

Female-biased size dimorphism in a diapausing caddisfly, *Mesophylax aspersus*: effect of fecundity and natural and sexual selection

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Abstract. 1. The effect of mating success, female fecundity and survival probability associated with intra-sex variation in body size was studied in *Mesophylax aspersus*, a caddisfly species with female-biased sexual size dimorphism, which inhabits temporary streams and aestivates in caves. Adults of this species do not feed and females have to mature eggs during aestivation.

2. Thus, females of larger size should have a fitness advantage because they can harbour more energy reserves that could influence fecundity and probability of survival until reproduction. In contrast, males of smaller size might have competitive advantages over others in mating success.

3. These hypotheses were tested by comparing the sex ratio and body size of individuals captured before and after the aestivation period. The associations between body size and female fecundity, and between mating success and body size of males, were explored under laboratory conditions.

4. During the aestivation period, the sex ratio changed from 1 : 1 to male biased (4 : 1), and a directional selection on body size was detected for females but not for males. Moreover, larger clutches were laid by females of larger size. Finally, differences in mating success between small and large males were not detected. These results suggest that natural selection (i.e. the differential mortality of females associated with body size) together with possible fecundity advantages, are important factors responsible of the sexual size dimorphism of *M. aspersus*.

5. These results highlight the importance of taking into account mechanisms other than those traditionally used to explain sexual dimorphism. Natural selection acting on sources of variation, such as survival, may be as important as fecundity and sexual selection in driving the evolution of sexual size dimorphism.

Key words. Body size, caves, mating behaviour, sex ratio, sexual size dimorphism, temporary streams, Trichoptera.

Introduction

Sexual size dimorphism, defined as the sex differences between body sizes of individuals of the same species, is a common and widespread phenomenon in nature that has traditionally attracted the attention of evolutionary biologists (Darwin,

1871; Andersson, 1994; Fairbairn *et al.*, 2007; Allen *et al.*, 2011). Several adaptive and non-adaptive explanations have been proposed to explain the considerable interspecific variation, not only in the degree of dimorphism, but also in which sex that is of larger size (Darwin, 1871; Hedrick & Temeles, 1989; Fairbairn *et al.*, 2007). Sexual size dimorphism has a strong phylogenetic component, which is likely associated with ecological conditions and life-history strategies (Brooks & McLennan, 1991). As an example, in birds and mammals,

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males are generally larger than females (Payne, 1984; Székely *et al.*, 2004; Lindenfors *et al.*, 2007), while the reverse occurs in the majority of insects and other ectothermic organisms (Darwin, 1871; Andersson, 1994; Fairbairn & Preziosi, 1994; Fairbairn, 1997; Fairbairn *et al.*, 2007). Although some quantitative genetic models point out that the sexual size dimorphism could be the result of non-adaptive processes (Lande, 1980; Leutenegger & Cheverud, 1982; Payne, 1984; Cheverud *et al.*, 1985; Brooks & McLennan, 1991), these phylogenetic associations might suggest a relationship with life history characteristics.

A vast amount of work offers adaptive explanations for sexual size dimorphism (e.g. Blanckenhorn, 2005; Fairbairn *et al.*, 2007). Among the several functional hypotheses of the evolution of sexual size dimorphism, the most popular refers to differences in reproductive roles, which is based on advantages related to fecundity (Honek, 1993; Blanckenhorn, 2000; Foellmer & Moya-Laraño, 2007) and sexual selection (i.e. mate choice) (Darwin, 1871; Andersson, 1994; Lindenfors *et al.*, 2007; Székely *et al.*, 2007). Large body size of females is often related to high fecundity and/or to the greatest fitness value of offspring of larger size. Therefore, body size of females is presumably related to reproductive success of the female as well as her mate (Honek, 1993; Andersson, 1994; Blackmore & Lord, 2000). In addition, the male's body size is probably related to a competitive ability to pair or defend resources in a context of sexual selection (Shuster & Wade, 2003). Small males, for instance, might have advantages associated with higher mobility in a scramble competition to gain access to gravid females, while in direct male–male competition for females or mating territories, large males will have an advantage (Banks & Thompson, 1985; Andersson, 1994; Moya-Laraño *et al.*, 2002).

Species-specific ecological conditions and life-history strategies may also explain the degree of sexual size dimorphism. It is known for instance that selection for fecundity is stronger in species of short lifespan that reproduce only once (Read & Harvey, 1989; Berger *et al.*, 2008). Moreover, natural selection in terms of survival probability could also affect the evolution of sexual size dimorphism if the relationship between body size and probability of survival differ for males and females. Natural selection may constrain the exaggeration of sexually dimorphic traits related to reproduction (i.e. mating success and fecundity), including body size, if it affects survival until reproduction (Allen *et al.*, 2011). Most studies of sexual dimorphism have addressed only one possible mechanism, but more than one may be operating simultaneously (Hedrick & Temeles, 1989). The net selection pressures on body size of females and males (i.e. survival probability, fecundity or mating success) would in any case depend on ecological conditions such as food availability. Therefore, the study of factors determining sexual size dimorphism in species living in particular ecological conditions with different life-history strategies is essential for a general understanding of agents driving the evolution of sexual size dimorphism in nature. Thus, here we explore the role of fecundity as well as natural and sexual selection to explain the sexual size dimorphism of an insect with very particular life-history traits.

Many insects do not feed during the adult stage and emerge with the energy reserves necessary for physiological activities and reproduction (i.e. capital breeders, Stearns, 1992; Wheeler, 1996). Females of some of these insects emerge with immature eggs (e.g. Masaki, 1980; Wiggins *et al.*, 1980) and, consequently, they expend energy reserves (i.e. body mass), not only for surviving until mating and laying the eggs, but also for egg maturation (Wheeler, 1996). Males of these species would need fewer resources than females would need for gamete maturation. In this scenario, natural selection would favour the evolution of female-biased size dimorphism given the higher relative needs of reserves for both survival and egg maturation of females. In this study, we explore possible causes underlying the sexual differences in body size of a caddisfly, *Mesophylax aspersus* Rambur (Trichoptera: Limnephilidae), a female-biased size dimorphic species adapted to temporary waters, with traits very similar to these described above.

Adults of *M. aspersus* emerge in spring and undergo a summer diapause (aestivation) in caves (Bouvet & Ginet, 1969; Botosaneanu, 1974; Salavert *et al.*, 2008). As occurs in other species of diapausing troglophile caddisflies, they do not feed during the adult stage, presumably surviving on the reserves of the adipose tissue accumulated during the larval phase (Bournaud, 1971). Moreover, the ovaries mature during aestivation at the expense of body reserves as well (Bouvet & Ginet, 1969; Botosaneanu, 1974; Bouvet, 1974, 1975). Because egg maturation is a resource-consuming activity that involves a trade-off with survival, the effect of body size (i.e. body reserves) on the probability of survival until reproduction should be particularly apparent in females. Moreover, as in other insects (Honek, 1993; Blackmore & Lord, 2000), the larger size of female *M. aspersus* could also have been selected because of its relation to fecundity. If this were the case, larger females should lay larger clutches.

Finally, another non-exclusive functional hypothesis that could account for sexual size dimorphism in *M. aspersus* may be related to possible advantages of smaller males in a scramble competition for mates (Blanckenhorn, 2000; Crompton *et al.*, 2003; McLachlan *et al.*, 2003; Moya-Laraño *et al.*, 2007). In such cases, a higher rate of mating success for smaller males should be found experimentally either because the smaller males arrive earlier to the focal females, or because of direct female preferences for smaller males (i.e. better flight performance; Ghiselin, 1974; Alcock, 1998; Rank *et al.*, 2006).

To test these hypotheses and predictions, we estimated sexual size dimorphism of *M. aspersus* in traits dependent on body reserves (body mass and body condition) and independent of them (wing length). Furthermore, we quantified the effect of aestivation on differential survival durations of males and females and the association of this parameter with wing length by comparing the sex ratio and wing length of individuals captured before and after the aestivation period. The association between body size and female fecundity, as well as that between mating success and body size of males were explored under laboratory conditions.

Materials and methods

Study site and species

This study was performed in a cave ('Cueva del Agua', 37°20.0'N, 3°30.4'W) located in Sierra Harana mountains (Iznalloz, Granada). The only known natural entrance lies at 1749 m a.s.l. (the maximum altitude within the cave), and the cave is 165 m deep. The caddisfly sampling area extends from the entrance to the first chamber, a length of approximately 135 m. Adults of *M. aspersus* arrive to the cave during the spring (March–May) and, after the aestivation period, they leave the cave, in autumn (October–December), when thermal inversion between outside and inside cave environments occurs (Salavert *et al.*, 2008). Caddisflies can be detected only in the first 135 m of the first cave gallery, a few days after the arrival or before the departure to rivers for egg-laying. During aestivation (June–September), caddisflies spend most of their time in inaccessible deeper locations of the cave. For more information on the cave and of the aestivating Trichoptera population see Salavert *et al.* (2008).

Sampling protocol

Adult caddisflies were searched for actively by visual inspection of the sampling area, on the walls and ceiling of the cave. Individuals were caught by hand nets or directly with forceps. At least two observers (VS, CZ-M or MR-R, and field collaborators) actively looked for caddisflies every second day during the arrival and departure dates of years 2000, 2002, 2003, 2004, and 2005. During the aestivation period the cave was also visited once per week, though caddisflies were never located, probably because they hide in the fissures in inaccessibly deeper locations (Tinaut, 1995; Salavert *et al.*, 2008). A total of 499 individuals, 130 females and 369 males were captured and measured (see Table 1).

Laboratory procedures

After capture, individuals were immediately transported to the laboratory inside isothermal boxes (6–10 °C). They were weighed on a digital balance (accuracy 0.0001 g; SV-120A, Gram Precision, Barcelona, Spain) and, under a stereomicroscope (Olympus CH-2, Barcelona, Spain), lengths of right and left forewings were measured to the nearest 0.01 mm using a digital calliper (Calb112, SESA Tools, Guipúzcoa, Spain). Caddisflies were placed into a small transparent vial while they were weighed and measured to avoid wing damage due to handling, and reduce measurement errors, as shown by the very high repeatability values registered for 35 randomly chosen individuals (measured three times; right wing: repeatability = 99%, one-way ANOVA, $F_{34,70} = 239$, $P < 0.001$; left wing: repeatability = 99%; $F_{34,70} = 283$, $P < 0.001$). Wing length was calculated as the mean values of both forewings.

After the measurements, caddisflies were sexed on the basis of their genitalia (see Malicky, 2004) and individually

Table 1. Number of *Mesophylax aspersus* individuals of different sex captured in spring and autumn at the aestivation location (Cueva del Agua) each study year. Resulting sex ratios for each year and season are also shown. Sex-ratio values are rounded to the nearest whole number.

Year	Season	Females	Males	Sex ratio
2000	Spring	3	4	1
	Autumn	9	65	7
	Total	12	69	6
2002	Spring	11	6	1
	Autumn	9	62	7
	Total	20	68	3
2003	Spring	10	7	1
	Autumn	33	76	2
	Total	43	83	2
2004	Spring	8	9	1
	Autumn	23	73	3
	Total	31	82	3
2005	Spring	9	25	3
	Autumn	15	42	3
	Total	24	67	3
All years	Spring	41	51	1
	Autumn	89	318	4
	Total	130	369	3

marked with a permanent felt-tip pen of different colours depending on their sex. Except for those used for the laboratory experiments described below, all individuals were returned to the cave the day after capture. Only one individual marked in spring was recaptured in autumn, indicating the difficulty of capture, probably due to the large size of the population, and suggesting a high rate of mortality during aestivation. Individuals collected in autumn and used for experimental trials were kept individually in terrariums (15 × 7 × 12 cm) supplied with water and housed in an incubator chamber at 10 °C, 95% of humidity, and total obscurity, simulating the environmental conditions of the cave (see Salavert *et al.*, 2008). After the experimental trials, a Petri dish with a wet substrate was placed in the terrariums to simulate close-to-river conditions and to stimulate the laying of eggs. The number of eggs was counted under a stereomicroscope.

Laboratory trials to detect male–male competition were performed in terrariums of 15 × 7 × 12 cm and consisted of arenas of one virgin female and two to four males; sex ratio very close to that observed in the cave after aestivation (see results below). The experiment finished at the end of the first copulation, which consistently occurred in less than 12 h. A total of 25 replicates were performed with a total of 25 females and 74 males. Aestivated experimental individuals were used only once. During the experiment, terrariums were kept in the chamber and every 2 h an experimental arena was observed for 5 min from outside the incubator (by VS). Based on previous experience and knowledge of the time necessary to detect copulation as well as the duration of copulation, this approach is appropriate for detecting the first individual male to copulate with the experimental female. For each visit, mating status was noted (i.e. whether or not a target male was copulating with the experimental female). Mating was

easily detected: the male, positioned parallel to the female, would bend his abdomen ventrally underneath the female abdomen in a characteristic 'S-form', inserting his aedeagus. Afterwards, the pair would remain in opposite directions. On three occasions, one male died during the experiment and was immediately replaced by another male to maintain the sex ratio. Data from death or replacing males were not used in the analyses.

Data analysis

In insects, body mass, body length, or wing or tarsus lengths are often measured as proxies of body size because all these estimates are strongly correlated. For holometabolous insects, however, while body mass may vary over the adult lifespan, body, wing or tarsus lengths do not change after adult emergence. Wing length of *M. aspersus* was positively correlated with the \log_e -transformed individual body mass in spring, both for males ($r = 0.57$, $n = 51$, $P = 0.00001$) and females ($r = 0.68$, $n = 41$, $P = 0.003$) and, thus, wing length was used as proxy of body size at the end of aestivation. Because some predictions are related to body-energy reserves, \log_e -transformed body mass was also used as a proxy of body size in some analyses. Furthermore, residuals of \log_e -transformed body mass after correcting for wing length were used, as an indicator of individual body condition (Schulte-Hostedde *et al.*, 2005). These variables, as well as between-sex differences (i.e. year \times sex interaction) did not significantly vary among study years (GLM, year as random factor, and sex as a fixed factor; all three independent variables: year effect: $P > 0.05$; sex \times year effect: $P > 0.09$). Therefore, data from different years were combined to increase statistical power. Frequency distributions of \log_e -transformed body mass, wing length, and body condition did not differ from normality (Kolmogorov–Smirnov test for continuous variables, $P > 0.05$).

Sex differences in survival during aestivation was estimated as the difference in sex ratio of caddisflies captured each year before (i.e. spring) and after (autumn) the aestivation period. Generalized linear models (GLZ) with a binomial error and logistic link function were used to explore the effect of year and season (fixed factors) on sex of captured individuals (dependent binomial variable). Sexual size differences were explored using general linear models (GLM), in which season and sex (fixed factors) were the predictor variables explaining body size, mass and condition. Standardized selection differentials (i.e. linear and quadratic) of wing length of males and females were quantified as estimates of selection on body size during the aestivation time. Endler (1986; pp. 171–172) was followed to test whether these estimates significantly differed from zero. Briefly, a positive linear selection differential (i) would suggest directional selection, while positive and negative values of quadratic selection differential (j), respectively, suggest disruptive and stabilizing selection (Endler, 1986).

The relationship between body size of females and clutch size was estimated with 19 females that were captured in autumn and laid eggs in the laboratory. This relation was

Table 2. Comparisons of body mass, wing length, and body condition of males and females of *Mesophylax aspersus* captured before (spring) and after (autumn) aestivation period (i.e. season effect).

	Sex effects		Season effects		Interaction	
	$F_{1,495}$	P	$F_{1,495}$	P	$F_{1,495}$	P
Body mass	117.11	<0.0001	16.46	<0.0001	8.59	0.004
Wing length	62.90	<0.0001	8.87	0.003	4.41	0.036
Body condition	39.81	<0.0001	50.09	<0.0001	3.05	0.081

analysed by means of Pearson's correlation coefficient using information of female's wing length because body mass and condition, but not wing length of caddisflies, change during the aestivation period, and the prediction tested refers to female size when arriving to the aestivating area (the cave). Clutch size was \log_e -transformed.

Association between male body size (i.e. wing length) and probability of mating was explored by comparing wing length of the successful male with the average wing length of males that did not copulate with a target female in a repeated-measures design.

Statistical analyses were performed by using STATISTICA 8.0 software[®].

Results

Sexual size dimorphism, selection on body size and sex ratio

Females of *M. aspersus* had larger body mass, wing length and better body condition than males, both before and after the aestivation period (Table 2 and Fig. 1). Moreover, females that survived the aestivation period were those with larger wing length given that, on average, those captured in autumn showed larger wings than females captured in spring (Fig. 1). This was not the case of males, as shown by the sex–season interaction term in Table 2 and Fig. 1. In addition, a significant standardized linear selection differential was detected for

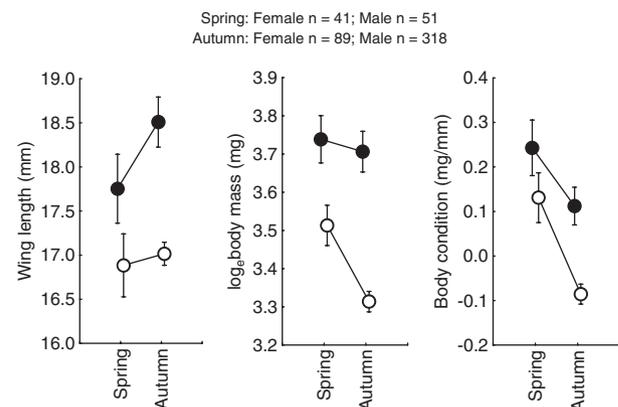


Fig. 1. Means ($\pm 95\%$ CI) of wing length, body mass, and condition of females (filled dots) and males (unfilled dots) of *Mesophylax aspersus* captured at the aestivation location (Cueva del Agua) on arrival (spring) and departure time (autumn).

wing length of females ($i = 0.560$, $t_{128} = 3.04$, $P = 0.0029$, suggesting directional selection) but not for wing length of males ($i = 0.110$, $t_{367} = 0.722$, $P = 0.47$). No evidence of disruptive or stabilizing selection was detected for females ($j = 0.159$, $F_{89,41} = 0.84$, $P = 0.75$) or males ($j = -0.236$, $F_{318,51} = 1.13$, $P = 0.30$) wing length during the aestivation period. Finally, a decrease in body mass and condition of caddisflies over the aestivation period was found, but trends were more pronounced in males than in females (Table 2 and Fig. 1).

Females of *M. aspersus* had a lower probability of survival than males, as shown by the differences in detected sex ratio of captured individuals before and after the aestivation events (Table 1), which changed from unbiased (1 : 1) (spring) to male biased (4 : 1) at the time of mating (autumn). This change in sex ratio was statistically significant (GLZ, binomial distribution and logistic link function; dependent variable: sex of captured individuals, factors: year and season; effect of season, Wald $\chi^2_1 = 21.79$, $P < 0.00001$) even after controlling for the non-significant effect of study year (Wald $\chi^2_4 = 5.85$, $P = 0.21$) and the between-years variation in the effects of season on sex-ratio estimates (interaction term, Wald $\chi^2_1 = 10.83$, $P = 0.029$).

These results taken together indicate that males survived the aestivation period better than did females and that larger females survived better than did smaller ones, resulting in a directional selection process towards larger size for females, but not for males.

Relationship between individual body size, fecundity, and mating success

Before dying, females laid a single clutch that varied in size between 191 and 668 eggs (mean \pm SE = 287.37 \pm 28.49). Wing length of females resulted positively related to clutch size ($r = 0.58$, $n = 19$, $P = 0.001$; Fig. 2), which is consistent with the predicted relationship between female size and fecundity.

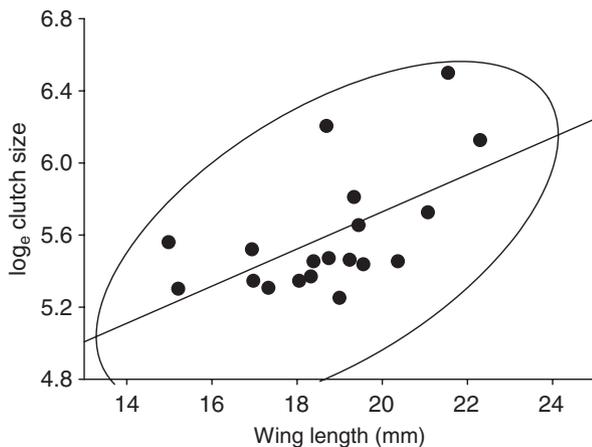


Fig. 2. Correlation between female wing length and clutch size. Regression line and the $\pm 95\%$ confidence ellipse are shown.

Finally, wing length of males that copulated with the females (mean \pm SE = 16.99 \pm 0.21) did not differ from that of other males in the same arena that did not copulate (mean \pm SE = 17.08 \pm 0.28) (repeated measures ANOVA, $F_{1,24} = 0.071$, $P = 0.79$), suggesting that males of small size had no advantage over those of large size when competing for females under the experimental conditions.

Discussion

The main findings on *M. aspersus* sexual dimorphism indicate that larger females survived the aestivation period better than did smaller ones, resulting in a directional selection process for females, but not for males, of larger size. Moreover, body size of females was associated with fecundity but that of males did not predict mating success in experimental arenas. These results suggest a role of fecundity and natural selection driving the evolution of sexual size dimorphism in this species. Special life-history traits of *M. aspersus* that may account for such results (i.e. not feeding during the adult stage and having to survive while developing eggs during aestivation) as well as alternative scenarios are discussed below.

Until emergence, limnephilid caddisfly species that do and do not inhabit temporary streams show very similar lifestyles (e.g. larvae build protective cases of silk, adding different materials and feed mainly on detritus; Wiggins, 2004). Species exploiting temporary habitats should, however, adopt life-history strategies allowing resistance to the dry period. A common strategy consists of emergence with immature eggs and the search for an appropriate aestivating location until the right time for laying them (Svensson, 1972; Wiggins, 1973; Botosaneanu, 1974; Bouvet, 1975; Masaki, 1980; Wiggins *et al.*, 1980). The study species follows this strategy and, because adult caddisflies do not feed (Bournaud, 1971; Bouvet, 1971, 1975; C. Zamora-Muñoz, pers. obs.), their energetic budget for aestivation and reproduction rely on the accumulated energy reserves in the adipose tissue. Egg maturation of *M. aspersus* occurs during the aestivation period (Bouvet & Ginet, 1969; Botosaneanu, 1974; Bouvet, 1974, 1975) and, thus, females need larger amounts of accumulated resources than do males for survival and reproduction. Individuals of large size are known to be able to accumulate more energy reserves and of better quality with respect to smaller individuals (Nijhout, 1994). Therefore, a larger body size will be differentially more advantageous for females than for males, and females of larger size will increase the probability of survival and the storing of a higher number of mature eggs, as has been observed in other insects (e.g. Rivero & West, 2002). Finally, *M. aspersus* adults have to fly from rivers to caves in spring and from caves to rivers in autumn and, therefore, flight performance would constrain the accumulation of reserves if accompanied by an increase in wing length (i.e. body size) (Alexander, 1999). All these peculiarities of *M. aspersus* make the evolution of sexual size dimorphism very likely in this species and in fact provides the background for the prediction of fitness advantages of females, but not of males, of larger size (body size should more closely

reflect survival of females than of males, and clutch size of larger females should exceed that of smaller females).

In accordance with this scenario, individuals captured after the aestivation period had lower body mass and conditions than those captured before this period, which evidence energetic costs associated with aestivation. The decrease in body mass and condition was, however, more pronounced in males, which at a first appears to suggest that, contrary to the prediction, males would consume more resources than females during aestivation. However, an alternative explanation is that females of lower body mass and poorer condition do not survive the aestivation period, while the strength of natural selection acting on body mass and condition is more relaxed in males. There are several pieces of evidence suggesting that the latter is the more likely explanation. First, sex ratio of captured individuals changed from unbiased at the beginning of the aestivation time to be male biased at mating time, which strongly implies a differential mortality rate of females during the aestivation period. The second piece of evidence revealed that, during the aestivation period, female body size (i.e. wing length) is under stronger directional selection than that of males, as shown by the standardized coefficients of linear selection differentials estimated for males and females. This directional selection process acting during the aestivation period provokes an increase in female body size but not male (see Fig. 2).

Sexual size dimorphism biased to females might also be explained by selection for fecundity or by an advantage of small males in scramble competition for mates. In accordance with the first possibility, it was found that females of larger size laid larger clutch sizes, but small males did not have any advantage when mating. In insects, there is ample evidence of selection for fecundity favouring large body size in females (e.g. Honek, 1993; Blackmore & Lord, 2000). Larger females have more space available to store larger numbers of eggs and the necessary nutrients for egg formation (Reiss, 1989; Preziosi *et al.*, 1996). The effect of fecundity on sexual size dimorphism is even more important in species that, as in the order Trichoptera, breed only once (Shuster & Wade, 2003). Support for hypothetical advantages of smaller males for pairing was not found, although it has been reported in several taxa (Andersson, 1994). However, experimental arenas may differ from natural conditions where smaller males could gain mating advantages, and more experiments are needed to draw a robust conclusion. Thus, as in most insect species (Blanckenhorn *et al.*, 2007), these results suggest that female-biased sexual size dimorphism of *M. aspersus* is influenced by fecundity selection, which favours a large body size in females, while the mechanism of sexual selection in males has not been conclusively identified.

In summary, these results highlight the importance of natural selection driving the evolution of sexual size dimorphism, for which the evidence has scarcely been documented (Allen *et al.*, 2011). Natural selection acting on body size of females during the aestivation period may explain sexual size dimorphism of *M. aspersus*. Selection for fecundity associated with large body size of females, but not sexual selection favouring males of small size, might also contribute to the evolution of sexual size dimorphism in this caddisfly.

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