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Body size and injury severity associated with mating strategies in male *Philotrypesis taida* fig wasps

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ABSTRACT: In theory, costs associated with fighting favor the assessment of resource value and relative fighting ability over indiscriminately attacking all opponents. This study explored how body sizes (head width and mandible length), morphs (typical and atypical), and injury severities are associated with mating strategies (fighting and sheltering) and outcomes (mated or unmated). We collected 75 ripe unexited figs from four *Ficus benguetensis* trees in Taipei, Taiwan. The figs were then opened and any male *Philotrypesis taida* fig wasps therein, involved in fighting, sheltering, or mating behaviors, were collected, categorized, and measured. The results indicated that body size and injury severity of the male fig wasps were significantly associated with their mating strategies; that is, larger males demonstrated considerably more fighting and sheltering behaviors, but less frequent severe injury conditions. However, no significant difference existed in body sizes, mandible morphologies, or injury severities between mated and unmated males. Our result suggested that all males may have an equal chance of mating, regardless of their body size and morphology.

KEY WORDS: Atypical morphology, Fig wasp, Sheltering, Mate competition, *Philotrypesis*, *Ficus benguetensis*.

INTRODUCTION

Costs associated with fighting, regarding energy and time, favor the assessment of resource value and relative fighting ability over indiscriminately attacking all opponents (Briffa and Elwood, 2004). Body size, which naturally reflects the fighting ability or strength of an animal, is one such cue commonly used for assessment by contestants (Arnott and Elwood, 2009). Massive body size potentially enables the contestants to assess each other's strengths without resorting to a fight (Davies and Halliday, 1978; Parker, 1974). Thus, individuals may avoid protracted contests with rivals that they are unlikely to defeat by comparing their strength with that of their opponent (Taylor and Elwood, 2003). Thus, the evolution of considerable size in males has generally been attributed to sexual selection for fighting ability (Prenter *et al.*, 2008). First, fighting favors large bulky males because they are physically stronger and heavier from a mechanistic perspective. Second, large males should be able to drive out smaller rivals from a competition pool more efficiently. The outcome of a contest will often depend on who is the largest, and many displays seem to involve assessment of body size alone (Neat *et al.*, 1998; Wells, 1988). Consequently, winners of fights should experience unusually high mating success (Hanks *et al.*, 1996).

How the body size of an individual is related to fighting has been examined using various models and led to three main hypotheses. (1) Failed assessment hypothesis (Maynard Smith and Parker, 1976): Fights occur when contest cannot be settled through an alternative mechanism. This hypothesis predicts that pairs of fighting males will be more similar in size than pairs chosen at random from relevant populations. (2) Future expectation hypothesis (Enquist and Leimar, 1990): Fights occur when the value of the currently contested mating opportunity is high in relation to expectations of future mating success. This hypothesis predicts that pairs of fighting males will be no more or less matched in size than randomly chosen pairs. (3) Impunity hypothesis (Cook and Bean, 2006): Fights occur if the risk of serious injury is low for one contestant. This hypothesis predicts that pairs of fighting males will be less similar than randomly chosen pairs.

Body size may be an indicator of fighting ability or male morphology, closely related to the mating strategies an individual will adopt. For example, fig wasp species exhibit a wide range of variations in male morphology—from heavily armored males bearing large mandibles that fight for mates to small flattened males that seek mates in and among the seeds and galls (Murray, 1990; Jousselin *et al.*, 2004). Most *Philotrypesis* species associated with African fig trees present at least two of three morphological adaptations: winged disperser, wingless fighter, and wingless sneaker (Jousselin *et al.*, 2004). Fighters are large, sclerotized, and have long mandibles, whereas sneakers have a thin body allowing them to crawl between fig flowers (Murray, 1990). Thus, rather than a direct head-on fight, some individuals will adopt a different mating strategy to achieve reproductive success. For instance, sheltering (i.e., staying inside an open gall with the mandibles near the exit hole) in male fig wasps provides a degree of self-protection during their mating period (Murray, 1987; Pereira and Prado, 2005). First, it reduces the risk of being injured, which increases survival rate. Second, the amount of time spent sheltering in empty galls is positively correlated to the overall cost of fighting (Murray, 1987; Pereira and Prado, 2005).

In this study, we aim to understand how body size, male morphs, and injury severity could be associated with the mating strategies in fig wasp. To investigate the relationships among these variables, we hypothesized that large males are more aggressive than their smaller opponents; sheltering behavior displayed by males was believed to reduced injury severity during their mating period; larger males should obtain higher mating success in this period.

MATERIALS AND METHODS

Study species

Philotrypesis taida Wong and Shiao 2018 (Chalcidoidea: Pteromalidae: Sycoryctinae) is a non-pollinating fig wasp species associated with the figs of *Ficus benguetensis* Merrill (Wong *et al.*, 2018). As a gynodioecious species, *F. benguetensis* trees bear either seed-producing female figs or wasp-producing male figs. Each fig is a closed round inflorescence containing hundreds of flowers and serves as the arena for mating competition in fig wasps. The fig wasp genus *Philotrypesis* is one of the most variable in terms of male polymorphisms, with winged and wingless males, as well as considerable variation in general body size and presence of fighting adaptations, such as large mandibles, body spikes, and a sclerotized thorax (Jousselin *et al.*, 2004; Cook and Bean, 2006). Moreover, two distinct male morphs which based on mandible morphology can be found in the *Philotrypesis taida*, namely "atypical" and "typical" morphs (D.M. Wong, unpublished data). Atypical males have significant longer mandible length and larger clypeal gap width for their body size than do typical males. Similar dimorphism was also reported by Moore *et al.* (2009) in *Philotrypesis* spp. associated with *F. rubiginosa*.

Sample collection

Ripe unexited figs (N = 75) were randomly collected from four *F. benguetensis* trees in Fuyang Eco Park, Taipei City (25°01′00.6″N, 121°33′25.9″E) between August and October 2015. The figs were then brought to a laboratory for behavioral experiments. The figs were cut into halves from stalk to ostiole at the beginning of the wasp hatching period. The behaviors of male fig wasps were observed in situ. Every fig was examined for 40–90 min under a stereomicroscope (Leica MZ125, Leica Microsystems, Germany). Males involved in any fighting, sheltering, or mating behaviors were removed from their natal fig and preserved in a tube of 75% ethanol to facilitate body measurement. Randomly selected individuals from the same fig in each behavior category were collected as well. Body measurement images were captured using a digital reflex camera (Canon EOS 550D, Canon, Japan). Head width (across the eyes) and mandible length were then measured using ImageJ 1.45a (National Institutes of Health, USA). Head width, rather than hind tibia length, was used to estimate "body size" because limbs are often lost during fights.

Male behaviors and injury severity

Males who initiated fights (physical contact > 3 s) - by crushing, piercing, and biting - were defined as "aggressive" and those being attacked or retreating as "passive." Sheltering behavior was defined as a male remaining within an empty gall with the mandible was facing outward. Mating behavior was defined as a male grasping a female until the copulation ended (mating success). The number of randomly selected individual males (non-fighting, non-sheltered, unmated) was consistent in each behavior category. The injury score was calculated according to a rating scale (Table 1), based on that given by Murray (1987). The original rating scale focused on the lethal effect of losing body fluid, but as this study focused on pre-mating behavior, the injury scale was modified. The new injury scale focused on impaired functions for searching for females, fighting, and locomotion. The injury score (IS) was categorized into three categories: uninjured (IS = 0), minor injury (IS < 8), and severely injured (IS ≥ 8).

Table 1. Criteria for scoring injuries of male fig wasps

Score	Description
1	Loss of part or whole tarsus
1	Loss of part or whole mandible
2	Loss of part or whole antenna†
2	Loss of part or whole tibia
3	Loss of part or whole femur
4	Loss of part or whole coxa
4	Laceration in abdomen
8	Decapitation

†Changed from 0.5 to 2 points

Data analysis

All statistical tests were performed on R (version 3.2.2, R Development Core Team). Shapiro-Wilk tests and Q-Q plots were used to examine the distribution of head width and mandible length in each male. Wilcoxon rank-sum tests were used to investigate the differences in head width and mandible length within each behavioral category (fighting, sheltering, or mating). Chi-squared tests were conducted to ascertain the relationship between the mandible morph and a behavioral category. Kendall's tau tests were performed to explore the relationship among injury level (uninjured, minor, or severe) within a behavioral category. Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test the difference in head width and mandible length in four fighting (aggressive-passive) pairs (atypical-atypical, atypical-typical, typical-typical, typical-atypical) along with additional randomly chosen pairs. The fighting pairs (N = 50) were sampled and compared with the randomly chosen pairs (N = 50) from the same patch.

RESULTS

Fighting behavior

The males usually spent most of their time in the lumen and rarely left the opened fig. Fights were preventable when two males met, and the passive individual could retreat. The head width and mandible length of the aggressive males were significantly larger than those of the passive or non-fighting males (Head: ANOVA, $F_{2,147} = 15.56$, $P < 0.001$; Mandible: ANOVA, $F_{2,147} = 3.85$, $P < 0.05$; Table 2). No pattern was discovered between male morph and fighting behaviors ($\chi^2_1 = 0.283$, nonsignificant [NS]). Regarding the fighting injuries, aggressive males had a significantly lower proportion of severely injured (IS ≥ 8) males than the passive males ($\tau = -0.189$, $z = -1.953$, $P < 0.05$).

Approximately 68% of the fighting pairs were typical–typical, and only 2% were atypical–atypical (Table 3). The differences between fighters in head width ($\chi^2_4 = 17.84$, $P < 0.001$) and mandible length ($\chi^2_4 = 19.76$, $P < 0.001$), and IS ($\chi^2_4 = 8.09$, $P < 0.05$) between fighting pairs among pair categories were significant, and pairing atypical-typical and typical-typical were significantly different from that of randomly pairing (Table 3). However, the injury score difference only coccured in the paring between typical and atypical.

Sheltering behavior

Seventy-six sheltering behavior events were observed in 30 of the 75 figs. Males created their own shelter by enlarging the entrance hole (Fig. 1). The comparison of the variables of sheltered and non-sheltered males revealed that the head widths (Wilcoxon rank sum: W = 1781, $P < 0.001$) and mandible lengths (Wilcoxon rank sum: W = 1163, $P < 0.001$) of the sheltered males were significantly greater than those of the non-sheltered males (Table 4). In addition, the sheltered males were significantly less injured, with a lower proportion of severely injured individuals ($\tau = 0.533$, $z = 6.941$, $P < 0.001$). However, no significant association between morphs and sheltering behavior was noted ($\chi^2_1 = 1.346$, NS).

Mating behavior

Only 16 events of mating behavior were observed in the 8 figs. No significant difference was revealed in head width (Wilcoxon rank sum: W = 175, NS) and mandible length (Wilcoxon rank sum: W = 112, NS) between mated and unmated males (Table 5). Moreover, no link

Table 2. Comparison among aggressive, passive, and non-fighting males

	Aggressive (N = 50)	Passive (N = 50)	Non-fighting (N = 50)
Body size (mm)			
Head width***	0.594[a] (0.498–0.788)	0.582[b] (0.293–0.721)	0.512[c] (0.325–0.719)
Mandible length*	0.243[a] (0.191–0.364)	0.234[b] (0.092–0.311)	0.233[b] (0.144–0.350)
Male morphology ($\chi^2_1 = 0.283$, NS)			
Atypical	7	10	8
Typical	43	40	42
Injury severity ($\tau = -0.189$, $z = -1.953$*)			
Uninjured	23	17	9
Minor	26	24	15
Severe	1	9	26

Ranges are given in parentheses; numbers with different letters indicate significant differences, *P < 0.05, ***P < 0.001

Table 3. Average difference in head width, mandible length, and injury score (in millimeters) between aggressive and passive males.

Aggressive	Passive	N	Head	Mandible	Injury score
Random	Random	50	-0.019[a]	-0.002[a]	1.4[a]
Atypical	Atypical	1	0.009[a]	0.072[a]	3.0[a]
Atypical	Typical	6	0.117[b]	0.087[b]	-3.0[a]
Typical	Atypical	9	-0.001[a]	-0.020[a]	-6.7[b]
Typical	Typical	34	0.037[b]	0.019[a]	-1.4[a]

Head ($\chi^2_4 = 17.84$***), Mandible ($\chi^2_4 = 19.76$***), Injury score ($\chi^2_4 = 8.09$*) Numbers with different letters indicate significant differences, *P < 0.05, ***P < 0.001

Table 4. Comparison between sheltered and non-sheltered males

	Sheltered (N = 76)	Non-sheltered (N = 76)
Body size (mm)		
Head width***	0.588[a] (0.388–0.719)	0.557[b] (0.372–0.673)
Mandible length***	0.249[a] (0.156–0.350)	0.215[b] (0.080–0.272)
Male morphology ($\chi^2_1 = 1.346$, NS)		
Atypical	9	4
Typical	67	72
Injury severity ($\tau = 0.533$, $z = 6.941$***)		
Uninjured	24	6
Minor	25	18
Severe	1	26

Ranges are given in parentheses; numbers with different letters indicate significant differences, ***P < 0.001

Table 5. Comparison between mated and unmated males, in the aspects of body size, mandible morphology, and injury severity

	Mated (N = 16)	Unmated (N = 16)
Body size (mm)		
Head width	0.563 (0.443–0.870)	0.545 (0.293–0.625)
Mandible length	0.216 (0.180–0.386)	0.222 (0.102–0.252)
Male morphology ($\chi^2_1 = 0.848$, NS)		
Atypical	1	4
Typical	15	12
Injury severity ($\tau = 0.466$, $z = 0.079$, NS)		
Uninjured	19	16
Minor	22	22
Severe	9	12

between male morphology and mating behavior was observed ($\chi^2_1 = 0.848$, NS), with no significant difference found in injury level among mated and unmated males ($\tau = 0.466$, $z = 0.079$, NS).

DISCUSSION

The main result of this study was that the males who initiated fights were not the largest males overall. However, considering only intra-morph fights, aggressive males were significantly larger than the passive males. Even though the atypical males were more massive on average than the typical males, they did not initiate more fights than the typical males (Table 3). Because no assessment behavior has been observed in this species (Elwood and Arnott, 2012), fighters do not know the fighting ability of their opponents. In theory, animal size is considered a secure signal for fighters to assess the resource-holding potential of their opponent (Schnell *et al.*, 2015). Moreover, the size of one individual is theoretically related to its quality as a mating partner (Maynard Smith and Parker, 1976). However, without assessment, aggressiveness becomes a signal of intention but not an indicator of Resource Holding Potential (Briffa *et al.*, 2015; Camerlink *et al.*, 2015). Aggressiveness can be linked with the success of the attack (Wilson *et al.*, 2013) or do not have any effect on the fights (McEvoy *et al.*, 2013; Camerlink *et al.*, 2015). In this study, although the fight outcome was not recorded, the injury scores indicated that the aggressive males were typically suffered less injuries than the passive males. Thus, their opponents may be terrified by their massive body size before the fight was escalated.

Another crucial result of this study was regarding the comparison of aggressive and passive males in the non-fighting category. The individuals from this category were randomly selected from other non-fighting males; they were severely injured individuals or significantly smaller than the fighters. These males could be new fighters that had been severely wounded and thus excluded from fights, or small males with alternate non-fighting strategies (Cook *et al.*, 1997). Behavioral observations have indicated that some males can barely move and some have slowly become moribund after a fight (Murray, 1987). The difference in size in the non-fighting category also revealed that some small males avoid fighting areas. Being attacked by an aggressive male required the individual to be in the vicinity of a receptive female. The smallest males were observed moving between galls and in the outer layer of ovules where the large males cannot go.

Only two studies have discussed sheltering behavior in fig wasps. Murray (1987) reported the time spent in galls depended on the number of the presence of other *Philotrypesis* spp. males, and Pereira and Prado (2005) noted that *Idarnes* males spent 23% of their time sheltering. In the present study, *Philotrypesis taida* males competed not only for mates but also for shelter. The sheltering behavior was observed throughout the mating period and after the competitive fights. A shelter can be acquired by either creating it or snatching it from others (D.M. Wong, unpublished data). Sheltered males tended to have larger body sizes and fewer injuries. However, two points must be addressed regarding the observations of sheltering in this study. First, it would be expected that males searching for shelter would be smaller or weaker, but this was not the case in *Philotrypesis taida* ex. *F. benguetensis*. Second, *Philotrypesis taida* males fought for open galls and tried to hide inside. If the males were fighting for these shelters, it meant that these empty galls could be quite valuable to them. For example, sheltering time may be important for males to rest or wait for mating opportunity because fighting fatigue was observed (Elwood and Arnott, 2012). This hypothesis is supported by the high proportion of uninjured and lightly injured males who sheltered within empty galls in our case(Table 3). In addition, the sheltered males were seen attacking actively from their gall shelter. Therefore, another hypothesis can be proposed as sheltered males can reduce their opponent number by injuring them from a good attacking spot with better protection, since the lumen space (the central space inside a fig) is tiny with little coverage.

This study demonstrated that no significant difference in mating opportunities among *Philotrypesis taida* males groups, regardless of their body size and morphology. This result suggests that smaller males could adopt non-fighting tactics and could also succeed in mating as well. This result, in combination with that in the non-fighting category, denotes the presence of an alternate non-fighting strategy. The similar average size between mated and unmated groups shows albeit that the smallest males have vital success in mating.

CONCLUSION

Body size and injury severity have a significant association with fighting and sheltering in male *Philotrypesis taida* wasps during their mating period. Aggressive and sheltering behaviors may be adaptations to the confined space of the fig lumen, which may explain that males do not assess their opponents before attacking. In conclusion, the different behaviors and strategies of the *Philotrypesis taida* males should be investigated by widening the focus of the study on non-fighting tactics.

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