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Body size sexual dimorphism affects mating behaviour in the parasitoid wasp, Lysiphlebus fabarum (Braconidae: Aphidiinae)

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Abstract

Body size has a profound effect on many aspects of animals' biology including sexual interactions. Hymenopteran parasitoids exhibit dimorphisms in which females are larger than males. A recent study has indicated that in the solitary koinobiont parasitoid wasp Lysiphlebus fabarum Marshall, offspring life history traits are influenced by maternal body size, which raises the questions of whether larger females are preferred and whether larger males have an advantage when it comes to accessing larger mates. To test this, females of L. fabarum were allowed to lay eggs in aphids (Aphis fabae Scopoli) at different growth stages to manipulate female and male body size. First, we conducted a choice experiment to determine whether large female wasps are preferred by males. Secondly, we examined the effect of male body size on the ability of males within a patch to access females. Males of L. fabarum lack mate preference, as both small and large females were almost equally selected as mates. Mate searching duration did not vary with male or female body size, suggesting that body size would not influence pre-copulatory interactions within the patch. Smaller males copulated significantly longer, and copulation duration increased with the sexual body size dimorphism. Our finding suggests that a "first-to-mate" strategy is favoured by males, mating with the female they encounter regardless of her quality. Also, small males copulate longer possibly because of lower sperm transfer rate. This study shed light on the evolutionary processes regarding mating behaviours in this parasitoid wasp.

Keywords: Sexual selection, mate preference, copulation, sperm competition

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Introduction

Body size is a significant sexual selection factor affecting many elements of animal biology, including sexual interactions (Andersson, 1994). By outperforming smaller males during intrasexual competitions, larger males in polygynous mating systems can access females and have a higher rate of successful mating (Clutton-Brock et al., 1977; Andersson, 1994) . Body size also plays an important role in sexual selection in which males may mate preferentially with larger females as they are more fecund (Byrne & Rice, 2006). Since body size can be a reliable predictor of physiological competence, females may also favour mating with larger males (Sheldon, 2000).

A substantial body of research describes the mating behaviours and life histories of parasitic Hymenoptera. However, studies of parasitoid mating structures have traditionally focused on how sex allocation is affected by the mating system (Hardy, 1994; Ayasse et al., 2001). Sexual selection can alter a range of reproductive behaviours in parasitoids despite their lack of obvious secondary sexual traits (reviewed in Boulton, Collins, & Shuker, 2015). Females are typically the larger sex in Hymenoptera, possibly because fecundity, a fitness benefit of size, is higher in females than it is in males. This suggests that selection on female and male sizes favours different optima 1994). (Stubblefield & Seger, dimorphisms may have functions for both males and females under various ecological context, including competition for mates (Fairbairn et al., 2007). For instance, males of Spalangia dozieri Burks wasps (Pteromalidae) have enlarged hind legs which involve grasping and holding females during mating or malemale competition (Gibson & Reigada, 2009). However, caution must be exercised using various size indices as equivalents for sexual size dimorphism. For example, ichneumonine wasps are mostly male-biased in hind tibia length but female-biased in body weight, suggesting sexual selection in males favours longer bodies and appendages rather than larger weight (Teder, 2005).

Lysiphlebus fabarum Marshall (Braconidae: Aphidiinae) is a generalist predator,

parasitizing a broad range of patchy distributed aphids (Rasekh et al., 2011). Females rarely mate more than one time (Astaraki et al., 2019); therefore, postcopulatory assessment of male quality is unlikely to occur in natural populations. Moreover, when L. fabarum adult wasps emerge nearly all their eggs are fully developed, and copulation is followed immediately by oviposition (Rasekh et al., 2010). It has recently been demonstrated that both maternal and paternal body significantly contribute to variation in offspring life history traits in L. fabarum (Rasekh et al., 2022). Offspring emerging from the eggs laid by large parents were larger and had quicker developmental times. Paternal body size was also significantly related to egg load in offspring, suggesting direct paternal effects occur in this species. This raises the question whether larger mates are more likely to be preferred and whether larger males are superior in accessing larger mates.

This study investigates whether body size of male and female wasps affects mating behaviours and mate preference under choice experiments in L. fabarum wasps. Female and male body sizes were manipulated by allowing females to deposit eggs in aphid hosts of different growth stages. First, we tested whether large female wasps are preferred by males under a choice experiment. Next, we tested the effect of body size on within patch performance of the males to access larger females. It is predicted that larger females are more preferred by males regardless of the size of the mating males. It is also predicted that males have greater performance accessing larger females compared to small males.

Material and Methods Study species

A stock colony of black bean aphids, *Aphis fabae* Scopoli (Hemiptera: Aphididae), was established from material collected in bean fields in Khuzestan province (31°190N, 48°410E), Iran, in the spring of 2018. Mummified aphids by the parasitoid *L. fabarum* were obtained from the same samples. The stock colony of the aphid, *A. fabae*, was

maintained on broad beans, *Vicia faba* L. (Fabaceae), grown in pots filled with fertilized sawdust. The stock colony of the parasitoid *L. fabarum* was reared on potted broad beans infested with the black bean aphid. All insects and experiments were held in a growth chamber at 21 ± 1 °C, 65-75% relative humidity, and 16:8 (light:dark) photoperiod.

Experimental procedure

Synchronous cohorts of black bean aphid were produced following (Ameri et al., 2014, 2015a) by allowing an adult aphid to deposit aphids on a young bean seedling for 12 h. The cut stem of the bean shoot was immersed in a small vial of fertilized water (N:P:K = 20:20:20) to maintain turgor and placed in a ventilated plastic cylinders (8.0×15.0 cm). Average age (± SE) of first and second instars of A. fabae used in the tests was 1.0 ± 0.4 and 2.25 ± 0.4 days, respectively. In each trail, cohorts of large and small parasitoid wasps were produced by rearing the parasitoid in the first and second instar of the aphids, resulting in small (males: 0.315 ± 0.004 ; females 0.318 \pm 0.003) and large (males: 0.371 \pm 0.003; females 0.381 ± 0.003) wasps, respectively. Males and females were randomly selected from the parasitoid stock and paired in 1.5 mL microtubes for 1 h to ensure the female is mated. These mated females were then introduced to bean seedlings containing 10 first or second instar aphids for 8 h. Before exposing the aphids to the wasp, seedlings were sprayed gently with water to avoid desiccation of the female wasps. After parasitisation the aphids were allowed to settle on the seedlings until the mummies formed whereupon they were kept in 1.5 mLmicro-tubes individually emergence of the adult wasps. The small and large parasitoid emerged from these mummies were used in the subsequent tests.

Female mate preference

In the first experiment, one large and one small female wasp were placed in each Petri dish with a diameter of 6 cm, which were allowed to habituate for 5 minutes. Thereafter, a male wasp was placed in the Petri dish where it could mate with either small or large female wasps. The same procedure was repeated in which a large male wasp was introduced to

females of different sizes (N = 2×40). At the end of each trial, male mate choice was determined and, hind tibia length of the mated pairs were photographed under a stereomicroscope equipped with a digital camera (Nikon Coolpix S10; Nikon Corporation, Tokyo, Japan) attached to a binocular microscope at $100 \times \text{magnification}$ and measured with a precision of 0.003 mm.

Competition between males

In the first experiment, one large and one small male wasp were placed in each Petri dish with a diameter of 6 cm, which were then allowed to habituate for 5 minutes. Next, a female wasp was placed in the Petri dish. The same procedure was repeated in which a large female wasp was introduced to males of different sizes. Mate choice, mate search duration (time required to find a female wasp and start copulation), and copulation duration (time taken from mounting a female wasp to dismount) were determined by observing the wasps directly (N = 2×40). At the end of each trial, hind tibia length of the mated pairs was photographed using the above mentioned method. All photographs were measured using ImageJ software (U.S. National Institutes of Health, Bethesda, Maryland).

Statistical analysis

All data were analysed with R 3.5.2 (R Core Team 2016). The distribution of the variables was checked before further analysis by calculating quantiles of each variable and then plot- ting them against theoretical quantiles (qq plot) to confirm that the empirical quantiles sat within the borders of the suitable theoretical distribution. The package lme4 (Bates et al., 2014) was used to fit a generalized linear model, followed by the Fisher's protected least significant difference (LSD), testing the significance of the fixed factors, including the effect of male and female body size and sexual body size dimorphism on mate choice, precopulation duration, and copulation duration. Binomial family distribution with logit link function was used for the mate choices data, and chi-square test was used to calculate pvalues. Gamma family distribution with log link function was used for pre-copulatory duration and copulation duration data, and

restricted likelihood ratio test was used to calculate p-values.

Results

Before copulation, males and females contacted where their antennae were held in a straight form and tapped each other several times, usually for a period of less than 5 seconds. Then, the male wasp mounted the female wasp and started to copulate. The female would stroke her hind legs until the mating male dismounts. There were no

significant differences between large and small males when selecting females with different sizes ($\chi^2 = 0.53$, P = 0.465).

Female body size did not influence the mate choice when small and large males were introduced to a female wasp ($\chi^2 = 0.81$, P = 0.371). Mate search duration did not vary with the body size of male and female (Table 1, Fig. 1A-B). While small males had significantly longer copulation time, female body size did not affect copulation duration (Table 1, Fig. 1C-D).

Table 1. Generalized linear models of the effect of male and female size on mate search duration and copulation duration in the parasitoid wasp, *Lysiphlebus fabarum*.

		Coefficient ± SE	t	df	P
Mate search duration	Male size	0.05 ± 0.19	0.24	73	0.805
	Female size	0.12 ± 0.21	0.54	73	0.591
	Male size × female size	0.4 ± 0.81	0.05	73	0.958
Copulation duration	Male size	0.13 ± 0.06	2.29	74	0.024*
	Female size	0.01 ± 0.06	0.06	74	0.949
	Male size × female size	0.71 ± 0.41	1.72	73	0.088

^{*}Statistically significant P value ($\alpha = 0.05$)

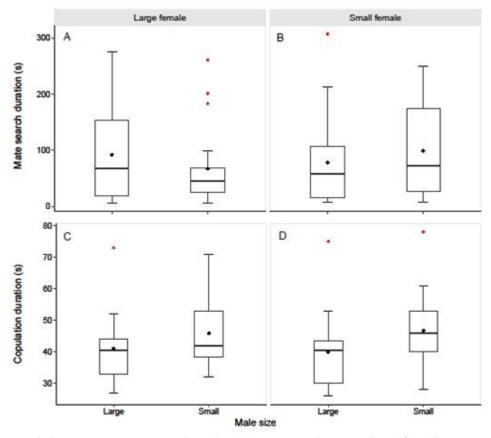


Fig. 1. Boxplot depicting mate search duration (A-B) and copulation duration (C-D) in the parasitoid wasp, Lysiphlebus fabarum at different size classes. The black dots indicate the average of the data.

There was no significant interaction between male and female body size for mate search and copulation duration (Table 1). Within individual regression revealed that mate search time was not affected by male and female body size (Fig. 2A-B), while small males copulated for a significantly longer time (Fig. 2C-D).

Sexual body size dimorphism did not affect mate search duration (Table 2, Fig 3A), however, pairs with higher body size dimorphism copulated for a longer time (Table 2, Fig. 3B).

Discussion

This study addressed mate preference and males' mating performance in accessing large, i.e. high quality, females in the parasitoid *L. fabarum*. We did not find mate preference in males when selecting between small and large females. Mate searching duration did not vary with male or female body size; however, larger males copulated for a significantly longer time. Sexual body size dimorphism had also a positive effect on copulation duration.

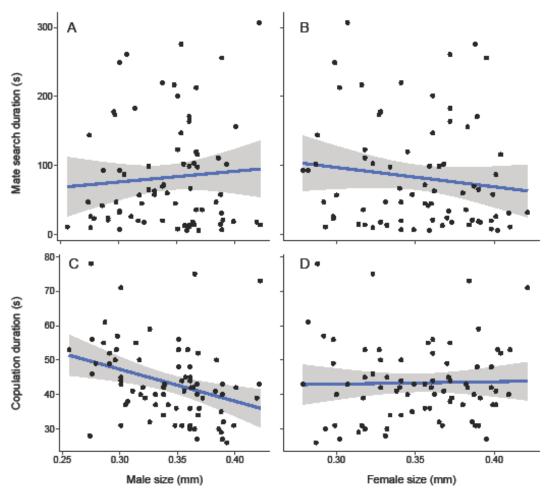


Fig. 2. The relationship between mate search duration (A-B) and copulation duration (C-D) with male and female body size in the parasitoid wasp, *Lysiphlebus fabarum*. The lines represent linear regression with standard error (shade area).

Table 2. Generalized linear models of the effect of sexual body size dimorphism on mate search duration and copulation duration in the parasitoid wasp, *Lysiphlebus fabarum*.

	Coefficient ± SE	T	df	P
Mate search duration	0.04 ± 0.02	1.42	74	0.158
Copulation duration	0.03 ± 0.01	2.46	75	0.015*

^{*}Statistically significant P value ($\alpha = 0.05$)

Females of L. fabarum species monandrous, lacking postcopulatory sperm competition (Astaraki et al., 2019; Rasekh et al., 2022). As male's reproductive success in a monandrous mating system is only determined by his access to mates, males are predicted to respond to precopulatory sexual selection where the mated male sires all the offspring (Arnqvist & Nilsson, 2000; Zeh & Zeh, 2003). This "first-tomate" mating pattern along with short longevity of males (Ameri et al., 2015b) can explain the lack of males' mate preference in this species as the males mate with the first female that happen to encounter as the fitness benefit of a single mating is very high, regardless of the female quality. Thus, males can increase their paternity by maximising the number of mating efforts in their reproductive lifetime (Parker, 1970; Cohen, 1973). Nevertheless, this has yet to be answered whether female L. fabarum wasps are truly monandry, i.e. a complete and irreversible loss of receptivity after an initial mating, or some key aspects of the mating ecology, such as postmating dispersal or mating plugs are involved.

For example, in *Nauphoeta cinerea* (Blattodea: Blaberidae), insertion of spermatophores in the bursa copulatrix inhibits sexual receptivity center in female brain (Roth, 1964) and the ability to remate will be recovered following the laying of the first egg clutch (Moore et al., 2001).

Mate searching duration did not vary with the body size of males, which was not consistent with our prediction. Males of L. fabarum mostly walked in the experimental patch during the trials to explore and find potential mates. Smaller males usually have the same walking speed as the large males (Rasekh A., unpublished data); thus, having a larger body size may not necessarily be advantageous within the patch. However, pre-copulatory sexual selection under monandry compared to a mix of pre- and post-copulatory forces can have profound effects on fitness of males. For example, exposure to rival males early in life is highly costly for males of a monandrous Drosophila subobscura Collin, reducing their ability to obtain a mate and shortening their longevity (Lizé et al. 2014).

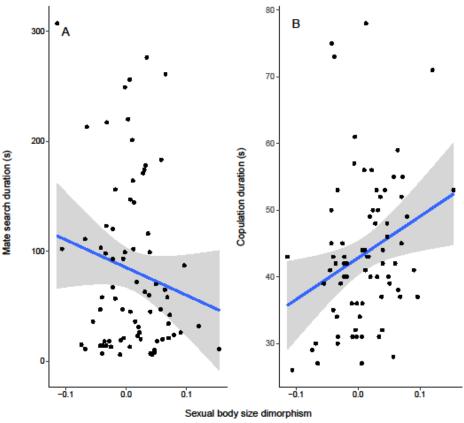


Fig. 3. The relationship between mate search duration (A) and copulation duration (B) with body size sexual dimorphism in the parasitoid wasp, *Lysiphlebus fabarum*. The lines represent linear regression with standard error (shade area).

Thus, males may suffer severe physiological costs from interactions with rivals, more importantly in smaller males where they physiological resources are restricted (Brown et al., 1993; Ameri et al., 2015a). One possible advantage for larger males can be their ability to mate females located away from the natal patch. It is likely that flight ability of *L. fabarum* males vary with body size as in animals where larger individuals have higher flight ability (Ellington, 1991; Shirai, 1995; Samejima & Tsubaki, 2010). Theoretical models have highlighted the importance of non-local mating (Hardy 1994), i.e. between patch mating, since it reduces the degree of competition between local males and the risk of inbreeding among offspring (Ruf et al., 2011; Heimpel, 2019).

Small males of L. fabarum wasps copulated for a longer time compared to their large counterparts which is supported by both interand intra-individual analyses of the males (Figure 1C-D, Figure 2CD). Interestingly, the copulation duration increased with body size sexual dimorphism (Figure 3B). Male size covaries with ejaculate size and increased fertilization success in many taxa (reviewed in Birkhead & Moller, 1998). Additionally, males with relatively large body and testes size, have high daily sperm production rates and relatively high numbers of sperm per ejaculate (birds: Moller, 1988; mammals: Moller, arthropods: Simmons et al., 1996; Engqvist & Sauer, 2003). Therefore, with equal copulation duration, larger males can gain more paternity, suggesting smaller males may copulate for a longer time to ensure a minimum level of fertilization as in L. fabarum males. This should be noted that while longer copulations were correlated with larger numbers of offspring, this may have resulted also from the positive correlation between female condition and

maternal investment (Ameri et al., 2019; Rasekh et al., 2022). Thus, the relationship between copulation duration and offspring number and performance may not necessarily represent an adaptive response.

Our findings suggest that males of L. fabarum wasp lack mate preference where they were introduced to small and large females. This suggests fitness benefit of mating is very high for males, and/or the costs of mating are low, regardless of the female quality. Therefore, males prioritize accessing females because of the lack of post-copulatory competition. Mate searching duration did not vary with male or female body size, suggesting body size does not influence pre-copulatory interactions within the patch. This has yet to be addressed if larger males can gain more access to females when travelling between patches, as they have higher flight capabilities. Interestingly, smaller males copulated for a significantly longer time, and sexual body size dimorphism had also a positive effect on copulation duration. This suggests smaller males may copulate for a longer time as a result of lower sperm transfer rate to ensure a minimum level of fertilization as in L. fabarum males. This study shed light on the evolutionary processes regarding mating behaviours in this parasitoid wasp. Assessing the role of body size on mate access and flight performance between patches and sperm allocation strategy would be the next step to widen our understanding of behaviours and pre-copulatory adaptations in parasitoid wasps.

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گیاه پزشکی (مجله علمی کشاورزی) جلد ٤٦، شماره ۳، یاییز ۱٤٠٢

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تأثیر دوشکلی جنسی ناشی از تفاوت در اندازه بدن، بر رفتار جفت گیری زنبور پارازیتوئید Lysiphlebus fabarum (Braconidae: Aphidiinae)

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ېكىدە

اندازه بدن تأثیر زیادی بر بسیاری از جنبههای زیستی جانداران از جمله برهمکنشهای جنسی آنها دارد. زنبورهای پارازیتوئید معمولا دارای دوشکلی جنسی ناشی از تفاوت در اندازه بدن هستند و عمدتا مادهها بزرگتر از نرها میباشند. مطالعه اخیر روی زنبور پارازیتوئید Lysiphlebus fabarum نشان داده که شاخصهای زیستی فرزندان تحت تأثیر اندازه بدن مادر میباشد. در این ارتباط این سؤالات مطرح میشود که آیا مادههای بزرگتر برای جفتگیری ترجیح داده میشوند و آیا نرهای بزرگتر با دسترسی به جفتهای بزرگتر مزیتی کسب مینمایند. در این مطالعه با پرورش زنبورهای £ fabarum در سنین مختلف رشدی دسترسی به جفتهای بزرگتر مزیتی کسب مینمایند. در این مطالعه با پرورش زنبورهای Aphis fabae در سنین مختلف رشدی این که آیا زنبورهای ماده بزرگ توسط نرها ترجیح داده میشوند، انجام شد. سپس تأثیر اندازه بدن زنبورهای نر بر توانایی آنها این که آیا زنبورهای ماده بزرگ توسط نرها ترجیح داده میشوند، انجام شد. سپس تأثیر اندازه بدن زنبورهای نر بر توانایی آنها برای دستیایی به مادهها بررسی شد. مطابق با نتایج بدست آمده، نرهای معنوان جفت انتخاب شدند. مدت زمان جستجوی برای دستیای به مادههای با اندازه کوچک و بزرگ تقریباً به میزان مساوی به عنوان جفت انتخاب شدند. مدت زمان جستجوی طول مدت زمان جفتگیری در نرهای کوچکتر به طور قابل توجهی بیشتر بود و همچنین مدت زمان جفتگیری با اولین ماده در دسترس» صرف نظر از کیفیت آن ماده، یک بین جفتها افزایش یافت. یافتههای ما نشان میدهد که «جفتگیری با اولین ماده در دسترس» صرف نظر از کیفیت آن ماده، یک راهبرد در نرها محسوب میشود. همچنین، نرهای کوچک احتمالاً به دلیل نرخ پایین تر انتقال اسپرم بر مدت زمان جفتگیری خود می افزایند. این مطالعه فر آیندهای تکاملی در مورد رفتارهای جفتگیری در زنبورهای پارازیتوئید را آشکار می سازد.

كليدواژهها: انتخاب جنسي، ترجيح جفت، جفت گيري، رقابت اسيرم

دبير تخصصي: دكتر سيد على اصغر فتحي

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