogus* (Saussure) (Hymenoptera: Vespidae: Eumeninae), and (2) to ascertain which of these elements predetermine mating success.

MATERIAL AND METHODS

The material for the laboratory observations was obtained in 1997–2002 in the locality Varnupys, at an old wooden building with numerous holes of xylophagous beetles, used as nesting cavities by the natural *S. allobrogus* population, the estimated size of which was 155–186 specimens (Budrys *et al.* 2004). Part of this wasp population nested in artificial reed trap-nests (Budrienė 2003).

Reed stem fragments from trap-nests with completed wasp nests were taken to the laboratory for further research several times per season. For mating observations in the laboratory, wasps were reared in April–June of the next year from the trap-nests that have hibernated in the laboratory. Males and females were kept individually or in groups of one sex in plastic cages (6 cm in height, 5 cm in diameter) or glass vials (20 cm in length, 2.5 cm in diameter) at room temperature (20–26°C), and fed with honey solution and water.

Mating was observed in the arena 22 cm in diameter, under a bell-glass 22 cm in height, surrounded by white paper on all sides, except that of the observer, and placed in a thermostat, at 28°C. It was exposed to daylight, with additional artificial illumination provided by two 25 W bulbs at a distance of 30 cm from the arena. A single virgin female was placed into the arena under the bell-glass. The cage with a single male was situated near the latter for the one-minute acclimation period. After that, the male was let into the arena, and the pair was observed for about 30 minutes, or, if mounting took place, until dismounting of the male.

We used the following terms with reference to mating phases. The ‘premounting phase’ refers to the period following the start of the observation until the male mounts the female. The ‘mounting phase’ refers to the period starting from the male’s mounting until the termination of mounting by the female or the male after

copulation or without it. The ‘precopulatory phase’ (also called ‘courtship’) refers to the part of the mounting phase before the female intromitting. ‘Copulation’ refers to the events after the female intromitting until the extraction of male genitalia. We classified the observed actions into fifteen mating behavioural elements, nine of which were characteristic of both sexes, four – of males and two – of females only (Table 1).

We quantified behavioural elements as independent variables, using their frequency: the number of recorded actions divided by the duration (in minutes) of the corresponding mating phase, or by the duration of the whole observation, if mounting did not take place. Mating success as a dependent variable was assessed according to the presence/absence of mounting (for the premounting phase elements), presence/absence of copulation (for the precopulatory phase elements), and duration of copulation (for the copulation phase elements).

The distribution of frequencies of behavioural elements was far from normal and could not be normalised, because in part of mating observations the elements did not occur at all, many of them being absent from more than 50% of mating observations (their frequency median was 0). Therefore, we analysed the dependence of mating success on behavioural elements of the premounting and precopulatory phases using non-parametric Kendall Tau correlation. The effect of elements in their interaction was assessed using logistic regression. We compared the frequency of elements in successful and unsuccessful mating using the Mann-Whitney U test. The impact of the interaction of behavioural elements of the copulation phase on mating success was assessed using multiple regression (duration of copulation as a dependent variable). We used the backward stepwise procedure for the selection of parameters in the models of logistic and multiple regression. Statistical analysis was performed using the computer program StatSoft Statistica, release 6.0.

Table 1. Mating behavioural elements of the solitary wasp *Symmorphus allobrogus*: definitions and average frequency. For elements of the premounting phase, N = 904, for those of the precopulatory phase, N = 606, for the copulatory phase N = 444.

Behavioural element	Definition	Acting sex	Mating phase and frequency (actions/min., mean ±SE)
aggression	sharp moving towards the partner with opened mandibles, sometimes followed by biting	both	premounting: female 0.065 ± 0.006, male 0.0017 ± 0.0004
alert posture	motionless position with antennae straightened forward to the sides and raising of the anterior part of mesosoma on hind and middle legs, hooked forelegs dangling in the air	both	premounting: female 0.029 ± 0.002, male 0.0023 ± 0.0005

Table 1 continued

approach	walking or flying towards the partner	both	premounting: female 0.074 ± 0.005 , male 0.124 ± 0.008
abdomen extending	lifting and telescopic stretching out of the metasoma over the substrate horizontally followed by the extension of genitalia	both	premounting: female 0.0003 ± 0.0002 , male 0.011 ± 0.001
falling backwards	abandoning of the typical male-above mating position during copulation by releasing leg-hold, falling backwards and hanging behind the female by the genitalia	male	copulation: 0.36 ± 0.03
jump	short (less than 2 cm) pouncing flight at the substrate in length	both	premounting: female 0.026 ± 0.006 , male 0.055 ± 0.006
mate antenna antennation	regular simultaneous stroking of the anterodorsal side of both female's antennae with the ventrolateral side (tyloidea) of male's ipsilateral antennae from pedicel to flagellum	male	precopulatory: 3.85 ± 0.15 ; copulation: 0.74 ± 0.06
mate body antennation	moving towards the partner followed by touching it with the tips of antennae	both	premounting: female 0.0016 ± 0.0005 , male 0.013 ± 0.003
moving back	gradual manoeuvring on the female posterad whilst mounting	male	precopulatory: 0.003 ± 0.002 ; copulation: 0.020 ± 0.007
shaking	small-amplitude movements of mesosoma with some rotating (or without it) around its longitudinal axis, curling metasoma forward ventrad and feeble kicking of the metasoma apex	female	precopulatory: 0.71 ± 0.06 ; copulation: 0.27 ± 0.02
struggle	large-amplitude rapid rocking motion of mesosoma around its longitudinal axis followed by the curling of metasoma forward ventrad, lifting metasoma against the substrate and thrusting it back on to the substrate, and forceful kicking of the metasoma apex	female	premounting: 0.0007 ± 0.0003 ; precopulatory: 1.1 ± 0.2 ; copulation: 0.73 ± 0.03
plopping	falling on the arena surface from the bell-glass wall or from the flight heavily with a sound	both	premounting: female 0.028 ± 0.006 , male 0.022 ± 0.003
abdominal stroking	male's probing with the underneath of metasoma and genitalia from the side toward the tip of female's metasoma	male	precopulatory: 2.80 ± 0.13
substrate antennation	inspection of the substrate with antennae by sweeping (male) or tapping (male and female) simultaneously and/or alternately	both	premounting: female 0.013 ± 0.002 , male 0.069 ± 0.005
wing vibration	rising and flicking of the wings with a buzzing sound whilst being on the substrate	both	premounting: female 0.0014 ± 0.0005 , male 0.0042 ± 0.0008 ; precopulatory: male 0.06 ± 0.01 ; copulation: male 0.014 ± 0.005

RESULTS AND DISCUSSION

We did 904 mating observations of *S. allobrogus* in the laboratory. Six hundred and six observations (67%) out of them resulted in the mounting of male, and in 444 cases (49.1% of all observations, 73.3% of mountings) copulation took place. In total, 18,712 actions of mates were recorded. Table 1 represents the observed mating behavioural elements and their average frequency. Figures 1 and 2 show average frequencies of behavioural elements of respectively the premounting and precopulatory phases in successful (mounting or copulation present) and unsuccessful experiments.

As it was earlier supposed (Budrienė 2001), *S. allobrogus* females seem to be monandrous, whereas males can copulate many times. The study of the influence of

behavioural elements of the premounting and precopulatory phases on mating success revealed significant correlations, part of which were confirmed by the logistic regression analysis (Table 2).

Generally we may assume that the male has higher average frequencies of various actions (Table 1) and tends to exhibit a greater repertoire of mating behavioural elements. However, female's activities proved to have significant influence on mating success as well. In the premounting phase, the probability of mounting negatively correlated with the frequency of the female approach and aggression to the male, although the average frequency of these behavioural elements was slightly higher (but median frequency was lower) in successful mating experiments than in those without mounting (Fig. 1). This controversy might be explained in the fol-

Table 2. Effect of the frequency of mating behavioural elements of the premounting phase on mating success of the solitary wasp *Symmorphus allobrogus* (N = 904; dependent variable: presence of mounting). Only significant values ($p < 0.05$) in the table; highly significant values ($p < 0.001$) in bold; n/s – not significant ($p > 0.05$).

Independent variables: frequency of behavioural elements (actions /min.)	Kendall Tau correlation	Logistic regression	
	τ	regr. coef. (b_i) \pm SE in the model with all parameters	regr. coef. (b_i) \pm SE in the model with parameters selected backward stepwise ($p < 0.05$)
Female's actions			
aggression*	-0.10	n/s	
alert posture	n/s	n/s	
approach*	-0.13	n/s	
abdomen extending	n/s	n/s	
jump	-0.05	n/s	4.8 \pm 2.3
mate body antennation	n/s	n/s	
struggle	n/s	n/s	
plopping	-0.06	n/s	
substrate antennation	n/s	n/s	
wing vibration	-0.05	n/s	
Male's actions			
aggression*	-0.14	-17.4 \pm 6.2	-15.6 \pm 6.1
alert posture*	-0.14	-12.2 \pm 6.2	
approach*	0.08	n/s	1.5 \pm 0.6
abdomen extending	n/s	8.6 \pm 3.2	8.8 \pm 3.1
jump	n/s	n/s	
mate body antennation	n/s	n/s	
plopping*	-0.10	n/s	
substrate antennation*	0.10	5.5 \pm 1.3	6.2 \pm 1.2
wing vibration	n/s	n/s	
	Intercept (b_0)	n/s	n/s
	Correct predictions	62.9%	67.5%

* – frequency of the element was significantly different (Mann-Whitney U test) in observations with successful mounting of male and in those without it

lowing way: attempts to mount by the active and finally successful male often caused stronger aggressive behaviour of the female that possibly reflected its assessment of the male, or indirect ('cryptic') choice (Thornhill 1983). The positive effect of female's jumps revealed by the backward stepwise selection of the logistic regression model parameters possibly shows that active females are easier detected by males, and suggests the importance of visual cues in the premounting phase of mating behaviour of eumenine wasps.

The male's activity in the premounting phase affected mating success in particular (Table 2). This may be in agreement with Bonduriansky's (2001) statement that in the systems with lower female mating frequency, males are likely to benefit by courting or pursuing every female they encounter and showing little choosiness. Behavioural elements that had the highest positive influence on mating success were male's abdomen extending and substrate antenation (Table 2, Fig. 1). Our observations revealed a difference in the manner of substrate antenation between the sexes (males' sweeping and/or tapping versus females' tapping). The relation between substrate antenation by the male and mounting success may let us presume that more active males react to the chemical cues produced by walking females. This chemical signal may also indicate female's receptivity. It has been shown in braconid wasp *Cardiochiles nigriceps* that male antenation and mounting are mediated by the cuticular hydrocarbons of males and females (Syverstein *et al.* 1995). Similar substrate antenation was shown in

Cerambycidae species having female contact pheromones (Wang *et al.* 2002). On the other hand, the male's extending of abdomen may give visual cues for the conspecific mate recognition by the female, thus increasing the probability of mating success.

The timid (alert posture) or aggressive behaviour of the male had the strongest negative correlation with mating success; this regularity was also confirmed by the logistic regression analysis and Mann-Whitney U test (Table 2), as well as the comparison of average frequency in successful and unsuccessful mating experiments (Fig. 1). The logistic regression model, selected by backward stepwise procedure, could correctly predict the success of the male in mounting in more than 2/3 of all mating observations (Table 2).

As to the precopulatory ('courtship') phase, behaviour of both sexes had influence on mating success in roughly equal degree (Table 3). The effect of all behavioural elements significantly correlating with copulation success was confirmed by logistic regression, the Mann-Whitney U test (Table 3) and the comparison of average frequencies (Fig. 2).

Vigorous struggle of the female had a negative influence on copulation, while slower shaking affected it positively. Therefore, we may expect some sort of female's choice at this phase: it is possible that the female uses the rejection response as an exercise of mate's assessment. Mating systems of some other insects such as flies (Blanckenhorn *et al.* 2000; Crean & Gilburn 2000) and water striders (Sih *et al.* 2002) involve a pre-mating vig-

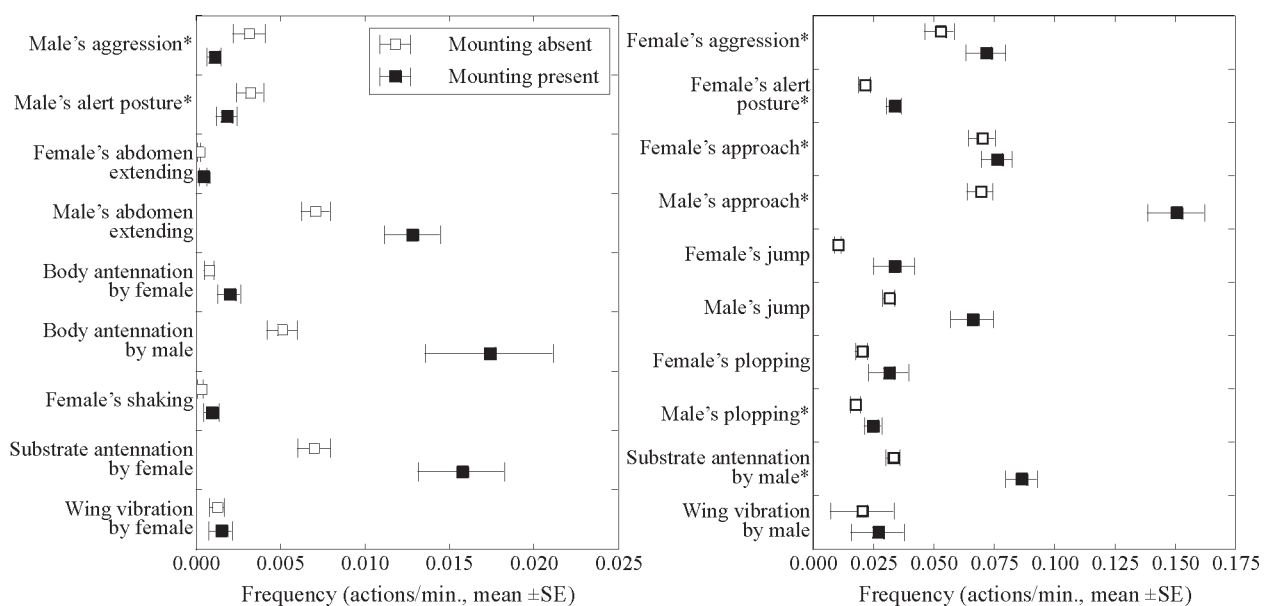


Figure 1. Average action frequency of *Symmorphus allobrogus* mates during the premounting phase in the observations resulting in mounting and those without it. * – frequency of the element was significantly different (Mann-Whitney U test) in the observations with mounting and in those without it.

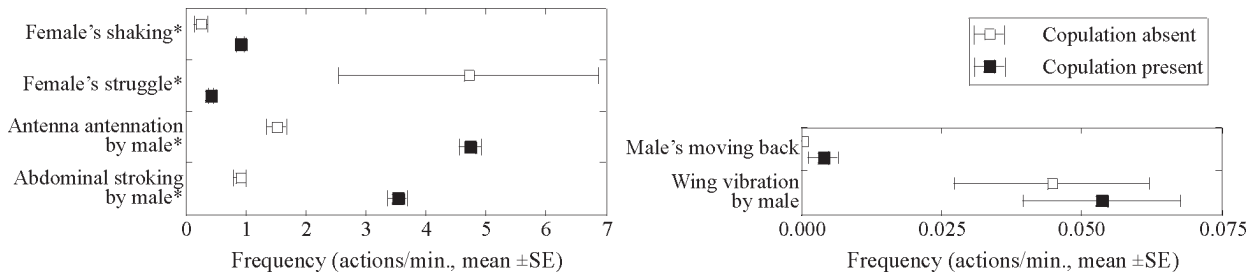


Figure 2. Average action frequency of *S. allobrogus* mates during the precopulatory phase of mounting in the observations resulting in copulation and those without it. * – frequency of the element was significantly different (Mann-Whitney U test) in the observations with copulation and in those without it.

Table 3. Effect of the frequency of mating behavioural elements of the precopulatory ('courtship') phase on mating success of the solitary wasp *Symmorphus allobrogus* (N = 606; dependent variable: presence of copulation). Only significant values ($p < 0.05$) in the table; highly significant values ($p < 0.001$) in bold; n/s – not significant ($p > 0.05$).

Independent variables: frequency of behavioural elements (actions /min.)	Kendall Tau correlation	Logistic regression	
	τ	regr. coef. (b_i) \pm SE in the model with all parameters	regr. coef. (b_i) \pm SE in the model with parameters selected backward stepwise ($p < 0.05$)
Female's actions			
shaking*	0.24	0.6 \pm 0.2	0.6 \pm 0.2
struggle*	-0.28	-0.2 \pm 0.1	-0.2 \pm 0.1
Male's actions			
mate antenna antenation*	0.43	0.4 \pm 0.1	0.4 \pm 0.1
moving back	n/s	n/s	
abdominal stroking*	0.26	0.2 \pm 0.1	0.2 \pm 0.1
wing vibration	-0.12	n/s	
	Intercept (b_0)	-0.7 \pm 0.2	-0.7 \pm 0.2
	Correct predictions	83.2%	82.7%

* – frequency of the element was significantly different (Mann-Whitney U test) in observations with copulation and in those without it

orous struggle that results in the rejection of undesirable males as well. The most important activities of the male, stimulating the female to copulate, were antenation and stroking by abdomen. The logistic regression model, including the listed behavioural elements could predict the success of the male in copulation in more than 4/5 of all mating observations (Table 3).

Budrienė (2001) earlier has hypothesised that male tyloids may function as integumentary glands of contact pheromones inducing readiness of the female to copulate. This hypothesis is indirectly corroborated by the revealed importance of male antenation in the precopulatory phase. The only behavioural elements of the copulatory phase, significantly affecting the duration of copulation in the multiple regression model, were shaking and vigorous struggle of the female (Table 4). Remarkably, antenation

of the male that was less frequent than in the precopulatory phase but still active (Table 1), did not significantly affect the duration of copulation in *S. allobrogus*. Thus we may conclude that in the copulatory phase activities of the female perform the major role.

CONCLUSIONS

1. In the premounting phase, mating success of *S. allobrogus* is mainly predetermined by the behaviour of the male. Actions exerting a positive impact on success of mounting include the male's abdomen extending that may give a visual signal for the conspecific female, and the substrate antenation that may reflect the activity of the male's response to chemical cues left by the female.

Table 4. Effect of the frequency of mating behavioural elements of the copulatory phase on the duration of copulation of the solitary wasp *Symmorphus allobrogus* (N = 444). Only significant values ($p < 0.05$) in the table; highly significant values ($p < 0.001$) in bold; n/s – not significant ($p > 0.05$).

Independent variables: frequency of behavioural elements (actions /min.)	Kendall Tau correlation	Multiple regression	
	τ	regr. coef. (b_i) \pm SE in the model with all parameters	regr. coef. (b_i) \pm SE in the model with parameters selected backward stepwise (F to remove = 8)
Female's actions			
shaking	-0.09	-70 \pm 24	-67 \pm 23
struggle	-0.55	-63 \pm 19	-59 \pm 16
Male's actions			
mate antenna antennation	n/s	n/s	
falling backwards	-0.20	n/s	
moving back	n/s	n/s	
wing vibration	0.08	n/s	
	Intercept (b_0)	141.4 \pm 18.4	135.6 \pm 17.4
	R	0.18	0.18

2. In the precopulatory ('courtship') phase of mating activities of both sexes are nearly equal in importance. Vigorous struggle of the female negatively affects mating success, while slow shaking of the female positively correlates with the resulting copulation. Antennation (simultaneous stroking of female antennae by male antennae, bearing tyloidea that possibly excrete contact pheromones) and stroking with lower part and apex of the abdomen are the behavioural elements of the male indispensable for successful copulation.

3. In the copulatory phase of mating visible activities of the male have little influence on the duration of copulation, while the intensity of shaking and struggle of the female have a crucial effect, inducing an earlier termination of mating.

ACKNOWLEDGEMENTS

Part of this study was capacitated by the grant of the Lithuanian State Science and Studies Foundation (contract No T-579).

REFERENCES

Abeelluck, D. and Walter, G.H. 1997. Mating behaviour of an undescribed species of *Coccophagus*, near *C. gurneyi* (Hymenoptera: Aphelinidae). *Journal of Hymenoptera Research* 6: 92–98.

Alcock, J. 1978. Notes on male mate-locating behavior in some bees and wasps of Arizona. *The Pan-Pacific Entomologist* 54: 215–225.

Alcock, J. 1994. Postinsemination associations between male and female insects: the mate-guarding hypothesis. *Annual Review of Entomology* 39: 1–21.

Alcock, J., Barrows, E.M., Gordh, G., Hubbard, L.J., Kirkendall, L., Pyle, D.W., Ponder, T.L. and Zalom, F.G. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zoological Journal of the Linnean Society* 64: 293–326.

Arnqvist, G. and Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60: 145–164.

Ayasse, M., Paxton, R.J. and Tengö, J. 2001. Mating behavior and chemical communication in the order Hymenoptera. *Annual Review of Entomology* 46: 31–78.

Batra, S.W.T. 1978. Aggression, territoriality, mating and nest aggregation of some solitary bees (Hymenoptera: Halictidae, Megachilidae, Colletidae, Anthophoridae). *Journal of the Kansas Entomological Society* 51: 547–559.

Blanckenhorn, W.U., Mühlhäuser, C., Morf, C., Reusch, T. and Reuter, M. 2000. Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. *Ethology* 106: 577–593.

Boake, C.R.B. and Hoikkala, A. 1995. Courtship behaviour and mating success of wild-caught *Drosophila silvestris* males. *Animal Behaviour* 49: 1303–1313.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: A synthesis of ideas and evidence. *Biologi-*

- cal Reviews* 76: 305–339.
- Boughman, J.W. 2002. How sensory drive can promote speciation. *Trends in Ecology & Evolution* 17: 571–577.
- Budrienė, A. 2001. Some aspects of mating behaviour of Eumenidae wasps (Hymenoptera). *Norwegian Journal of Entomology* 48: 41–44.
- Budrienė, A. 2003. Prey of *Symmorphus* wasps (Hymenoptera: Eumeninae) in Lithuania. *Acta Zoologica Lituonica* 13 (3): 306–310.
- Budrys, E., Budrienė, A. and Pakalniškis, S. 2004. Population size assessment using mark-release-recapture of 12 species of Orthoptera, Diptera and Hymenoptera: a comparison of methods. *Latvijas Entomologs* 41 (in press).
- Crean, C.S. and Gilburn, A.S. 2000. Sexual selection as a side-effect of sexual conflict in the seaweed fly, *Coelopa ursina* (Diptera: Coelopidae). *Animal Behaviour* 59: 121–126.
- Cowan, D.P. 1986. Sexual behaviour of Eumenid wasps (Hymenoptera, Eumenidae). *Proceedings of the Entomological Society of Washington* 88: 531–541.
- Cowan, D.P. 1991. The solitary and presocial Vespidae. In: K.G. Ross and R.W. Matthews (eds) *The Social Biology of Wasps*, pp. 33–73. Ithaca, NY: Cornell University Press.
- Cunningham, E.J.A. and Birkhead, T.R. 1998. Sex roles and sexual selection. *Animal Behaviour* 56: 1311–1321.
- Eberhard, W.G. 2001. Species-specific genitalic copulatory courtship in sepsid flies (Diptera, Sepsidae, Mocssepsis) and theories of genitalic evolution. *Evolution* 55: 93–102.
- Edvardsson, M. and Arnqvist, G. 2000. Copulatory courtship and cryptic female choice in red flour beetles *Tribolium castaneum*. *Proceedings of the Royal Society of London B* 267: 559–563.
- Eickwort, G.C. and Ginsberg, H.S. 1980. Foraging and mating behavior in Apoidea. *Annual Review of Entomology* 25: 421–426.
- Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.
- Jachmann, F. and van den Assem, J.A. 1996. A causal ethological analysis of the courtship behaviour of an insect (the parasitic wasp *Nasonia vitripennis*, Hym., Pteromalidae). *Behaviour* 133: 1051–1075.
- Markow, T.A., Bustoz, D. and Pitnick, S. 1996. Sexual selection and a secondary sexual character in two *Drosophila* species. *Animal Behaviour* 52: 759–766.
- McClintock, W.J. and Uetz, G.W. 1996. Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Aranea: Lycosidae). *Animal Behaviour* 52: 167–181.
- Miller, K.B. 2003. The phylogeny of diving beetles (Coleoptera: Dytiscidae) and the evolution of sexual conflict. *Biological Journal of the Linnean Society* 79: 359–388.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45: 525–567.
- Qvarnström A. and Forsgren, E. 1998. Should females prefer dominant males? *Trends in Ecology & Evolution* 13: 498–501.
- Reinhold, K., Kurtz, J. and Engqvist, L. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. *Journal of Evolutionary Biology* 15: 201–209.
- Ringo, J. 1996. Sexual receptivity in insects. *Annual Reviews of Entomology* 41: 473–494.
- Sauter, A. and Brown, M.J.F. 2001. To copulate or not? The importance of female status and behavioural variation in predicting copulation in a bumblebee. *Animal Behaviour* 62: 221–226.
- Shimron, O. and Hefetz, A. 1985. Mating behavior and sex attraction of *Eucera oalestinae* Friese (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* 58: 526–531.
- Sih, A., Lauer, M. and Krupa, J.J. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water strider. *Animal Behaviour* 63: 1079–1089.
- Smith, A.P. and Alcock, J. 1980. A comparative study of the mating systems of Australian eumenid wasps (Hymenoptera). *Zeitschrift fuer Tierpsychologie* 53: 41–60.
- Syverstein, T.C., Jackson, L.L., Blomquist, G.L. and Vinson, S.B. 1995. Alkadienes mediating courtship in the parasitoid *Cardiochiles nigriceps* (Hymenoptera: Braconidae). *Journal of Chemical Ecology* 21: 1971–1989.
- Thornhill, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *American Naturalist* 122: 765–788.
- Thornhill, R. and Alcock, J. 1983. *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press.
- Van Dongen, S., Matthysen, E., Sprengers, E. and Dhondt A.A. 1998. Mate selection by male winter moths *Operophtera brumata* (Lepidoptera, Geometridae): adaptive male choice or female control? *Behaviour* 135: 29–42.
- Wang, Q., Zeng, W., Chen, L., Li, J. and Yin, X. 2002. Circadian reproductive rhythms, pair-bonding, and evidence for sex-specific pheromones in *Nadezhdiella cantori* (Coleoptera: Cerambycidae). *Journal of Insect Behavior* 15: 527–539.
- Wedell, N., Gage, M.J.G. and Parker, G.A. 2002. Sperm competition, male prudence and sperm-limited females. *Trends in Ecology & Evolution* 17: 313–320.

**ELGSEŅOS ELEMENTAI, ĪTAKOJANTYS
KLOSČIAVAPSVĒS *SYMMORPHUS*
ALLOBROGUS (HYMENOPTERA:
EUMENINAE) PORAVIMOSI
SĒKMEĀ**

A. Budrienē, E. Budrys

SANTRAUKA

Straipsnyje aprašyti klosčiovapsvēs *Symmorphus allobrogus* poravimosi elgsenos komponentai, ĩvertinta jū ĩtaka susiporavimo sēkmei. *S. allobrogus* patinai pateliū aptikimui naudoja regējimą. Statistinė analizē (Kendall Tau koreliacija ir logistinė regresija) parodē,

kad priesužtūpimo fazēje didžiausią ĩtakā poravimosi sēkmei turi patino aktyvumas, ypač jo pilvelio ištiesimai ir substrato antenavimas. Prieskopuliacinēje fazēje abiejū lyčīū elgsena yra mažauga vienodai svarbi. Iš patelēs elgsenos elementū „kova“ turi neigiamā ĩtakā poravimosi sēkmei, tuo tarpu „kratymasis“ didina kopuliacijos tikimybę. Antenavimas ir braukymas pilveliu yra svarbiausi patino elgsenos elementai, užtikrinantys kopuliacijā. Kopuliacinēje poravimosi fazēje patino matomas aktyvumas mažai ĩtakoja kopuliacijos trukmē, tuo tarpu patelēs „kratymasis“ ir „kova“ salygoja ankstesnē jos pabaigā.

Received: 20 November 2003

Accepted: 14 June 2004