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COMPARISON OF MATING OF TEN EUMENINAE WASP SPECIES WITH A BRIEF REVIEW OF SEXUAL SELECTION THEORIES: A FRAMEWORK FOR FUTURE RESEARCH

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Abstract. This paper represents an initial attempt to examine mating phases of ten wasp species of the genera *Ancistrocerus*, *Discoelius* and *Symmorphus*, posing the questions as to what species traits are potentially involved in interactions between sexes, and what forms of sexual selection impel the evolution of these traits. The studied species significantly differ in the sex ratio and the relative body size of sexes, their willingness to mount and copulate, male displays (mode and frequency of antennation and position while copulating), female displays (intensity and frequency of rejecting behaviour), the presence of the male's copulatory and postcopulatory courtship. Results of the comparative study of mating behaviour are discussed in parallel with the review of literature on sexual selection and sexual conflict, defining the framework for future research. Single locus complementary sex determination (sl-CSD), regular inbreeding and female uniparental care in combination with predominant monandry are the features of these wasps that allow to use them as a model for studies into understanding of the evolutionary maintenance of monandry.

Key words: courtship, female rejecting behaviour, monandry, sexual conflict, sexual selection, sl-CSD

INTRODUCTION

The lifetime reproductive success of animals depends largely on male-female behavioural interactions that result in choosing a high-quality partner. Most animal males including insects are more active competitors for their mates than females (e.g. Andersson 1994; Andersson & Iwasa 1996), and their mating efforts are usually higher than parental efforts (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Arnold & Duvall 1994). This difference in reproductive interests between males and females provides a potential for sexually antagonistic selection that may result in the antagonistic coevolution of sexes (Parker 1979, 2006; Alexander *et al.* 1997; Chapman *et al.* 2003; Arnqvist & Rowe 2005). The latter is thought to shape mating behaviour like the precopulatory 'struggle' between males and females in aquatic isopods (Jormalainen & Merilaita 1995; Jormalainen 1998), dung flies (Parker 1979) and water striders (Arnqvist 1992; Rowe 1994; Rowe *et al.* 1994; Lauer *et al.* 1996; Arnqvist 1997; Watson *et al.* 1998; Arnqvist & Rowe 2002). Sexually antagonistic selection is predicted to influence biological diversity not only by affecting speciation rates (Parker & Partridge 1998; Arnqvist *et al.* 2000; Gavrilets 2000; Gavrilets *et al.* 2001; Martin & Hosken 2004), but also by altering the likelihood of extinction (Kokko & Brooks 2003).

Most discussions on sexual selection mechanisms have focused on polyandrous species. Their reproductive success may be affected by pre-mating events, resulting in male and female choice, as well as post-mating events, including male-male competition in the form of sperm competition (Parker 1970; Danielsson 1998) and cryptic female choice (Eberhard 1996). The latter two forms of postcopulatory sexual selection are assumed to be powerful evolutionary forces working both at molecular and population levels (Birkhead & Pizzari 2002; Neff & Pitcher 2005; Snook 2005). Positive consequences of female promiscuity have been generally divided into direct effects on female fecundity and lifespan, e.g. acquisition of nutritious accessory gland substances (Gwynne 1984; Arnqvist & Nilsson 2000; Møller & Jennions 2001), as well as indirect (genetic) effects on offspring fitness, e.g. by selecting compatible or good genes (Zeh & Zeh 1997; Møller 1998; Jennions & Petrie 2000; Birkhead & Pizzari 2002; Tomkins *et al.* 2004; Neff & Pitcher 2005; Simmons 2005). According to theoretical models, the preferred male must provide genes that increase net offspring fitness as compared to the genes provided by less desirable males (Kokko *et al.* 2003; Mead & Arnold 2004). However, the prevalence of indirect benefits is controversial because its genetic and physiological background is poorly understood.

It is suggested that females of most Hymenoptera species mate only once during their lifetime (Alcock 1978; Boomsma & Ratnieks 1996; Schmid-Hempel & Schmid-Hempel 2000; Baer & Schmid-Hempel 2001; Strassmann 2001; Baer 2003; Boomsma *et al*. 2005). Nonetheless, social Hymenoptera are better known than the solitary ones in terms of the incidence of polyandry in some genera (Crozier & Fjerdingstad 2001; Paxton 2005), thus increasing the genetic diversity of a colony (Crozier & Page 1985; Palmer & Oldroyd 2000; Tarpy & Page 2001; for alternative hypotheses see Brown & Schmid-Hempel 2003; Kraus *et al*. 2004; Schlüns *et al*. 2005). Therefore, the question is why females do not copulate more than once, if polyandry brings some fitness benefits. In the evolution of mating systems, costs of searching for and discriminating among males (costs of being too choosy) and costs of mating too often (costs of being not choosy enough) are important (Kokko *et al*. 2003). Indeed, mating at very high rates is costly to insect females in general (Thornhill & Alcock 1983; Arnqvist & Nilsson 2000), including the social Hymenoptera. Among the latter, monandry is favoured due to a narrow time window for mating, lack of material gain from males, lack of paternal care and apparent lack of any post-copulatory sperm discrimination mechanisms (Strassmann 2001).

Solitary Eumeninae are important because, as a sister group of the social subfamilies Stenogastrinae, Polistinae and Vespinae of the family Vespidae (Carpenter 1981; Brothers 1999; Carpenter & Wheeler 1999), they possess behavioural features which may have explanatory implications for the evolutionary trajectories of sociality in insects (Kurzenko 1980; Itino 1986; Cowan 1991; Chapman & Stewart 1996; Hunt 1999; Wcislo 2000; Hunt & Amdam 2005). Solitary wasp females gain little from additional matings, thus tend to be monandrous (O'Neill 2001). They are often receptive on emergence, therefore, the ability of males to select sites of waiting for emerging virgin females is crucial for their reproductive success (Alcock 1978; Batra 1978; Seidelmann 1999). Protandry (males emerge several days earlier than females) is a common feature of the species, whose males seek freshly enclosed females, and represents an adaptive aspect of the male's life-history strategies (Evans 1966; O'Neill 2001). The intensity of competition among males measured by their operational sex ratio (OSR) is defined as the ratio of the number of sexually active males in a population to the number of receptive females (Emlen & Oring 1977). It is presumed to be much higher than the population sex ratio even in species with a small degree of protandry (O'Neill 2001). Becoming biased towards the less investing sex, OSR increases the competition for mates among individuals of the more abundant sex and choosiness among those of the less abundant sex (Trivers 1972; Emlen & Oring 1977). In solitary wasps, the female choosiness is possible because females of many species can reject suitors as they can physically dominate smaller males (O'Neill 2001; Budrienė & Budrys 2004).

As the mating behaviour of solitary wasps, including Eumeninae, is difficult to observe in nature, earlier knowledge is mainly based on anecdotal reports, detailed investigations being rare (O'Neill 2001). Only a few studies have compared the mating behaviour of Eumeninae (Cowan 1986; Budrienė 2001), even less attention being given to the mode of sexual selection to which this behaviour may be subject. This paper provides new data on the mating behaviour of six species of Eumeninae and additional information on four previously studied species.

The first objective of this study was to shed light on the basic features of the mating systems of Eumeninae wasps, i.e. (1) their choosiness while selecting a mate, (2) the behavioural elements that are involved in mate choice, and (3) their traits related to sexual selection such as sexual size dimorphism (SSD) and the sex ratio. The second objective was to review the latest achievements in sexual selection theories and to assess the potential of Eumeninae as a model group for the future research and testing the hypotheses.

MATERIAL AND METHODS

Mating was observed in captivity, using wasps reared from trap-nests. Also, occasional field observations of mating were used for comparison.

The reed bundle trap-nests were exposed in four localities of Lithuania, Varnupys (55°24'N 25°17'E), Bilšiai (55°08'N 25°16'E), Kaunas city (54°54'N 23°54'E) and Papiškiai (55°56'N 24°16'E) in 1991–2003 (details in Budrienė 2003). Insects obtained before the year 1997 were used for the estimation of sex weight and sex ratio only. Wasps reared in 1997–2003 were used for observations of mating.

We studied mating behaviour of ten Eumeninae species: *Ancistrocerus antilope* (Panzer), *A. gazella* (Panzer), *A. nigricornis* (Curtis), *A. trifasciatus* (Müller), *Discoelius dufourii* (Lepeletier), *D. zonalis* (Panzer), *Symmorphus allobrogus* (Saussure), *S. crassicornis* (Panzer), *S. gracilis* (Brulle) and *S. murarius* (L.). Of these species, mating of *A. gazella*, *A. nigricornis*, *A. trifasciatus*, *S. crassicornis*, *S. gracilis* and *D. dufourii* was studied for the first time.

Reed internodes containing wasp nests were reactivated in the refrigerator. The sex of insects was determined at the pupal stage. After that the latter were kept in small plastic vials until hatching of adults. Males and females were kept individually in plastic cages (6 cm height × 5 cm diameter) or glass vials (20 cm length × 2.5 cm diameter) at ambient temperature (22–26°C), with honey solution and water available. In total, 439 males and 1,037 females of ten species were used in mating trials.

Pairings were observed on a white paper arena of 22 cm diameter, under a bell-glass 22 cm in height, surrounded by white paper in all sides, except the side of the observer, in a thermostat, at a temperature of 27–29°C. The thermostat was exposed to daylight, with additional artificial illumination (two 25 W light sources at a distance of 30 cm). In such artificial setting, the conspecific partner had to be the only stimulus to mating behaviour.

A single virgin female (or an inseminated female in cases of remating experiments) was let into the arena under the bell-glass and the cage with a single male was placed near the latter for a 1 minute acclimation period. Afterwards, the male was admitted into the arena, and the pair was observed for 30 minutes. If mounting took place, the insects were observed until dismounting. In order to prevent wasps from responding to odour cues of previous pairings, we changed the paper layer between trials. In total, data of 1,060 observations of pairing were used for analysis.

We used term 'Precopulatory phase' (which may include 'precopulatory courtship') for the part of mating from the start of mounting until intromitting the female (Cowan 1986). 'Copulatory phase' (and 'copulatory courtship', if present) refers to the events after intromitting the female until extraction of male genitalia. 'Postcopulatory phase' (and 'postcopulatory courtship', if present) refers to the part of the mating following termination of copulation and until the end of mounting. The 2 × 2 Chi-square test ($\chi^2_{df=1}$) was applied for the pairwise inter-specific comparison of proportions of experiments that resulted in mounting and copulation. The Mann-Whitney U test was performed to compare frequencies of female antennae antennation by males of different species. Statistical analysis was done using the computer program StatSoft Statistica, release 6.0.

RESULTS

Sexual size dimorphism and sex ratio

The average female weight of the studied wasp species ranged from ca. 30 mg (*A. gazella*, *A. trifasciatus*, *S. allobrogus*, *S. gracilis*) to nearly 80 mg (*A. antilope*) (Table 1). The average weight of males made up from 45% (*D. zonalis*) to 62% (*A. trifasciatus*, *S. allobrogus*, *S. gracilis*) of the average female weight.

The male/female abundance ratio varied among the studied species. Three of them had the ratio close to one-to-one (*A. antilope*, *D. dufourii*, *S. crassicornis*). In two species (*D. zonalis* and *S. murarius*) males were considerably more abundant than females. The other five species had a female-biased sex ratio (Table 1).

Mating observations in the field

Out of ten studied species, *S. allobrogus* was the only one, which mating behaviour could be observed at their nest aggregations. Males of the other studied wasp species were never seen at the nesting sites.

Table 1. Average size of males and females, male-to-female size ratio, and sex ratio of 10 Eumeninae wasp species.

Wasp species	*n* of males measured	Weight of male (mg)	*n* of females measured	Weight of female (mg)	Male/female mean weight ratio	Estimated male/ female sex ratio*
A. antilope	63	39.0 ± 1.4	92	77.7 ± 2.1	0.50	1.24 ± 0.36, *n* = 10
A. gazella	2	16.8 ± 0.6	8	28.7 ± 2.1	0.59	0.25, *n* =1
A. nigricornis	13	30.4 ± 1.5	6	50.0 ± 1.3	0.61	0.31 ± 0.09, *n* = 3
A. trifasciatus	36	17.7 ± 0.6	61	28.5 ± 0.8	0.62	0.44 ± 0.17, *n* = 10
D. dufourii	23	20.6 ± 1.3	23	37.7 ± 1.7	0.55	0.94 ± 0.24, *n* = 8
D. zonalis	29	28.7 ± 1.4	24	64.2 ± 3.0	0.45	2.24 ± 0.35, *n* = 10
S. allobrogus	639	19.1 ± 0.2	962	31.0 ± 0.2	0.62	0.67 ± 0.06, *n* = 10
S. crassicornis	23	21.4 ± 1.2	37	46.0 ± 1.9	0.47	1.17 ± 0.61, *n* = 7
S. gracilis	6	18.5 ± 1.0	31	29.7 ± 0.9	0.62	0.29 ± 0.20, *n* = 3
S. murarius	43	31.0 ± 1.7	67	64.3 ± 2.5	0.48	1.82 ± 0.42, *n* = 10

** – average of yearly ratios; n – number of years when species nests were obtained*

S. allobrogus males were emerging a few days earlier than females and were active for about three weeks. Males spent much time at nesting sites waiting and searching for receptive females. These activities of *S. allobrogus* males were defined as follows:

- patrolling of nest aggregations and continuous inspecting of surfaces with cavities;
- locating cavities with females (in the observed cases the females were apparently underdeveloped, with unformed wings) and attempting to pull them out with their mandibles;
- brief touching of conspecific foraging females in flight resulting in their refusal to copulate and occasional abandonment of their load;
- brief pouncing on conspecific males or dead females as well as other dark objects of similar shape and size.

Female hatching and mating period was short, as we watched females already performing nesting activities 4 or 5 days after the first observations of males. In that time, copulation of *S. allobrogus* was never observed at the nesting sites. Therefore, we suppose that the majority of copulations occurred immediately after the females' emergence.

Probability of mating in captivity

Of total 1,037 pairing trials with virgin females, 583 (56% of all observations) resulted in mountings. Of them, 353 (34% of all trials, 61% of all mountings) ended in copulation.

The species showed considerable differences in readiness of mates to take up a mounted position (Table 2; Fig. 1). Observations of mounting attempts by *Symmorphus* species showed that they were successful in more than half of cases, while representatives of the other genera showed less than 50% of mountings. The differences were statistically significant for most inter-generic comparisons (Table 3).

The highest probability of copulation (more than 70% of all mountings) was also observed in *Symmorphus* species (except *S. murarius*; Table 2, Fig. 1). In contrast, *A. nigricornis*, *A. antilope*, and *S. murarius* copulated in less than half (11%, 12% and 38% correspondingly) of all trials, and the difference was significant in comparison with most other species (Table 4).

Taking into account that the partner was the only stimulus to initiate mating behaviour in the trials, we assume that the observed differences of mounting and copulation probability reflect the intrinsic differences in mate recognition and discriminatory ability of the wasp species.

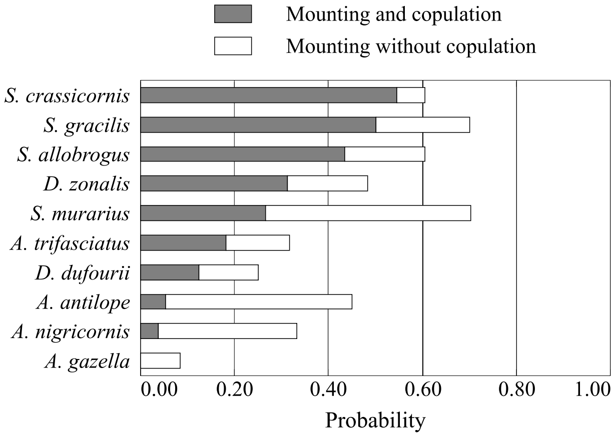

Figure 1. Mating behaviour of 10 Eumeninae wasp species in the laboratory: probability of mounting and copulation.

Table 2. Number of mating trials that resulted in mounting and copulation of 10 Eumeninae species.

Wasp species	*n* of mating trials	*n* of trials that resulted in mounting	% of trials that resulted in mounting	*n* of trials that resulted in copulation	% of trials with mounting that resulted in copulation
A. antilope	133	60	45%	7	12%
A. gazella	12	1	8%	0	0%
A. nigricornis	27	9	33%	1	11%
A. trifasciatus	22	7	32%	4	57%
D. dufourii	8	2	25%	1	50%
D. zonalis	93	45	48%	29	64%
S. allobrogus	606	367	61%	264	72%
S. crassicornis	33	20	61%	18	90%
S. gracilis	10	7	70%	5	71%
S. murarius	94	66	70%	25	38%

Table 3. Pairwise comparison of the number of trials that resulted in mounting and those without mounting among 10 wasp species: 2×2 χ^2_1 values*.

	S. murarius	*S. gracilis*	*S. crassicornis*	*S. allobrogus*	*D. zonalis*	*D. dufourii*	*A. trifasciatus*	*A. nigricornis*	*A. gazella*
A. antilope	**14.0**			10.6					6.1
A. gazella	**17.5**	9.0	9.7	**13.3**	6.9				
A. nigricornis	**12.1**	4.0	4.4	7.9					
A. trifasciatus	**11.3**	4.1	4.4	7.2					
D. dufourii	6.8			4.2					
D. zonalis	9.2			4.9					
S. allobrogus									
S. crassicornis									
S. gracilis									

** – only significant ($p < 0.05$) values are presented in the table; highly significant ($p < 0.001$) values are shown in bold. n – see Table 1*

Mating behaviour in captivity

Precopulatory phase. Typically, the male took a horizontal position over the female on her dorsum with head above head. However, in 22 cases (nearly 3.8% of all mountings) the male initially mounted the female in antiparallel position. He started to antennate her abdominal tip but after a few seconds of such behaviour, returned to the typical position. Males of *S. allobrogus* demonstrated this behaviour in 4.4% of all mountings of the species (16 observations), *D. zonalis* in 6.7% of all mountings (3 observations), *A. antilope* in 3.3% of all mountings (2 observations), and *S. crassicornis* in 5% of mountings (one observation). Such behaviour occurred both in virgin males (11 cases) and those having earlier mating experience (11 cases). Thus we may conclude that such behaviour does not depend on the male's experience.

When mounted, male of any of the studied species, except *A. antilope* and *D. dufourii*, held his forelegs on the sides of the female's pronotum, his mid legs on the sides of her propodeum, and his hind legs close to her petiole. In contrast, males of *A. antilope* and *D. dufourii* splayed out their mid legs horizontally, directed in opposite sides.

Antennation of female antennae was one of male behavioural elements distinctive of each studied species. In contrast to irregular tapping by switching antennae of *A. antilope*, males of other species stroked female antennae from pedicel to flagellum regularly. The manner of stroking differed among the species studied. It was mostly a straight simple movement in *A. gazella*, *A. trifasciatus*, *D. dufourii*, *D. zonalis*, and *S. murarius* males in contrast to the jerking motion

Table 4. Pairwise comparison of the number of observations with mounting that resulted in copulation and those without copulation among 10 wasp species: 2×2 χ^2_1 values*.

	S. murarius	*S. gracilis*	*S. crassicornis*	*S. allobrogus*	*D. zonalis*	*D. dufourii*	*A. trifasciatus*	*A. nigricornis*	*A. gazella*
A. antilope	**11.4**	**15.2**	**42.8**	**80.5**	**31.8**		9.5		
A. gazella			6.3						
A. nigricornis		6.1	**17.1**	**15.6**	8.6		3.9		
A. trifasciatus									
D. dufourii									
D. zonalis	7.6		4.5						
S. allobrogus	**29.1**								
S. crassicornis	**16.7**								
S. gracilis									

** – only significant ($p < 0.05$) values are presented in the table; highly significant ($p < 0.001$) values are shown in bold. n – see Table 1* exhibited by males of *A. nigricornis*, *S. allobrogus*, *S. crassicornis*, and *S. gracilis*. In addition to simple stroking, males of *A. trifasciatus* sometimes demonstrated trembling antennal movements similar to those of *A. nigricornis* observed during copulation (see copulatory phase).

Rejecting behaviour, or the 'struggle' of females (described in Budrienė 2001, 2004; Budrienė & Budrys 2004) of varied intensity during the initial phase of mounting was more or less characteristic of all the studied species (Table 5).

Copulatory phase. Copulation always took place on the substrate: the bell-glass wall or the layer of the arena. In most cases, each mounting resulted in a single copulation. The exception was *A. antilope*. Of the total number of 7 pairing trials of this species that resulted in copulation, four pairs copulated once, two pairs copulated twice and one pair copulated three times. Therefore, each successful pairing of *A. antilope* included 1.6 ± 0.3 (here and further average ± standard error) copulations. In addition, 2.7% of pairing trials of *S. allobrogus* that resulted in copulation (7 pairings) included two copulations each, the interval between them lasting from 9 to 259 seconds.

Male antennal strokings were less common during copulation than during the precopulatory phase of mounting in most species (Table 5). The only exception was males of *S. gracilis* demonstrating significantly higher probability of presence of antennal stroking during copulation than males of any other species (Mann-Whitney U test, $p < 0.05$). Unlike the other species, the male of *A. nigricornis* moved his trembling antennae alternately from side to side, if the female became restless. That movement bore some similarity with the precopulatory antennal switching of *A. antilope*.

After the initiation of copulation, males of *A. trifasciatus*, *D. zonalis*, *D. dufourii* and *S. murarius* always (except a single observation of *D. zonalis*) released their leg-hold and fell backwards behind the female, remaining attached to the female by their genitalia. Sometimes, males of *S. allobrogus*, *S. crassicornis* and *S. gracilis* fell backwards, as well (Table 5). Such behaviour of males was observed in cases when the female exhibited vigorous rejection behaviour. After the termination of copulation, males of *A. trifasciatus*, *D. zonalis*, *S. allobrogus* and *S. murarius* sometimes remained immobile for 272 ± 25 (n = 4), 147 ± 9 (n = 28), 5.7 ± 1.2 (n = 137) and 308 ± 31 (n = 25) seconds, correspondingly.

Females demonstrated a different degree of rejecting behaviour, mostly by the end of copulation (Table 5). It was expressed as kicking and wriggling of their abdomens in order to release themselves from males, and/or walking on the substrate dragging the attached male behind. The most vigorous 'struggle' was demonstrated by females of *A. antilope*, *S. allobrogus* and *S. crassicornis* and a more moderate one by *A. gazella*,

Table 5. Selected features of mating behaviour in 10 Eumeninae wasp species.

Species	Female		Male			
	'struggle'		Antennal strokings			Falling backwards**
	Precopulatory*	Copulatory**	Precopulatory**	Copulatory**	Mode	
A. antilope	57%	85%	82%	0%	tapping /switching	0%
A. gazella	100%		100%		simple	
A. nigricornis	78%	100%	11%	0%	jerking/ trembling	0%
A. trifasciatus	43%	100%	86%	50%	simple /trembling	100%
D. dufourii	50%	100%	100%	0%	simple	100%
D. zonalis	27%	93%	71%	28%	simple	97%
S. allobrogus	66%	97%	84%	29%	jerking	52%
S. crassicornis	50%	100%	95%	28%	jerking	17%
S. gracilis	57%	100%	71%	100%	jerking	20%
S. murarius	73%	88%	85%	20%	simple	100%

** – percentage of mating trials with the precopulatory 'struggle' and antennal stroking of the total number of trials that resulted in mounting;*

*** – percentage of mating trials with the copulatory 'struggle', antennal stroking and male falling backward of the total number of trials that resulted in copulation*

A. nigricornis, *A. trifasciatus*, *S. gracilis* and *S. murarius* females. Although predominantly feeble kicking of *D. dufourii* and *D. zonalis* females contrasted with quite uniform rejection behaviour of the other species, we recognised it as the 'struggle', as well. In addition to kicking, the female of *D. dufourii* arched her body and seized the motionless male with her mandibles repeatedly. This 'aggressive kicking' strikingly differed from the rejection behaviour of *D. zonalis*.

Postcopulatory phase. Following the termination of copulation, males of *A. antilope* demonstrated the postcopulatory courtship behaviour, which was similar to the precopulatory courtship and lasted from 1.9 minutes to 19.5 hours. Each pair of the other studied Eumeninae species usually separated immediately after copulation. However, there were some exceptions. In 13% of all copulation cases of *S. allobrogus* (33 observations) and in 67% copulations of *S. crassicornis* (12 observations) the male remained on the female in mounted position from 1 to 841 seconds and from 1 to 24 seconds, correspondingly, after the termination of copulation. Generally, the male simply rode the female, but in three trials with *S. allobrogus* and in one trial with *S. crassicornis*, within 12 to 841 seconds the male initiated courtship behaviour. The similar simple riding after the end of copulation was demonstrated in some pairings of *A. nigricornis*, *D. zonalis*, and *S. gracilis*, as well.

Remating experiments. In order to check the monandry of the studied Eumeninae wasps, we tested eight copulated females of *S. allobrogus* and three females of *D. zonalis* in additional mating trials. Each inseminated female was allowed to pair with one male once per day. Out of 23 trials of *S. allobrogus*, two females were tested during four subsequent days, three females were tested during three subsequent days, and three females were tested during two subsequent days. Out of six trials of *D. zonalis*, three females were tested in two subsequent days. In all experiments the females rejected males that attempted to copulate. This regularity was significant for *S. allobrogus* ($\chi^2_1 = 21.77$, $p < 0.001$), however, it was not significant for *D. zonalis* at the current number of observations ($\chi^2_1 = 3.11$, $p = 0.08$).

Males of *S. allobrogus* (70% of all test trials) as well as those of *D. zonalis* (50%) showed nearly as high mounting frequencies as those in the trials with virgin females (67% of all trials of *S. allobrogus*, $\chi^2_1 = 0.67$, $p = 0.41$, and 51% of *D. zonalis*, $\chi^2_1 = 0.07$, $p = 0.80$). These results support our field observations (see above) demonstrating that female's mating status is recognised (possibly by chemical or tactile cues) only after an immediate contact, e.g. mounting, has occurred.

DISCUSSION

Though multiple matings have been reported for a few species (Cowan & Waldbauer 1984; Cowan 1986), monandry is thought to be the most frequent feature of Eumeninae females (Smith & Alcock 1980; O'Neill 2001). It has been assumed that:
- for insects in general, monandrous systems are characterized by weaker selection for mate choosiness (Bonduriansky 2001);
- for social Hymenoptera, sexual selection is relatively weak in both males and females as the obligatorily singly mating ants, bees, and wasps may not have any sexual selection beyond premating partner choice (Boomsma *et al.* 2005); and
- for solitary bees, the variance in male mating success, and, hence, the opportunity for sexual selection is low in species that practise male scramble competition which is thought to be the most frequent male mate seeking behaviour among bee species (Paxton 2005).

One of the aims of the present discussion is to highlight the degree to which these assumptions may match the mating systems of Eumeninae wasps.

Mate searching tactics. The behaviour of *S. allobrogus* observed in the field shows that males use virgin female emergence site-patrolling tactics like many other protandrous species (Evans 1966; Cowan 1979, 1981). Immediate refusal of foraging (mated) females confirms that an *S. allobrogus* male is likely to recognise the mating status of a female instantly on contact, as it occurs in other Eumeninae species (Cowan 1991). We assume that olfactory cues are applied for ultimate identification of mate as it has been observed in other Aculeata (Barrows 1975). Females' refusals imply that they usually mate once and that males' attempts to grasp them incur costs to females. Indeed, attempts of males to mate with foraging females of the solitary bee *Anthophora plumipes* could have significant negative consequences for females' fitness as they reduced their ability to provision cells (Stone 1995).

The absence of other than *S. allobrogus* males at nesting sites may imply that they use other mate searching tactics. For example, males of *A. antilope* search for conspecific females in patches of suitable inflorescences (Cowan & Waldbauer 1984). In general, rendezvous sites of Eumeninae wasps seem to be species-specific.

According to Wickmann and Rutowski (1999), the mating strategy and mating site choice depend on ecological and behavioural variables that include population density and female mating frequency. High population density and low female mating frequency favour the patrolling of female emergence sites, whereas low population density may determine more specific mating tactics, as rendezvous sites, pheromonal or other signals. Therefore, the reason behind the patrolling of virgin female emergence sites by *S. allobrogus* males may be nesting of this species in colonies of higher density, in comparison with the other species (Budrys *et al*. 2004). The mating system of *S. allobrogus* may be classified as scramble competition polygyny (Thornhill & Alcock 1983), when the occurrence of females is focused in space and time, and males do not compete with each other directly defending territories or resources but compete in a race for receptive females.

Sexual size dimorphism and sex ratio. The fact that only 56% of all trials with Eumeninae resulted in mountings suggests that selective forces influencing mates' decision 'to mount or not to mount' need not necessarily be weak. The mate location system and strength of premating sexual selection in Hymenoptera are assumed to be associated with sexual size dimorphism (SSD) (Boomsma *et al*. 2005; Paxton 2005). According to this assumption, female-biased SSD (males are smaller than females) predicts non-territorial male mate seeking tactics. The fact that all the studied species have female-biased SSD is consistent with this prediction (Table 1: the male/female weight ratio). However, there is a variation in SSD among species, thus the intensity of selection that drives SSD may vary, as well. It is supposed that in the case of male scramble competition for mates, a common phenomenon among solitary wasps (O' Neill 2001), the selection is directed toward a smaller male size, associated with agility and in-flight manoeuvrability during mate search and courting (Blanckenhorn 2005). However, our data on SSD do not support this assumption. *S. allobrogus*, the species with scramble competition tactics and a higher frequency of mounting attempts (high agility), has relatively larger males (Table 1). In contrast, some species, most likely applying other mating tactics, possibly, rendezvous sites on flowers or leaves, and demonstrating a lower probability of mounting attempts (lower agility), such as *A. antilope*, or *D. dufourii*, have relatively smaller males (Table 1). It is assumed that these male tactics and SSD are associated with the sex ratio (e.g., Hardy & Mayhew 1998). In Eumeninae, the species with relatively large males (*A. nigricornis*, *A. trifasciatus*, *S. allobrogus* and *S. gracilis*) have a distinctly female-biased sex ratio, while males of the species having a male-biased ratio (*D. zonalis, S. murarius*) are relatively small (Table 1).

Sexual selection for small males is thought to be comparatively rare, thus it is important to integrate all the three sexual selection episodes: the mate search, the precopulatory and the postcopulatory episode (Blanckenhorn 2005). The study of SSD should test the applicability of Rensch's rule to Eumeninae and that of the assumption that the taxa deviating from it must be affected by female fertility selection (Székely *et al*. 2004) as well.

In summary, selective processes driving the sex-specific body size evolution in Eumeninae remain poorly understood and a further comparative analysis of the SSD is needed.

Recognition and assessment of mate. The interaction between cues is a common phenomenon influencing mate choice or facilitating its assessment (Candolin 2003). Within Hymenoptera, the visual cues, as facial and abdominal markings, are used to recognise the quality of conspecifics, e.g. hierarchical state of colony members in paper wasps (Tibbetts 2002; Tibbetts & Dale 2004). A positive relationship between the frequency of display of abdominal stripes and male mating is found in stenogastrine wasps (Beani & Turilazzi 1999). The inter- and intra-specific variability of colour patterns in the studied Eumeninae species (Budrienė & Budrys, unpubl.) may function not only as species identity cues but mate quality signals, as well. However, the misdirected mounting orientation of males, regularly occurring in *A. antilope*, *D. zonalis*, *S. allobrogus* and *S. crassicornis*, may reflect rather limited visual capabilities of these wasps. The correct orientation of mates during courtship may be a non-trivial problem in the species with scramble competition polygyny that may be solved using tactile and pheromonal stimuli (Shine *et al*. 2000). The presence of antennal glands in Eumeninae males (Budrienė 2001) and the occurrence of antennation in all the studied species (Table 5) suggest generality of tactile and chemical signals in sexual advertisement displays.

Differences among species in antennation modes indicate their functional importance in recognition and assessment of conspecific mate. In Hymenoptera, the antennation type is related to the species-specific number and location of glanded antennomeres (Romani *et al*. 2003). It is hypothesized that antennation is associated either with the spreading of a paste-like secretion onto female gustatory receptors while contacting the mate's antennae (Isidoro *et al*. 1996) or with the release of a volatile pheromone in the case of antennal fanning without contact (Felicioli *et al*. 1998). The co-occurrence of these two types of antennal movements in *Polistes dominulus* could be related to the release of two different secretions (Romani *et al*. 2005). A positive relationship between the intensity of precopulatory antennation and the occurrence of copulation in *S. allobrogus* (Budrienė & Budrys 2004) as well as excretion from male flagellomeres during antennation

(Budrienė 2004) confirm that male antennae may be regarded as one of the main sexually dimorphic signal structures in Eumeninae. They perform tactile and chemical communication, recognition and assessment of mates thus being essential to selective processes in conventional sexual selection models (e.g. 'good genes', 'Fisher's runaway'). Indeed, the antennal play used by males of Eumeninae wasps during their courtship is thought to be subject to the runaway component of Fisher's model of female choice (Cowan 1986). In addition, olfaction signalling can be considered as a handicap due to physiological costs of excrete production and can serve as an indicator of sender's quality to females (Gosling *et al.* 2000). Females benefit from the use of such signals both directly and indirectly. The indirect advantage is the inheritance of genes that increase viability and attractiveness of offspring. The direct benefits include decreased predation vulnerability and increased foraging time due to male search and courtship time-saving (Endler & Basolo 1998).

Obviously, Eumeninae wasps may recognise and assess their mates using multiple cues. Therefore, studies of the individual variation and behavioural manipulative experiments are needed to further clarify the functioning of species-specific traits (colour markings, structural features and behavioural elements) as signals.

Sexual conflict. High occurrence of the precopulatory rejection by females (Table 5) indicates the presence of sexual conflict. Parker (2006) defines the latter as a contradiction between evolutionary interests of different sexes that may, or may not, be generated by sexual selection. According to Lessells (2006), not all cases of sexual conflict lead to the evolution of manipulative behaviour or ongoing antagonistic co-evolution of sexes. In the sexual antagonism model, the female's preference is described as a general avoidance of male-imposed direct costs (Chapman *et al.* 2003). However, the precopulatory female resistance, which is interpreted as a cryptic mating preference, can help to indirectly assess the male's quality (Kokko *et al.* 2003). As the potential for the conflict is ubiquitous, there is a controversy in the understanding of the relative importance of sexual conflict co-evolution and the sexual co-evolution that is caused exclusively by indirect selection (Cunningham & Birkhead 1998; Kokko *et al.* 2003; Arnqvist 2004; Cordero & Eberhard 2005; Parker 2006; Tregenza *et al.* 2006). Therefore, it is difficult to judge from the available data on the studied Eumeninae species whether the precopulatory rejecting behaviour of females minimizes mating costs arising from male interests, or increases indirect benefits by selecting the strongest and the most persistent male. At present, the simplest explanation is that the female 'struggle' is a behavioural trait allowing females to assess mates as it has been earlier suggested for *S. allobrogus* (Budrienė & Budrys 2004). A similar interpretation has been proposed to explain the female reluctance observed in four monandrous species of ichneumonine wasps (Teder 2005).

Two major forms of sexual conflict are associated with mating and parental investment (Parker 2006). Manipulative behaviour or rapid evolutionary changes, which may be symptomatic of sexually antagonistic co-evolution, are more rare as outcomes of conflict over parental investment than conflict over mating (Lessells 2006). In haplodiploids, where males pass their genes to daughters only, there is selection on males to ensure that females produce more daughters by increasing the fertilization rate (Jennions & Petrie 2000). The resulting differences in optimal male and female sex ratios may lead to the sexual conflict over sex allocation (Shuker *et al.* 2006). It has been established that males of the parasitoid wasp *Nasonia vitripennis* may partly influence the sex allocation behaviour of females. One of the possible explanations for that phenomenon is that males deliberately attempt to increase their fitness by influencing daughter production (Shuker *et al.* 2006). Furthermore, the situation can become even more complicated taking into account the single locus complementary sex determination (sl-CSD) mechanism in most Hymenoptera, including Eumeninae. Under sl-CSD, in contrast to the standard arrhenotokous situation of uniparental haploid males, biparental diploid males (often infertile) result from the so-called matched matings in which parents share an allele at the sex locus (Wilgenburg *et al.* 2006). Although in some solitary Hymenoptera sl-CSD can result in a sharply increased probability of extinction under inbreeding conditions (Hedrick *et al.* 2006), it is not a case in the naturally inbreeding Eumeninae wasp *Euodynerus foraminatus* where diploid males have near-normal fertility and father fully fertile diploid daughters (Cowan & Stahlhut 2004).

It has been suggested that there is a potential conflict between mates over the ploidity of sons that should be produced in species with a combination of inbreeding and sl-CSD (Cowan & Stahlhut 2004; Stahlhut & Cowan 2004). From the female's point of view, the production of diploid sons results in loss of control over the offspring sex (ability to adjust the amount of provisions given to each offspring according to its sex). Diploid sons have only half of the value of haploid sons to females, while haploid sons have no value to males because they do not receive genes from the latter. It must be noted, that in the case of low inbreeding costs, mating with kin increases an individual's inclusive fitness (Parker 2006; Kokko & Ots 2006). This view is in concordance with the assumption that the advantage of mating with a brother and thus achieving greater genetic representation in offspring for an *E. foraminatus* female outweigh the costs of lower genetic variation among her offspring (Cowan & Stahlhut 2004; Stahlhut & Cowan 2004).

A possibility to avoid inbreeding was recently described in the solitary crabronid *Philanthus triangulum* (Herzner *et al*. 2006). This wasp seems to recognise kin mates by the similarity of a genetically variable male sex pheromone. The authors point out that the complementary mate choice maintains diversity in contrast to the 'good genes' model that is associated with strong directional selection and 'the paradox of the lek'.

Copulation between siblings does occur in some of Eumeninae species in captivity (Budrienė & Budrys, unpubl.). The ability of kin recognition and inbreeding avoidance, the fertilization success of sibling matings and the ability of females to adjust their offspring sex ratios in response to mating with brothers has not been investigated yet. However, the potential for both forms of sexual conflict, i.e. over the precopulatory mating decision (within the context of mate quality and/or mating between siblings) and over parental investment (within the context of what kind of progeny should be produced and how much to invest in it) is likely to be present in Eumeninae.

The studies aimed at the identification of potentially sexually antagonistic traits in populations are challenging in terms of examining the interaction between population ecology and the level of sexual conflict (Rowe & Day 2006; Tregenza *et al*. 2006). In Eumeninae, the latter should be taken into account applying the multifaceted model of the parental investment for offspring provisioning and sex allocation tactics (Rosenheim *et al*. 1996).

Choosiness of mates. Our observations of the copulatory behaviour of Eumeninae lead to two main assumptions: (1) the fact that only 34% of all trials and 61% of all mountings resulted in copulation infers the existence of mate choice; (2) inter-specific differences in willingness to copulate and hence choosiness are potentially causally linked to differences in mating systems that in turn are likely to be the target of different forms and strength of sexual selection. Therefore, we argue here that the assumptions about the weakness of selection on mate choosiness need not necessarily be applied to all the Eumeninae species studied. Additionally, the readiness to mate seems to be skewed among individual males in Eumeninae: some of them may copulate up to six times during their lifetime whereas others do not copulate in any of trials. Even species with scramble competition and the predicted low variance of male mating success, such as *S. allobrogus*, demonstrate high variation in the willingness of males to copulate (Budrienė & Budrys, unpubl.). Hence, the opportunity for sexual selection in Eumeninae is not as low as it is assumed. According to Reynolds and Gross (1990), the greater possibility for female choice in leks and related scramble mating systems can be explained by lower costs of mate search activities, and thus direct, rather than genetic benefits through either 'good genes' or the 'runaway' selection. It has been suggested by Werner and Lotem (2006) that lekking males may be also much choosier than it was previously supposed. Male choosiness, in combination with other factors, may help to solve the 'paradox of the lek'. Nevertheless, high probability of copulation within most of the studied *Symmorphus* (except *S. murarius*) may indicate a relatively low choosiness of both sexes, hence it implies a rather low actual intensity of sexual selection.

Male's copulatory courtship. Antennal stroking during copulation, characteristic of *S. gracilis* and often present in other monandrous species (Table 5), is a kind of copulatory courtship. However, the latter has traditionally been explained as the male's attempt to influence the female's cryptic choice, which represents a post-copulatory aspect of sexual selection in polyandrous species (Eberhard 1996). This is inconsistent with the assumption that premating sexual selection is the only form of mate choice operating in singly mating Hymenoptera. Nevertheless, Simmons *et al*. (2000) have associated the presence of the copulatory courtship in monandrous bee *Amegilla dawsoni* with the possibility for cryptic female choice. Permanent loss of female receptivity of this bee is caused by the presence of ejaculate in spermatheca, the filling of which is stimulated by the copulatory courtship. Insufficient courtship may result in a renewed receptivity of the female and mating with another male. To date, ejaculate peculiarities in Eumeninae have not been studied yet, but there is growing evidence that seminal fluid of male insects is a complex medium containing molecules and cells (apart from spermatozoa) that may have many effects on females (Simmons 2001; Gillott 2003; Arnqvist & Rowe 2005; Poiani 2006). The comparison of male sexual organs among species of Attinae ants has revealed a negative relationship between the degree of polyandry and the relative size of accessory glands, potentially indicating the male's ability to monopolize paternity (Mikheyev 2004; Baer & Boomsma 2004). Also, males of bush crickets can reduce the lifetime degree of polyandry of their mates by means of the transfer of large ejaculate volumes (Vahed 2006). Monandry is thought to be maintained by sexual conflict in the house fly *Musca domestica* (Arnqvist & Andrés 2006) and the bumble bee *Bombus terrestris* (Baer & Schmid-Hempel 2001), males of which are able to enforce monandry upon their mates despite the beneficial for females effects of multiple mating.

These facts allow us to hypothesize that the copulatory courtship via antennal strokings and possibly some yet unknown characteristics of ejaculate may enable the male to influence the female's reproductive investment in monandrous Eumeninae (though we could not reject their possible function in induction of the female unreceptivity too). It means that females may adaptively allocate investment depending on the quality of their mates or that the male's ability to manipulate the female's investment is associated with his quality. Such abilities were discovered in parasitoid wasps *Nasonia vitripennis* and *Uscana semifumipennis*. Males of *N. vitripennis* can affect the sex ratio of their progeny (Shuker *et al.* 2006), while those of *U. semifumipennis* vary in their capacity to inseminate females, larger males producing a more female-biased sex ratio (Henter 2004). The demonstration that a female allocates investment differentially, depending on the quality of her mate, is challenging, because the experiment must include the determination of the subsequent success of both the female and her offspring (Sheldon 2000). Again, to decide whether the intraspecific variation in male traits is related to differences in his manipulative ability, or to female choice, is a difficult task for empiricists (Danielsson 1998). An example of such difficulty is seen in recent experimental studies of differential allocation in crickets, *Acheta domesticus* (Head *et al.* 2006) and *Gryllus bimaculatus* (Bretman *et al.* 2006).

Female's rejecting behaviour. The similar problem arises when interpreting the female's copulatory 'struggle', where two explanations may be equally applied. First, this behavioural trait is aimed at 'screening' the male's genetic quality, thus it is maintained by indirect benefits to the female (Eberhard 1996). Second, the rejecting behaviour may reduce direct costs potentially associated with male attempts to monopolize paternity and to influence the offspring sex ratio. Differences in costs and benefits of parental investment to males and females result in conflict. Hence, the two sexes are selected to produce different sex ratios (Wedell *et al.* 2006). This may be true in the species with a combination of inbreeding and sl-CSD, such as Eumeninae. Their fathers may prefer to produce diploid offspring (daughters and inbred diploid sons), since they do not provide parental care and do not contribute any of their own genome to haploid sons. At the same time, mothers do bear parental care and may be interested in haploid sons, because both daughters and inbred diploid sons are more costly (but see Reece *et al.* 2004 for understanding of female-biased sex ratios in haplodiploid species). For instance, diploid male larvae of *Philanthus triangulum* cost twice as much as haploid males (Strohm & Linsenmair 1999, 2000). According to the multifaceted model of nest-building Hymenoptera (Rosenheim *et al.* 1996), these costs can be attributed to at least three limiting components of parental investment of Eumeninae females: nesting cavities, resources for offspring provisioning and oocytes. The former two involve the interplay between the female's postinseminating decisions and environmental factors. Since female control over the offspring sex ratio is partly influenced by the interaction between sexes during mating phases, we hypothesize that the female-biased sex ratio (Table 1) may at least partly reflect the sexual conflict that has been won by males. In contrast, male-biased sex ratios may imply that females 'have kept the upper hand in the coevolutionary arms races with males'. At the same time, female-biased offspring sex ratio might be achieved by means of females' optimal control under a local mate competition model (Hamilton 1967), that is, a single female should produce just enough sons to inseminate all daughters without increasing competition among themselves for mates. However, in populations, where male offspring will compete with mostly unrelated males, the effect of local mate competition on the sex investment ratio is supposed to be weak (Helms 1994). It is essential to establish the relative importance of each of the components discussed, and future studies may lead to the re-evaluation of the offspring sex-ratio control currently held as being performed purely by females (Shuker *et al.* 2006).

We may also expect that there is a link between the intensity of female rejecting behaviour and the sex ratio. For instance, forcibly struggling females of *S. allobrogus* produce a female-biased sex ratio, while moderate kicking mainly occurs in the group of species with a male-biased or nearly equal sex ratio (Tables 1; 5). Males of the latter group (*D. dufourii*, *D. zonalis* and *S. murarius*) fall backwards after the initiation of copulation remaining cataleptically immobile until copulation is ended or even longer. To dislodge the mounted male is a much more difficult task for a female (especially in the species with relatively large males, e.g. *S. allobrogus*) than to detach a motionless lying partner. Therefore, an increased rate of rejecting behaviour may reflect a more overt sexual conflict and the resulting decrease or loss of the opportunity for the female to control copulation. If it is so, the negative relationship between the duration of copulation and the female rejecting behaviour ('struggle') in *S. allobrogus* (Budrienė & Budrys 2004) may indicate an attempt of the female to affect the copulation length in the 'co-evolutionary arms race' with the male. However, this attempt seems to be unsuccessful, since the species has a female-biased sex ratio. The question, why feebly kicking females and 'cataleptically' falling backwards males of *A. trifasciatus* still produce a female-biased sex ratio, is still without an answer. Hypothetically, males of this species might evolve a counter-adaptation to the female's rejecting behaviour by increasing the copulation duration and, consequently, direct effects of ejaculate substances. The fact that the duration of *A. trifasciatus* copulation is one of the longest among the species with the 'cataleptic' behaviour of males (Budrienė & Budrys, in prep.) supports this speculative scenario. The decreased ability of the *A. trifasciatus* female to resist her partner's manipulation could be also mediated by low SSD (relatively large male) in this species. Further understanding of why offspring sex ratios differ among species in Eumeninae requires empirical studies into relative aspects of interactions between two parental sexes: degree of control over mating phases, balance between costs and benefits associated with mating and, consequently, identification of behaviour, traits and mechanisms that are responsible for it.

Multiple copulation. Repeated copulation observed in *A. antilope* and *S. allobrogus* is thought to be quite rare in Eumeninae, and its significance is obscure (Smith & Alcock 1980). This pattern has been described by Smith and Alcock (1980) in polyandrous wasp *Abispa*. *A. antilope* females are also known to mate more than once during their reproductive cycle (Cowan & Waldbauer 1984). Therefore, it is possible that multiple copulation per one pairing is associated with female's promiscuity. According to Cowan (1986), repeated copulation in *A. antilope* is comparable to post-insemination displays of other Hymenoptera and may be viewed as an adaptation that increases chances of obtaining a mate with 'good genes' by females, and decreases the probability of their remating with another male. Interestingly, this behaviour sometimes occurs in the expectedly monandrous *S. allobrogus*. Therefore, we may speculate that repeated copulation reflects intraspecific variation in mating tactics and relativity of females' monandry, thus endowing the mating system with evolutionary flexibility.

The fact that in the remating experiments males of *S. allobrogus* and *D. zonalis* mounted inseminated females almost as frequently as the virgin ones suggests that mating has reduced female receptivity, but not attractiveness, and this attractiveness of female is persistent at least up to four days after mating. Within other monandrous Hymenoptera, mating reduces receptivity but not attractiveness in parasitoids, *Spalangia cameroni* (King 2000) and *Aphytis melinus* (Allen *et al*. 1994), as well as in solitary bees, *Centris pallida* (Alcock & Buchmann 1985) and *Amegilla dawsoni* (Simmons *et al*. 2000). However, in the latter species this holds true only for recently mated females because nesting females are unattractive to searching males. This phenomenon may be viewed as female adaptation to avoid time and energy costs associated with resistance to unwanted harassment, given that females nest at dense emergence sites (Simmons *et al*. 2003). In this context, additional studies into ontogenetic aspects of the behaviour of mated Eumeninae females are needed.

Postcopulatory behaviour. If postcopulatory male displays in *A. antilope* as well as multiple copulation are understood as male response to female promiscuity, our explanations for the adaptive function of multiple copulation should be applied here. It has been suggested that male behaviour during postcopulatory guarding might signal the male's genetic quality to the female (Thornhill & Alcock 1983; but see Bussière *et al*. 2006 in terms of the maintenance of postcopulatory guarding due to sexual conflict over insemination). If so, female choice (expressed as differential allocation) may be associated with the male's ability to perform postcopulatory displays (particularly in *S. crassicornis*, demonstrating frequent occurrence of this behaviour). Thus, the function of postcopulatory behaviour could be analogous to that of the copulatory courtship discussed above.

Postcopulatory mounting is viewed as a form of mate guarding, aimed at maximizing fertilization success and inducing female unreceptivity (Alcock 1994). Postcopulatory courtship is responsible for the induction of loss of both receptivity and attractiveness of *Spalangia endius* females (King & Fischer 2005) and only loss of receptivity of *A. melinus* (Allen *et al*. 1994) and *C. pallida* females (Alcock & Buchmann 1985). We can only speculate that reduction or loss of receptivity might occur during either copulatory or postcopulatory events in Eumeninae species with the presence of postcopulatory behaviour and during copulatory episodes in those with the absence of postcopulatory behaviour. Hence, there is a need for studies designed to determine which aspect of each consecutive mating sequence is involved in loss of receptivity and attractiveness of Eumeninae females. This need becomes even more important with the recognition that changes in both receptivity and attractiveness are potentially associated with mechanisms leading to monandry. The manipulative experimental design including interruption of mating phases (e.g. King & Fischer 2005; Arnqvist & Andrés 2006) could yield insights into these mechanisms in Eumeninae.

Conclusion

The results of our discussion on the comparative aspects of mating systems in the Eumeninae species studied are summarized in Table 6. Our understanding of evolutionary processes of sexual selection in this group of solitary Hymenoptera is obviously insufficient. However, we should emphasize the potential importance of the sl-CSD, female uniparental care and presence of regular inbreeding at least in some species, in combination with predominant monandry, as idiosyncratic features of them. These features may provide Eumeninae with the opportunity for becoming a promising model system for testing hypotheses of sexual selection and understanding of the evolutionary maintenance of monandry.

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Table 6. Summary of the predicted types of sexual selection discussed in the studied Eumeninae species.

Feature	Variability of the feature (alternative states) observed in the studied Eumeninae wasp species	Type of sexual selection likely to be associated with the feature	Sexual selection episode with involvement of the feature
Sex ratio	1. Close to one-to-one (*A. antilope*, *D. dufourii*, *S. crassicornis*) 2. Male-biased (*D. zonalis*, *S. murarius*) 3. Female-biased (most *Ancistrocerus*, *S. allobrogus*, *S. gracilis*)	Indirect (good genes); sexually antagonistic	Mate search, precopulatory, postcopulatory
Sexual size dimorphism	1. Lower – male less smaller than female (*S. allobrogus*, *S. gracilis, D. dufourii,* most *Ancistrocerus*) 2. Higher – male much smaller than female (*A. antilope*, *D. zonalis*, *S. crassicornis*, *S. murarius*)	Direct (time saving etc.); indirect (good genes); sexually antagonistic	Mate search, precopulatory, postcopulatory
Willingness to mount	1. High (>50%) mounting attempt (*Symmorphus*) 2. Low (<50%) mounting attempt (*Ancistrocerus*, *Discoelius*)	Direct (time saving etc.); indirect (good genes)	Mate search, precopulatory
Willingness of mates to copulate	1. High copulation rate (most *Symmorphus*) 2. Low copulation rate (*Ancistrocerus*, *Discoelius*, *S. murarius*)	Indirect (good genes); sexually antagonistic	Precopulatory
Mode of male's antennation	1. Stroking combined with trembling and switching (most *Ancistrocerus*) 2. Jerking (most *Symmorphus*) 3. Simple stroking (*Discoelius*)	Direct (time saving etc.); indirect (good genes, Fisher's runaway)	Precopulatory, postcopulatory
Position of a copulating male	1. Copulation while lying behind the female (*A. trifasciatus*, *Discoelius*, *S. murarius*) 2. Copulation while mounted (others)	Sexually antagonistic	Postcopulatory
Female rejecting behaviour	1. Feeble (*Discoelius*) 2. Higher magnitude (others)	Indirect (good genes); sexually antagonistic	Precopulatory, postcopulatory
Postcopulatory behaviour	1. Present (*A. antilope*, *S. allobrogus*, *S. crassicornis*) 2. Absent (others)	Indirect (good genes); sexually antagonistic	Postcopulatory

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DEŠIMTIES EUMENINAE POŠEIMIO KLOSČIAVAPSVIŲ PORAVIMOSI PALYGINIMAS, TRUMPAI APŽVELGIANT LYTINĖS ATRANKOS TEORIJAS: TOLESNIŲ TYRIMŲ KRYPTYS

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SANTRAUKA

Straipsnyje pirmą kartą apibendrinami duomenys apie dešimties klosčiavapsvių rūšių iš genčių *Ancistrocerus*, *Discoelius* ir *Symmorphus* poravimosi fazes, iškeliant klausimus: kurie rūšims būdingi elgsenos bruožai svarbūs lyčių tarpusavio sąveikai poravimosi metu ir kurios lytinės atrankos formos galėtų skatinti šių bruožų evoliuciją. Ištirtos rūšys patikimai skiriasi patinų ir patelių skaičiaus santykiu populiacijose ir santykiniu jų kūno dydžiu, prekopuliacinės ir kopuliacinės elgsenos aktyvumu, patino poravimosi elgsenos elementais (antenų judesių pobūdžiu ir dažnumu, kūno orientacija kopuliuojant), patelės elgsenos elementais (poravimosi vengimu: partnerio atstūmimo elgsenos intensyvumu ir dažnumu), patino tuoktuvių, kopuliacijos ir postkopuliacine elgsena. Klosčiavapsvių poravimosi elgsenos lyginamojo tyrimo rezultatai aptariami apžvelgiant lytinės atrankos ir lyčių antagonistinių sąveikų hipotezes ir apibrėžiant tolesnių tyrimų kryptis. Vieno lokuso komplementariojo lyties nustatymo (sl-CSD), ženklaus inbrydingo ir tik vieno iš tėvų rūpinimosi palikuonimis derinys su monandrija yra klosčiavapsvių bruožai, ypač tinkami šias vapsvas naudoti modeliais tyrimuose, kuriais bus siekiama geriau suprasti monandrijos išlikimo evoliucijos eigoje galimybes.

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