

Male-biased size dimorphism in ichneumonine wasps (Hymenoptera: Ichneumonidae) – the role of sexual selection for large male size

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Abstract. 1. Sexual differences in body size are expected to evolve when selection on female and male sizes favours different optima.

2. Insects have typically female-biased size dimorphism that is usually explained by the strong fecundity advantage of larger size in females. However, numerous exceptions to this general pattern have led to the search for selective pressures favouring larger size in males.

3. In this study, the benefits of large size were investigated in males of four species of ichneumonine wasps, a species-rich group of parasitoids, many representatives of which exhibit male-biased size dimorphism.

4. Mating behaviour of all ichneumonine wasps are characterised by pre-copulatory struggles, in the course of which males attempt to override female reluctance to mate. A series of laboratory trials was conducted to study the determinants of male mating success.

5. A tendency was found for larger males as well as those in better condition to be more successful in achieving copulations. Size dimorphism of the species studied, mostly male-biased in hind tibia length but female-biased in body weight, indicates that sexual selection in males favours longer bodies and appendages rather than larger weight.

6. The qualitative similarity of the mating patterns suggests that sexual selection cannot completely explain the considerable among-species differences in sexual size dimorphism.

7. The present study cautions against using various size indices as equivalents for calculating sexual size dimorphism.

8. It is suggested that female reluctance in ichneumonine wasps functions as a mechanism of female mate assessment.

Key words. Mate choice, parasitoids, protandry, sexual conflict, sexual size dimorphism.

Introduction

The adaptive significance of sexual differences in animal body sizes has attracted considerable interest (e.g. Ding & Blanckenhorn, 2002; Ferguson & Fairbairn, 2000; Monnet

& Cherry, 2002; Cox *et al.*, 2003). Sexual size dimorphism (SSD) is expected to develop when the net effect of phenotypic selection on body size differs for males and females (Arak, 1988; Fairbairn, 1997). Accordingly, the sex gaining more from a large body size in terms of fitness is presumed to evolve towards a larger size. Being a relative measure of male and female sizes, SSD is sensitive to sex-specific differences in selection on body size rather than selection acting on body size *per se* (Preziosi & Fairbairn, 1996).

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In insects, size dimorphism is usually female-biased, which has primarily been ascribed to the strong fecundity advantage of large size in females (Honek, 1993; Blanckenhorn, 2000). Females appeared to be the heavier sex in about 85% of the 158 insect species, widely spread over major insect orders (Teder & Tammaru, 2005). However, in a considerable proportion of insect species males are as large as or even larger than females. Given the generality of fecundity selection in females, there should exist some strong selective advantage of large size in males for male-biased size dimorphism to evolve.

This study was conducted to shed light on possible mechanisms contributing to the evolution and maintenance of male-biased size dimorphism in Ichneumoninae (Hymenoptera: Ichneumonidae). This particularly species-rich group of parasitoid wasps is exceptional in that males tend to be larger than females (Hurlbutt, 1987; but see also Gauld & Fitton, 1987); however, the causes underlying this pattern are still unknown (Hurlbutt, 1987; Godfray, 1994).

Mating behaviour of all Ichneumoninae involves a pre-copulatory struggle, during which males attempt to override female reluctance (Hinz, 1987; Hilpert, 1992; this study). Pre-copulatory struggles in insects have been repeatedly shown to result in non-random mating patterns with respect to male traits (e.g. Arnqvist, 1992; Preziosi & Fairbairn, 1996; Crean & Gilburn, 1998; Blanckenhorn *et al.*, 2000). If larger males show a greater ability to withstand female reluctance, sexual selection should favour an evolutionary increase in male size, and thus a shift towards male-biased size dimorphism.

In the present study, a series of laboratory mating trials were conducted to examine male mating success in Ichneumoninae with respect to body size and individual condition. Four species, varying in the degree and direction of size differences between males and females, were used for this purpose. It will be shown that larger males tend to be more successful in achieving copulations. The potential evolutionary mechanisms modifying SSD of Ichneumoninae are discussed.

Materials and methods

Species

The mating trials were conducted with four solitary parasitoid wasps, each representing a different genus of the ichneumonine wasps (Hymenoptera: Ichneumonidae) – *Chasmodon paludator* Desv., *Exephanes occupator* Grav., *Spilichneumon limnophilus* Thoms., and *Vulgichneumon saturatorius* L. These species, although closely related taxonomically and similar in ecological characteristics, differ in the degree and direction of weight-based SSD. In *E. occupator*, females are clearly heavier than males, whereas in *S. limnophilus*, males are significantly heavier than females. In contrast, size differences of conspecific males and females in *V. saturatorius* and *C. paludator* are negligible (Fig. 1).

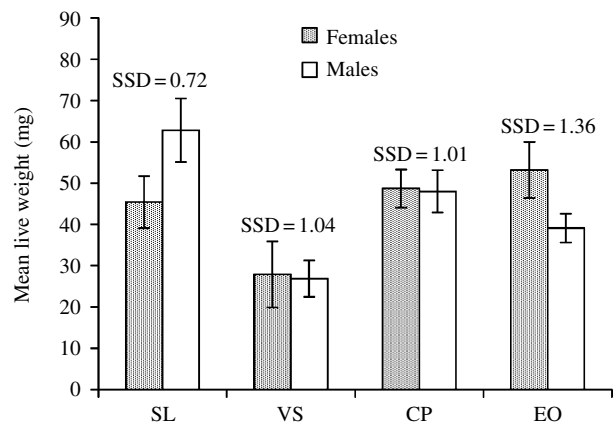


Fig. 1. Adult male and female body sizes (mean live weight) of the species examined. Sizes are based on samples collected from the field and reared to adults in the laboratory in 2002 (SL, *Spilichneumon limnophilus*; VS, *Vulgichneumon saturatorius*; CP, *Chasmodon paludator*; EO, *Exephanes occupator*). Error bars indicate SD.

Adults of these species appear in the second half of summer, with males emerging several days earlier, on average, than females (protandry). Both males and females are ready to mate on the day of adult emergence. Male longevity usually does not exceed a month, whereas fertilised females overwinter and lay their eggs on moth larvae in late spring or early summer (*E. occupator*, *S. limnophilus*, and probably also *V. saturatorius*), or on moth pupae in mid-summer (*C. paludator*) (T. Teder, pers. obs.). Adult wasps emerge from moth pupae. The three former species thus represent koinobiont life-history strategy, whereas *C. paludator* is an idiobiont. All four species are common parasitoids of the two noctuid moths – *Nonagria typhae* Thunb. and *Archanara sparganii* Esp. (Lepidoptera) – the larvae and pupae of which are easy to collect in high numbers from the shoots and leaves of their principal host plant, *Typha latifolia* L. (Typhaceae) (Teder *et al.*, 1999; Teder & Tammaru, 2002, 2003).

Mating trials

All mating trials were conducted in Tartu, Estonia, in 2000 and 2002. The insects for the mating trials were collected as parasitised moth pupae (both *N. typhae* and *A. sparganii*) from a wild population. The collected pupae were transferred to the laboratory, and were then kept individually in Petri dishes until the emergence of adult parasitoids. Dates of emergence were recorded to determine the age of individuals at the time of trial. Live weight of freshly emerged individuals (males and females in 2002), dry weight (males and females in 2000), and hind tibia length (males in 2002) were measured as indices of body size. Weighing a Petri dish with and without an insect by an analytical balance was used as a standard procedure for determining live weight of particular individuals. Hind tibia length was measured by means of an ocular micrometer

under a stereomicroscope. All individuals used in the mating trials in 2002 were regularly provided sucrose solution as food, whereas those used in 2000 were kept unfed. The latter was carried out to facilitate the study of individual condition as a possible factor influencing male mating success: when kept unfed, the condition of males declined with age. The strong effect of feeding on longevity suggests that the effect of feeding on individual condition of wasps was likely to override any other effects that might have been associated with different years.

The mating trials were carried out in Petri dishes with a diameter of 10 cm. A female and a male were released to this mating arena, and their behaviour was observed. The following set of parameters were recorded for each couple: (1) the number of male attempts to mount the female; (2) the duration of each attempt (the time when the struggling couple were in physical contact); (3) the outcome of the pre-copulatory struggle (acceptance or rejection); and (4) the duration of copulation. An attempt to mount was considered a separate one when at least 5 s had passed from the last physical contact between the members of the struggling couple. The trial was terminated (1) after a copulation, (2) if a male, having once or repeatedly tried to mount the female, started to avoid her, or (3) if the male avoided or ignored the female from the beginning of trial. In the latter case, the decision to stop a particular trial was made when the male had ignored/avoided the female for 4 min after the first contact with the female (see also Results). The adult age of males at the time of the trial varied from 1 to 22 days (median = 9 days in 2000, and 6 days in 2002).

Additional mating trials were conducted to obtain data on mating frequency in the two sexes, and the possible presence of male–male competitive interactions. The respective trials followed the same scheme as described above. However, already mated females or males were used instead of virgin ones in the first set of mating trials, and two males instead of one were released to a mating arena in the other set.

Data analysis

Logistic regression analysis (PROC GENMOD; SAS Institute Inc., 2001) was applied to examine determinants of mating outcomes. Binomial probability distribution was assumed, and logit was chosen as the link function. The

binary outcome scores of the pre-copulatory struggles (acceptance vs. rejection) were treated as the response variable, whereas male and female parameters – size (weight or hind tibia length) and age – were used as independent variables. Similarly, a logistic regression analysis was performed, while analysing the effect of the duration of pre-copulatory struggles on corresponding outcome scores. In the latter analysis, the natural logarithm of the average duration of male mating attempts (= the duration of all attempts performed by a particular male divided by the number of attempts) and the natural logarithm of the duration of the first mating attempt were used as indicators of male ability to override female rejection response.

Qualitative similarities in the mating patterns of the four species examined (see below) suggest that the pre-copulatory struggles in different ichneumonine wasps serve the same function. It was therefore justified to base the conclusions about sexual selection on the basis of (1) the size differences between successful and unsuccessful males within species, as well as (2) the qualitative similarities of the mating patterns of the four species. The logistic regression analyses examining the effect of male and female parameters on mating outcomes were therefore performed both for each species separately as well as for all species combined. The combined analyses were conducted to increase the power of the tests.

Results

Qualitative aspects of mating behaviour

Despite the among-species differences in SSD, no qualitative differences were observed in mating behaviour of the four species examined. Mating was always initiated by the male who, perceiving the presence of a female, started chasing and grasping her in order to mount the female and achieve a genital contact. As a rule, females tried to disengage from the mounting males, moving around, kicking males with legs, and/or biting with mandibles. If a first attempt to mount a female failed, males either continued to attempt mounting or started avoiding the female (Table 1). A single mounting attempt usually did not last longer than 10 s (84% of attempts across all species; Table 1), and only occasionally more than 30 s. Females that accepted a male calmed down for the time of genital contact. The average

Table 1. The duration and number of mating attempts and the duration of copulations (for the mating trials conducted with fed males).

Species	Median duration of single mounting attempts (s)	Average number of mating attempts made by successful/unsuccessful males	Average duration (\pm SD) of copulation (s)
<i>Chasmius paludator</i>	5.2	1.3/2.2	55.0 \pm 16.0
<i>Exephanes occupator</i>	3.7	1.2/2.6	86.1 \pm 14.1
<i>Spilichneumon limnophilus</i>	4.3	1.2/1.9	33.8 \pm 5.7
<i>Vulgichneumon saturatorius</i>	6.0	1.3/2.0	38.4 \pm 7.2

duration of copulations ranged from 34 s in *S. limnophilus* to 86 s in *E. occupator* (Table 1). Copulations were normally terminated by the female, who actively disengaged from the male.

The results of the additional mating trials suggest that females of the studied species are monandrous: numerous trials conducted with mated females never ended in a copulation. Several hours after copulation, females became, and remained, unreceptive as indicated by males invariably ignoring such females. In contrast, males appeared to be able to copulate with more than one female: soon after a successful insemination of a female they were ready to copulate with another female (see also Hilpert, 1992).

No indications of contest competition between males for mating opportunities were observed. Two males, simultaneously released to a mating arena with one female, typically ignored each other. The male that was the first to recognise the presence of the female tried to copulate with her, whereas the other male typically avoided the struggling couple.

In all species examined, males frequently ignored or even avoided females (especially in *S. limnophilus*) in the laboratory trials, making no attempts to mate with them. As a likely explanation, temporal unreceptivity of females may have caused males' indifference, although this phenomenon may deserve further study. The mating trials in which males ignored or avoided the female were not considered in the subsequent analyses.

The effect of male and female parameters on mating success

The numbers of couples used in the mating trials were 176 and 302 in 2000 and 2002 respectively (Table 2). Pre-copulatory struggles between the male and female were observed in 77 couples (44%) in 2000, and in 124 couples (41%) in 2002 (Table 2). In the rest of the couples, males were documented to ignore or to avoid females. Pre-copulatory struggles ended in a copulation in 62% of the couples in 2000, and in 75% in 2002. The remaining struggles ended in the female rejecting the male (Table 2).

In the trials conducted with fed individuals, males of all four species that achieved copulation were larger on average than males rejected (Fig. 2). The effect of male size on mating success attained statistical significance for all species combined, and separately for *E. occupator* (Table 3, parts a, b). The results of the analyses were qualitatively

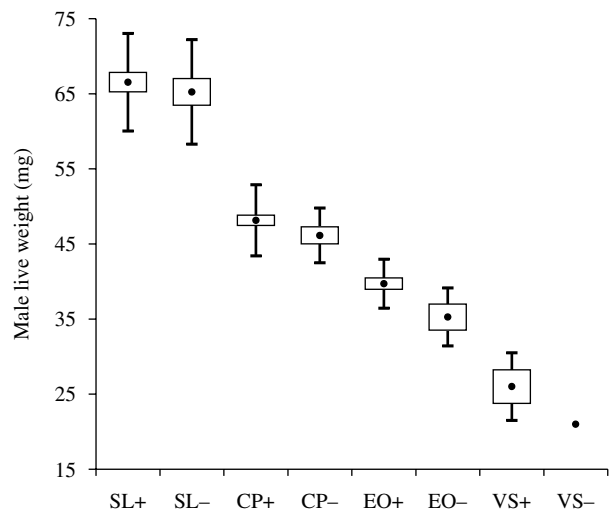


Fig. 2. The effect of male size on the mating outcomes (SL, *Spilichneumon limnophilus*; CP, *Chasmias paludator*; EO, *Exephanes occupator*; VS, *Vulgichneumon saturatorius*; successful males are marked with '+', unsuccessful ones with '-'). Black dots indicate means, boxes indicate SE, and whiskers indicate SD.

insensitive to the index of male body size (weight or hind tibia length) used in the model. The effect of female body size on mating outcomes cannot be excluded either, as the corresponding *P*-value was close to 0.05 in the analysis with all species combined (Table 3, part a).

As indicated by the average duration of mating attempts, successful males of all species were able to withstand female rejection response for longer (Table 4, part a, Fig. 3). The differences were significant separately for *C. paludator* and *S. limnophilus*. Successful males were able to resist for longer in first mating attempts as well (logistic regression analysis with species combined: $n = 124$, $\chi_4^2 = 11.1$, $P = 0.02$). However, even though male mating success was significantly affected both by male size and ability to withstand female rejection response, no correlation was found between the duration of pre-copulatory struggles and male size.

Mating outcomes were influenced by female age as well (Table 3, part a). Yet surprisingly, older females were more reluctant to copulate than younger ones. Hinz (1987) reports a similar behavioural pattern in some other

Table 2. The number of couples (trials) in which males attempted to mate and the percentage of couples in which a copulation occurred

Species	Fed males (mating trials conducted in 2002)		Unfed males (mating trials conducted in 2000)	
	No. of couples	Mating success	No. of couples	Mating success
<i>Chasmias paludator</i>	57	82.5	20	80.0
<i>Exephanes occupator</i>	22	77.3	11	72.7
<i>Spilichneumon limnophilus</i>	40	60.0	32	43.8
<i>Vulgichneumon saturatorius</i>	5	80.0	14	71.4

Table 3. The results of the logistic regression analyses (significance tested by type III analysis), examining the effect of male and female parameters on mating outcomes. The binary outcome scores of the pre-copulatory struggles (copulation occurred/copulation did not occur) were used as the response variable. Weight is used in the models as the index of male size. (a) The mating trials with *Exephanes occupator*, *Spilichneumon limnophilus*, and *Chasmius paludator* (the number of trials conducted with *Vulgichneumon saturatorius* was too low for inclusion) combined in a single analysis (fed males); (b) mating outcomes as a function of male size in *E. occupator* (fed males); (c) the mating trials with all four species combined in a single analysis (unfed males).

Source	d.f.	χ^2	<i>P</i>
<i>(a) Mating outcomes (species combined; fed males)</i>			
Female age (Species)	3	14.2	0.003
Female weight (Species)	3	7.6	0.055
Male age (Species)	3	4.4	0.222
Male weight (Species)	3	11.9	0.008
<i>(b) Mating outcomes (E. occupator only; fed males)</i>			
Male weight	1	7.8	0.005
<i>(c) Mating outcomes (species combined; unfed males)</i>			
Female age (Species)	4	2.0	0.733
Female weight (Species)	4	9.0	0.061
Male age (Species)	4	9.5	0.050
Male weight (Species)	4	1.0	0.909

ichneumonine wasps. The causes underlying this phenomenon remain out of the scope of the present study, but may deserve further attention.

The mating trials conducted with unfed males showed a marginally significant negative relationship between male age and mating success, but there was no effect of male size on the outcomes of pre-copulatory struggles (Table 3, part c). Analysed separately, the effect of male age on mating success was significant for *C. paludator*. Again, males that were able to withstand female rejection response longer, gained a higher mating success (Table 4, part b). The effect of female weight on mating outcomes appeared to be marginally significant also in this set of trials (Table 3, part c).

Finally, the duration of copulations did not depend on any of the factors (male and female sizes, and male and female ages at the time of trial) examined, either when the results of the mating trials conducted with fed (Table 5) or unfed males were considered.

Discussion

Mating behaviour of ichneumonine wasps typically involves an intense pre-copulatory struggle between the

two sexes, characterised by males attempting to mate with reluctant females. Due to variable performance in these struggles, males exhibit differential mating success. The closer examination of mating patterns in four species of ichneumonine wasps revealed a dependence of mating outcomes on male characteristics: the proportion of males accepted vs. rejected appeared to be higher among larger males, and those in a better condition. Moreover, males that were able to resist the female rejection response longer gained a mating advantage.

The non-random mating patterns observed suggest that sexual selection for large male size is likely to be a factor contributing to the evolution and maintenance of male-biased size dimorphism in ichneumonine wasps. Yet, despite the qualitative similarity of the mating patterns, males were the heavier sex only in one of the studied species (*S. limnophilus*), whereas three others showed slightly (*V. saturatorius* and *C. paludator*) or clearly (*E. occupator*) female-biased size dimorphism (Fig. 1). Moreover, the species showing the effect of male size on mating outcomes most clearly (*E. occupator*; Fig. 2) appeared to be the only species with pronounced female-biased size dimorphism. This suggests that observed differences in SSD cannot be ascribed to variation in sexual selection intensity alone, and

Table 4. The results of the logistic regression analysis (significance tested by type I analysis) examining the effect of male ability to withstand female rejection response (the natural logarithm of the average duration of male mating attempts) on mating outcomes. (a) The mating trials conducted with fed males, (b) the mating trials conducted with unfed males. In both cases, all four species were analysed together.

Source	d.f.	χ^2	<i>P</i>
<i>(a) Mating outcomes</i>			
Species	3	5.0	0.171
The average duration of mating attempts (Species)	4	14.6	0.006
<i>(b) Mating outcomes</i>			
Species	3	8.5	0.037
The average duration of mating attempts (Species)	4	37.0	<0.001

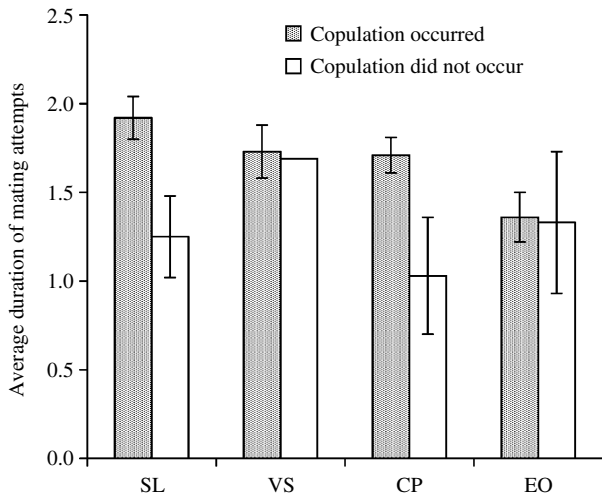


Fig. 3. The natural logarithm of the average duration of mating attempts (see *Data analysis*) separately for males that eventually achieved/did not achieve copulation (SL, *Spilichneumon limnophilus*; VS, *Vulgichneumon saturatorius*; CP, *Chasmodon paludator*; EO, *Exephanes occupator*). Error bars indicate SE.

sexual selection acting on male size is not necessarily the primary determinant of the frequent occurrence of male-biased size dimorphism in ichneumonine wasps. There should thus exist some factors favouring either large female size or small male size that override the large male mating advantage, and maintain female bias in body weight.

A major evolutionary force, widely accepted as contributing to female-biased size dimorphism in many organisms, is the fecundity selection for large size in females (Blanckenhorn, 2000). This is because in most insects, egg production has been shown to increase with body size (e.g. Honek, 1993). However, depending on the presence/absence of adult feeding there are considerable differences in the strength of body size–fecundity relationship among species (Tammaru & Haukioja, 1996). Reproductive potential of capital breeders, i.e. species with non-feeding adults, is largely determined by the resources accumulated during the larval stage. Accordingly, there is usually a strong correlation between fecundity and female body size. In contrast, the relationship between body size and fecundity

in income breeders, i.e. insects for which adult feeding is crucial for reproduction, is often less obvious (e.g. Karlsson & Wiklund, 1984; Braby & Jones, 1995; Sokolovska *et al.*, 2000). Fecundity of these insects depends primarily on resources available for adults rather than weight at eclosion.

All parasitoids examined represent income-breeding species (Hinz, 1983, 1991; Teder & Tammaru, 2002), suggesting thus a rather weak correlation between body size and potential fecundity. Moreover, parasitoid life histories further obscure the relationship between body size and (realised) fecundity (Hardy *et al.*, 1992; Ellers & van Alphen, 1997). In particular, the reproductive success of parasitoids depends critically on the encounter rates with suitable hosts, the distribution of which may vary both spatially and temporally. Potential fecundity is thus quite a poor indicator of realised fecundity in parasitoids. Fecundity selection for large body size in females is therefore presumably rather weak in the species examined.

Another factor, commonly argued to contribute to female-biased size dimorphism, is selection for protandry (Singer, 1982; Wiklund & Solbreck, 1982; Zonneveld, 1996). According to this hypothesis, by emerging earlier males would increase their mating success. If males and females grow at the same rate, the trade-off between development time and final size should lead to female-biased size dimorphism. Similarly to many other insects, males of all species examined emerged earlier on average than females, the difference between emergence dates exceeding 1 week in *S. limnophilus*. Surprisingly, the single species with male-biased size dimorphism, *S. limnophilus*, showed the largest gap in emergence dates, suggesting a rather unconstrained schedule of development. Consequently, selection for protandry is not likely to constitute an important factor in the evolution of male body size in these parasitoids.

The advantage of large male size in physical contacts with females may counterbalanced by lower agility and manoeuvrability of heavier males. Several authors (McLachlan & Allen, 1987; Crompton *et al.*, 2003) have shown that in three-dimensional arenas, smaller males may gain mating advantage due to their superior aerobic abilities. The current research was conducted in small and simple structured mating arenas, in which females could

Table 5. The results of the analysis of variance (significance tested by type III analysis) examining the effect of male and female parameters on the duration of copulations (the mating trials conducted with fed males). All species were analysed together (the number of mating trials conducted with *Vulgichneumon saturatorius* was too low to include it in the analysis); male and female parameters were nested within species. The results did not change qualitatively when the trials with unfed males were analysed. Neither were any significant effects found in the analyses conducted separately for each species.

Source	d.f.	F	P
Duration of copulations			
Female age (Species)	3	0.16	0.92
Female weight (Species)	3	1.03	0.39
Male age (Species)	3	0.36	0.78
Male weight (Species)	3	0.57	0.64

not escape male mating attempts. It is likely that under natural conditions, males' ability of chasing females is likely to play a far more significant role in determining their mating success. Further research is therefore needed to investigate mating behaviour of ichneumonine wasps in more complex environments.

The actual target of sexual selection needs not necessarily be the larger body size itself, but some correlated trait(s). For example, Tseng and Rowe (1999) examined SSD in a water strider exhibiting pre-copulatory struggles, and showed that male mating success was dependent on the length of legs rather than large body size. The situation may well be analogous in the Ichneumoninae. In the species examined, males use their legs, abdomen and antennae to effectively grasp and hold a female during a mating attempt. Sexual selection may thus favour longer bodies and appendages in males instead of a heavier body. In concordance with this, SSD, based on hind tibia lengths, was male-biased in three species, and the fourth species (*E. occupator*) showed only a slight female bias, whereas SSD, calculated on the basis of body weights, was male-biased in one species only (*S. limnophilus*) (Fig. 4). Similarly, Hurlbutt (1987) found that in most of the 81 Ichneumoninae species examined, SSD, based on body lengths, was male-biased. The present study implies that different size indices commonly used for assessing SSD, like weight and tibia length, may produce values of SSD that differ not only in degree, but also in direction. Hence, caution should be exercised when considering various size indices as equivalents for calculating SSD, and/or deducing mechanisms underlying particular patterns of SSD (see also Gauld & Fitton, 1987).

The results of this study also consider the functional significance of female reluctance. It is suggested that by being reluctant to mate, females either assess mate quality or avoid excessive copulations (e.g. Arnqvist, 1992; Blanckenhorn *et al.*, 2000; Dunn *et al.*, 2002). The present results seem to preclude the latter possibility as the primary function of female reluctance. In numerous trials, no male was observed to succeed in copulating with a female that had already been fertilised. The studied ichneumonine wasps thus seem to have a monandrous mating system, in which females possess an effective control over copulation: males appear not to be able to force females to copulate. Moreover, a few hours after copulation, females apparently lost their receptivity to males as indicated by males ignoring the presence of females that had already been fertilised. Unreceptivity of mated females has been observed also in some other ichneumonine wasps (Hinz, 1987). It is therefore unlikely that female reluctance has evolved to function as a mechanism of avoiding extra copulations.

Instead, the reluctance of females to mate in ichneumonine wasps may facilitate assessing the quality of mating partners. The results of the mating trials conducted with unfed males indicate, however, that instead of assessing male quality directly by some morphological indicators, females apparently rely on the ability of males to withstand the female rejection response. In particular, the mating

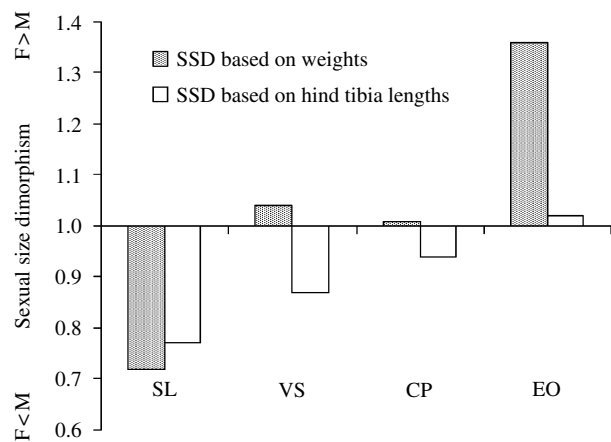


Fig. 4. Sexual size dimorphism (females/males) calculated on the basis of live weights and hind tibia lengths (SL, *Spilichneumon limnophilus*; VS, *Vulgichneumon saturatorius*; CP, *Chasmias paludator*; EO, *Exephanes occupator*).

success of unfed males was a function of male age (= individual condition, see *Mating trials*) at the time of the trial rather than their size. Accordingly, the duration of pre-copulatory struggles by successful males exceeded that of unsuccessful males in all species both in the mating trials with fed and unfed males.

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