

Fighting injuries, fig exit, and dimorphism in two species of sycoryctine fig wasp (Chalcidoidea, Pteromalidae)

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Academic editor: Petr Jansta | Received 23 May 2019 | Accepted 27 November 2019 | Published 30 December 2019

<http://zoobank.org/5CA95318-B1ED-46AE-919A-5547A01D6C82>

Citation: Wong D-M, Bain A, Shiao S-F, Chou L-S (2019) Fighting injuries, fig exit, and dimorphism in two species of sycoryctine fig wasp (Chalcidoidea, Pteromalidae). Journal of Hymenoptera Research 74: 105–121. <https://doi.org/10.3897/jhr.74.36461>

Abstract

Similar to many vertebrate and invertebrate species, many fig wasp species are fighting other members of their species for mates. Fighting between the males of many non-pollinating fig wasp species involves injuries and fatalities. Studies have shown that large males fight for mates, whereas conspecific small males tend to adopt nonfighting, sneaky behaviors. To analyze male morphs in two non-pollinating fig wasps (*Philotrypes taida* Wong & Shiao, 2018 and *Sycorycteria taipeiensis* Wong & Shiao, 2018) associated with the fig tree *Ficus benguetensis*, the head and mandible allometry and injuries were examined as well as the morphologies of their heads and mandibles. Male fig wasps of these two nonpollinating species can be divided into two morphological groups according to their head and mandible shapes. Approximately 88% of the *Philotrypes* and 62% of the *Sycorycteria* males were injured and no males belonging to largest morphs were decapitated. Moreover, nearly 31% of the *Philotrypes* and 45% of the *Sycorycteria* males left their natal figs. No difference in injury level or male exit rate between the male morphs was observed. This study reveals slight morphological and behavioral differences that may hint towards different mating strategies among morphs.

Keywords

Ficus benguetensis, fatal fighting, male dimorphism, male dispersal, *Philotrypes*, *Sycorycteria*

Introduction

Fighting is ubiquitous in the animal kingdom (Hardy and Briffa 2013; Huntingford 2013; Vieira and Peixoto 2013), and intraspecific fighting is mainly caused by the need to defend for food and territory (Backwell and Jennions 2004) or for mating opportunities (Baxter et al. 2015). For example, many Cervidae stags fight for the control of the females (Clutton-Brock et al. 1979; McElligott et al. 1998); such activity is common in mammals (Packer 2001; Casey et al. 2015). Fighting is also extremely common in invertebrate species such as cephalopods (Schnell et al. 2015) and weaponless butterflies (Kemp and Wiklund 2001). Hymenopterans, such as ants, wasps, and bees, are well-known to engage in intraspecific fighting, either to protect their colonies (Gloag et al. 2008; Rudolph and McEntee 2015) or to compete for the queen position (Berthelot et al. 2017). Fighting often causes many casualties, especially in reproductive castes of social insects (Kärcher et al. 2013; Heinze et al. 2016). Fatal fighting may occur when the following two conditions are met (Enquist and Leimar 1990): the value of the contested resource (e.g. a limited number of mating partners) is particularly high and the value of future reproduction is extremely low (e.g., the organism's lifespan is short). Many examples of fatal fights between males have been documented in the hymenopteran superfamily Chalcidoidea: in the genus *Melittobia* (Hartley and Matthews 2003) and in numerous fig wasp species (Cook 2005). For example, the males of several fig wasp species can only live for up to one day, and the numbers of females within a mating arena in these species are often low (Cook et al. 2017). Thus, the non-pollinating fig wasp model fits the conditions required for the evolution of fatal fighting (Enquist and Leimar 1990).

Fig wasps are small insects that are obligately associated with plant of genus *Ficus* (Kjellberg et al. 2005). As larvae, all fig wasp species (pollinators and non-pollinating fig wasps) are confined inside closed inflorescences called figs. Because of the following aspects of their peculiar life cycle, non-pollinating fig wasps provide a unique opportunity for studying non-pollinating male fig wasp fights: (1) Each fig is a spherical enclosed inflorescence containing hundreds of flowers with one single exit (the ostiole), and (2) limited variation in environmental factors, and the number of figs produced by each tree enable easy replication of experiments in a known environment. In each fig, one or a few female pollinators enter receptive fig, pollinate the flowers inside the fig and lay eggs into the fig ovaries. Wasp larvae then develop inside galled flowers over several weeks. Non-pollinating fig wasps mostly colonize figs after pollination and parasitize fig ovules or pollinating or non-pollinating fig wasp larvae; they do not enter the fig but rather use their long ovipositor to lay eggs through the fig wall into ovules (Kerdelhué and Rasplus 1996). Male pollinating fig wasps hatch first and mate with unhatched pollinating female fig wasps.

Fighting among male fig wasps occurs in both pollinating and non-pollinating species (Bean and Cook 2001; Nelson and Greeff 2009) and tend to be fatal (Bean and Cook 2001; Pereira and Prado 2008; Dunn et al. 2015). The fights take place in the fig: more precisely in the central cavity (the lumen) of the fig and during the short period

before the fig opens (or is opened by male fig wasps) to let the female fig wasps disperse. A considerable proportion of fighting occurring between individuals results in severe injuries or death (Bean and Cook 2001). Fig wasp males belonging to the same species can exhibit a range of morphologies, including armored males bearing large falcate mandibles that fight for mates and flattened males that stealthily seek mates (Murray 1990; Cook et al. 1997; Joussetin et al. 2004). Moreover, some species have dispersing morphs such as winged males (Joussetin et al. 2004) and apterous dispersing males (Greeff and Ferguson 1999); however very little is known about the dispersal rate and behavior of the male fig wasps. Theoretically, a male reaching a fig other than its native fig would be able to mate with female wasps that likely are genetically very different.

The aim of this study was to document morphological variations, the fighting outcomes, and the exit rates of two species of non-pollinating fig wasp living on *Ficus benguetensis*. Preliminary observations of *Philotrypesis taida* Wong & Shiao, 2018 and *Sycorycteridea taipeiensis* Wong & Shiao, 2018 males had revealed that: (1) males are fighting inside the figs, (2) fighting may result in death by decapitation, (3) males vary in size, and (4) males may exit figs. On the basis of these observations, this study raised the following questions concerning male interactions among the studied species: (1) How different in size and morphology are these males? (2) How common are injuries and fatal injuries? (3) How often do males exit their natal figs? (4) What are the factors (e.g., fig diameter linked with the fighting space, sex ratio linked with the number of fighters) affecting the level of injury and the exit rate?

Methods

Study species

Philotrypesis taida and *Sycorycteridea taipeiensis* belong to the Sycoryctinae subfamily (Chalcidoidea: Pteromalidae) and are the two non-pollinating fig wasp species associated with the gynodioecious *Ficus benguetensis* Merrill (Berg 2011; Wong et al. 2018). The trees bear either seed-producing female or wasp-producing “male” figs. Until recently (Segar et al. 2012), the genus *Sycorycteridea* and three other genera (*Arachonia*, *Sycoryctes*, and *Sycoscapteridea*) were synonymized under the *Sycoscapter* genus (Bouček 1988).

Sample collection and behavior observation

Thirty ripe unexited figs were haphazardly collected from five *F. benguetensis* trees in Taiwan from October 2011 to July 2012 (see Suppl. material 1: Table S1). Unripe figs are dark green and firm to the touch, whereas ripening figs gradually change to yellowish green and yield to gentle pressure. The diameters of all sampled figs were measured before the figs were stored at room temperature in transparent plastic pots covered with mesh for 24 h with their ostioles facing upward. A fig's diameter is an

indicator of its size and correlates with the size of the lumen, i.e. the space available for the male fig wasps to fight. Onset of wasp exit was identified by the presence of a hole chewed through the fig-wall. All wasps that exited from their natal figs were collected and stored in 75% ethanol. The figs were then dissected and the wasps inside them were collected. All the collected wasps were then identified, sexed, and counted under a stereomicroscope at 6.3× magnification. Images were captured using a digital reflex camera. Head width (across the eyes) and mandible length were measured using the 1.45a image processing software (National Institutes of Health, USA). Head width, rather than the hind tibia length, was used to estimate body size because limbs are often lost during fighting.

Fighting injuries and exit

The collected *Philotrypesis* and *Sycorycteridea* males were examined for their fighting injuries. All observed lacerations and amputations were noted. The injury level of an individual male was estimated according to a rating scale developed for fighting fig wasps (Murray 1987). However, because the behavior of male fig wasps is specialized to the dark environment of a fig, the scale was modified in the present study; loss of antenna was changed to from 0.5 point to 2 points (Table 1). The original scale developed by Murray (1987) focused on the fluid loss, whereas the modified scale considers the necessity for the male wasps to locate females in dark environments by using only their antennae. Mate-seeking ability is severely impaired when an individual loses part or all of its antennae. Hence, it was assigned a heavier weight in the present study. Injury level per fig was estimated according to the following three variables proposed by Murray (1987): (1) lifetime extent of injury (LEI), the injury scores of all males from the same fig divided by the total number of males; (2) injury frequency (IF), the proportion of injured males; and (3) severe injury frequency (SIF), the proportion of injured males with injury scores greater than 8 points.

Male exit was estimated as the proportion of males exiting their natal fig, namely the “male exit proportion”, and was calculated as the number of exited males divided by the total number of males per fig.

Table 1. Criteria used in 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

Data analysis

The sex ratio for each species was calculated as the number of male wasps divided by the total number of wasps within a fig. All statistical tests were performed using the R 3.6.1 statistical software (R Development Core Team 2019). The dataset was not normally distributed so the used tests were nonparametric. To investigate the factors affecting male exit proportion, multiple linear regression (which do not require a normally distributed dataset) was performed, with five variables: average head width, fig diameter, LEI, morph ratio, and wasp sex ratio.

Results

Male morphology and sex ratio

One hundred eighty-two *Philotrypesis* and 42 *Sycorycteridea* male wasps were collected. The average sex ratio of the sampled figs was 0.36 ± 0.03 for *Philotrypesis* and 0.47 ± 0.09 for *Sycorycteridea*, which was significantly different from the 1:1 ratio for *Philotrypesis* ($t = 4.44$, $df = 48$, $P < 0.001$) but not for *Sycorycteridea* ($t = 0.39$, $df = 22$, NS). The sex ratio of the two species was not different ($t = -1.16$, $df = 14.03$, NS).

Two *Philotrypesis* male morphologies, namely “atypical” and “typical” morphs, were identified. They were distinguished by the shapes of their mandibles (Fig. 1; alternative images in Suppl. material 2: Fig. S1); the atypical males (7% of the males) have scythe-shaped mandibles, whereas the typical males have three-tooth mandibles. In addition, atypical males were significantly larger than the typical males (Table 2). The largest *Philotrypesis* male was approximately twice the size of the smallest, and its mandible was approximately three times as long (Table 2; Fig. 2a). The sizes of the two morphs overlapped; the smallest *P. taida* atypical males were smaller than many of the typical males (Fig. 2a). The *Sycorycteridea* males were divided into two morphs according to their size (Table 2): the “small” morph, having head widths narrower than 0.425 mm (57% of the individuals), and the “large” morphs, having heads wider than 0.425 mm (Fig. 2b). The largest *Sycorycteridea* male was approximately thrice the size of the smallest and had a mandible approximately four times as long. *Sycorycteridea* mandible length and head width were discontinuously distributed. No male with a

Table 2. Head width and mandible length of each male morph.

	Morph	N	Mean head width	Head width range	Mean mandible length	Mandible length range
<i>Philotrypesis</i>	Atypical	13	0.673 ± 0.187^a	0.550–0.719	0.323 ± 0.089	0.242–0.370
	Typical	169	0.576 ± 0.044^b	0.366–0.675	0.233 ± 0.018	0.134–0.310
<i>Sycorycteridea</i>	Large	18	0.502 ± 0.118^c	0.453–0.562	0.290 ± 0.068	0.243–0.326
	Small	24	0.336 ± 0.069^d	0.215–0.388	0.153 ± 0.031	0.078–0.230

Means are given \pm SE. Numbers with different letters indicate significant differences.

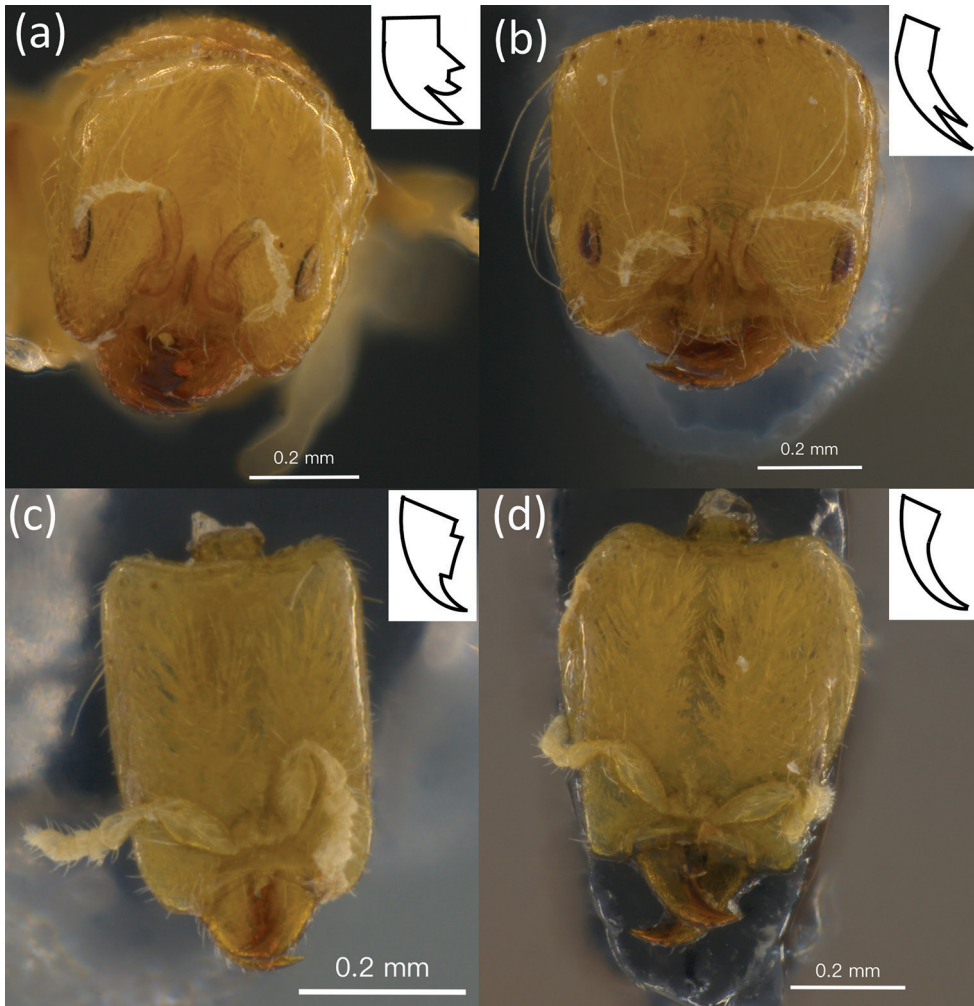


Figure 1. Frontal view of the males of the two studied species and mandible outline (a) a “typical” *Philotrypesis* male: rounded back of the head and broad mandibles (b) “atypical” *Philotrypesis* male: head more square and falcate mandibles (c) *Sycorycteridea* small male, rectangular head (d) *Sycorycteridea* large male, lantern-shaped head.

head width between 0.400 and 0.450 mm was found. The measurement gap between the two morphs represents approximately 12% and 19% of the average male head width and mandible length, respectively.

The mandible length of *Philotrypesis* males correlated positively with head width (Spearman rank correlation test: $\rho = 0.759$, $df = 180$, $P = 2.58E-35$; Fig. 2a). In addition, significantly positive correlations were independently observed in the atypical morph (Spearman rank correlation test: $\rho = 0.714$, $df = 167$, $P = 1.09E-27$) and typical morph (Spearman rank correlation test: $\rho = 0.828$, $df = 11$, $P = 0.000473$). The mandible length of the *Sycorycteridea* males exhibited a positive relationship with their

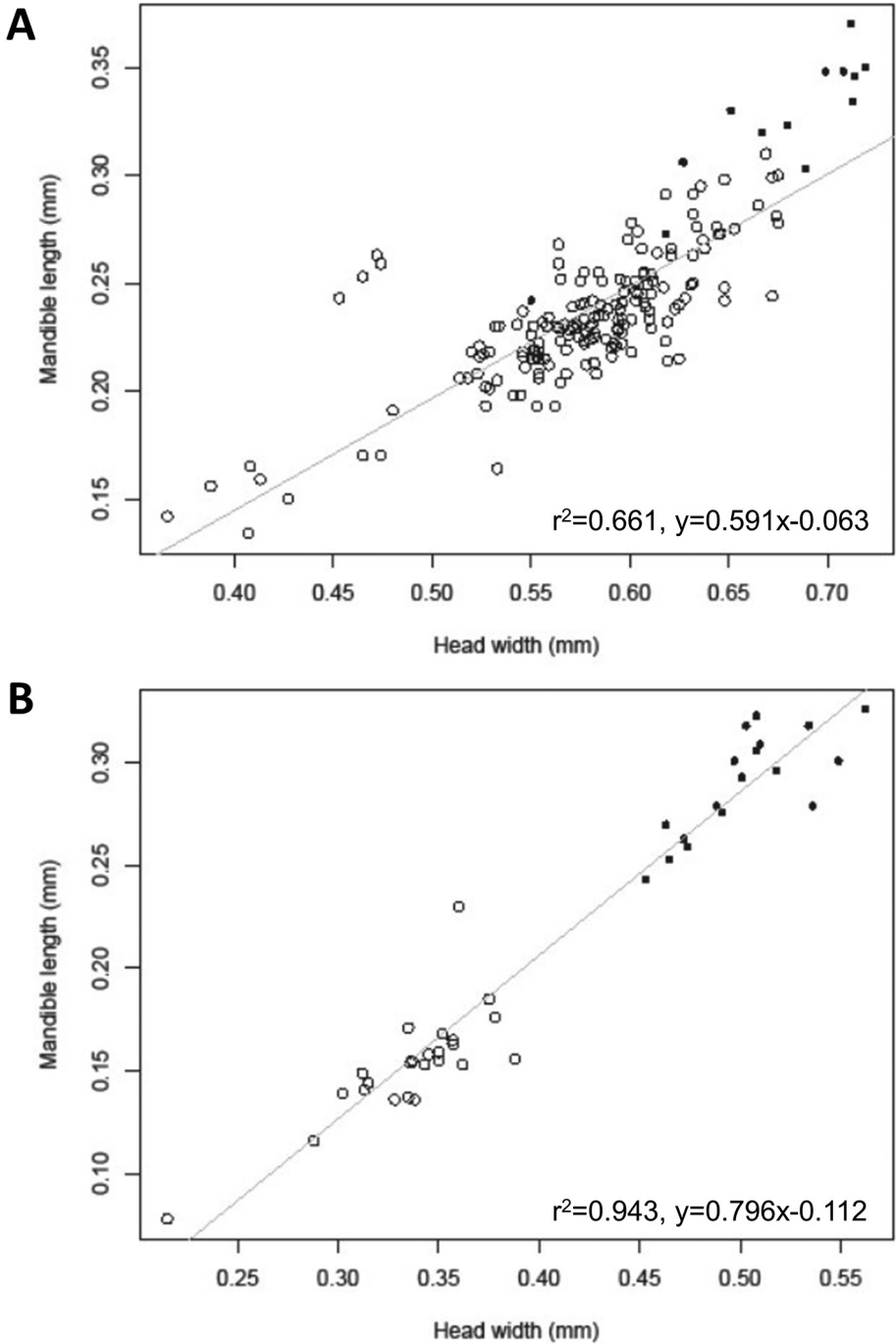


Figure 2. Relationship between head width and mandible length in **a** *Philotrypesis* and **b** *Sycorycteridea*. Typical *Philotrypesis* and small *Sycorycteridea* are represented by the unfilled circles whereas atypical *Philotrypesis* and large *Sycorycteridea* are represented by filled circles.

head width (Spearman rank correlation test: $\rho = 0.939$, $df = 40$, $P = 3.82E-20$; Fig. 2b). Furthermore, the same positive correlation existed independently for the large males (Spearman rank correlation test: $\rho = 0.765$, $df = 22$, $P = 1.35E-05$) and small males (Spearman rank correlation test: $\rho = 0.765$, $df = 22$, $P = 1.35E-05$).

Fighting injuries

The number of *Philotrypesis* males of each morph in each injury level was not different ($\chi^2_1 = 0.48$, NS), same for the *Sycorycteridea* morphs ($\chi^2_1 = 0.00$, NS; Table 3). Additionally, no difference was observed in average injury score between the atypical and typical *Philotrypesis* males (Wilcoxon rank sum test: $W = 1096.5$, $P = 0.99$; Table 4) or between the *Sycorycteridea* male morphs (Wilcoxon rank sum test: $W = 197.5$, $P = 0.64$; Table 4). Finally, half of the *Sycorycteridea* large males were uninjured (Table 3; Fig. 3b), whereas more than half of the atypical *Philotrypesis* were severely injured (Table 3).

Philotrypesis had a significantly higher LEI value ($t = 3.11$, $df = 35$, $P < 0.01$; Table 5) and a higher proportion of injured males than did *Sycorycteridea* ($\chi^2_1 = 15.58$, $P < 0.01$; Table 5); however, the proportion of severe injury was not different between the two species ($\chi^2_1 = 7.86$, NS). Rates of decapitation were low in *Philotrypesis* and *Sycorycteridea* males and all decapitated specimens were small *Sycorycteridea* and typical *Philotrypesis* males (Table 4; Fig. 3). The femur and tarsus were the most commonly injured body parts for the *Philotrypesis* males, whereas for the *Sycorycteridea* males, the antenna and tarsus were the most commonly injured parts (Table 4).

The calculation of the injury score differs from Murray’s scoring (1987) from the points allotted to the antenna injuries, increasing their score from 1.5 or 3 points from

Table 3. Proportion of injured males.

	<i>Philotrypesis</i>		<i>Sycorycteridea</i>	
	typical (N = 169)	atypical (N = 13)	small (N = 24)	large (N = 18)
Uninjured (injury score = 0)	0.11	0.15	0.29	0.50
Minor (injury score <8)	0.46	0.31	0.50	0.33
Severe (injury score ≥8)	0.43	0.54	0.21	0.17

Means are given ± SE.

Table 4. Mean injury score per individual and injury proportion distributed among different body parts.

	<i>Philotrypesis</i>		<i>Sycorycteridea</i>	
	typical (N = 169)	atypical (N = 13)	small (N = 24)	large (N = 18)
Mean injury score	7.4 ± 0.6 ^a	7.1 ± 2.0 ^a	3.8 ± 0.8 ^b	3.5 ± 0.8 ^b
Abdomen	0.01	0.00	0.00	0.00
Antenna	0.37	0.62	0.25	0.28
Coxa	0.31	0.23	0.21	0.11
Decapitation	0.08	0.00	0.04	0.00
Femur	0.49	0.46	0.25	0.22
Tarsus	0.42	0.38	0.29	0.22
Tibia	0.32	0.46	0.17	0.22

Means are given ± SE. Numbers with different letters indicate significant differences.

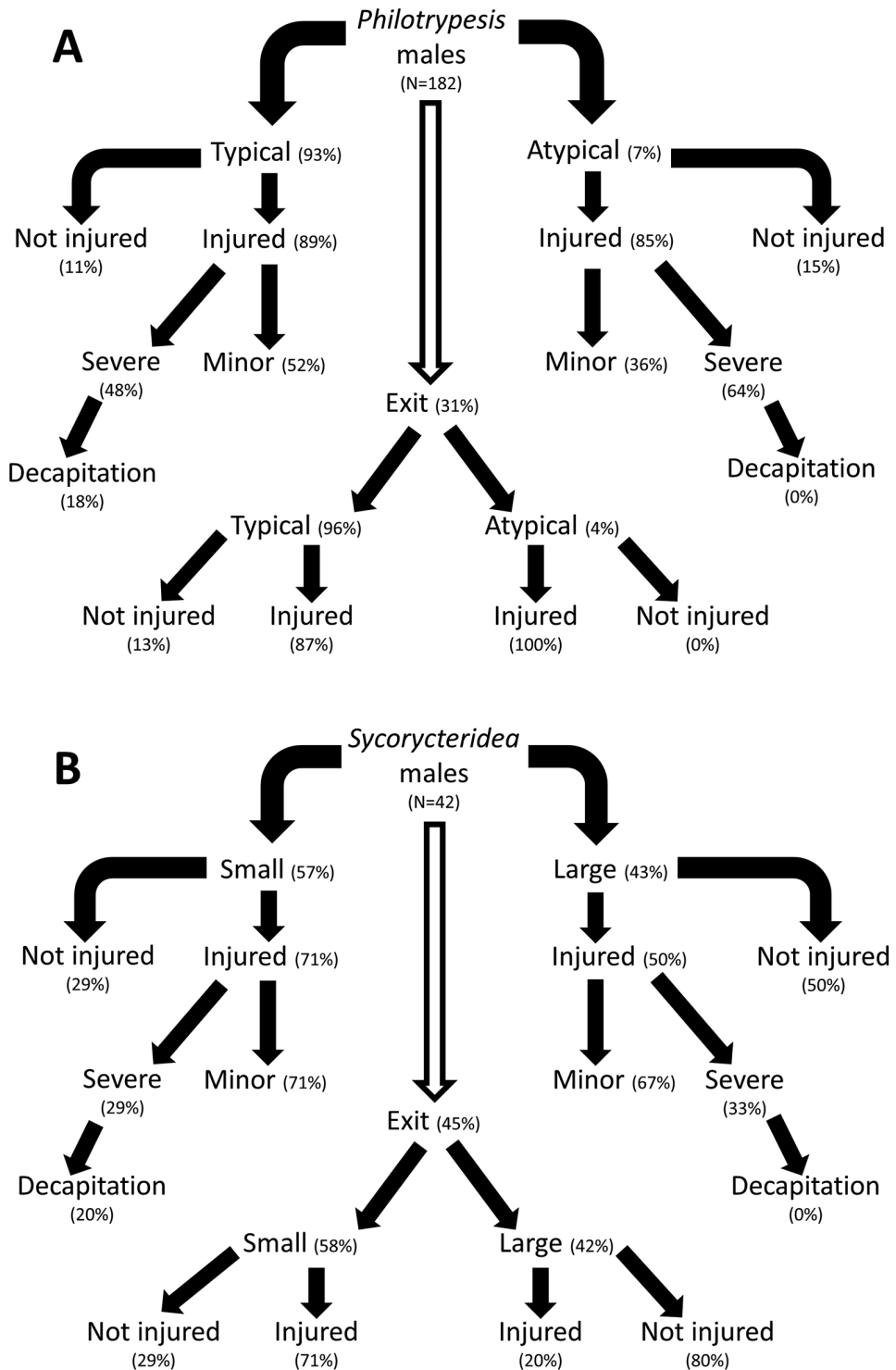


Figure 3. Proportions of **a** *Philotrypesis* and **b** *Sycorycteridea* exited and injured males.

Table 5. Average numbers per fig and injury rates for the two non-pollinating fig wasp species (N = 30 figs).

	<i>Philotrypesis</i>	<i>Sycorycteridea</i>
Mean wasp number	21 ± 5	12 ± 3
Male exit rate	0.31 ± 0.06	0.45 ± 0.13
Lifetime Extent of Injury (LEI)	5.6 ± 0.6 ^a	2.5 ± 0.7 ^b
Proportion of injured males (IF)	0.88 ± 0.02 ^a	0.62 ± 0.07 ^b
Severe Injury Frequency (SIF)	0.23 ± 0.03	0.10 ± 0.05

Means are given ± SE. Numbers with different letters indicate significant differences.

Table 6. Result of the multiple linear regression model with the male exit proportion as dependent variables.

	<i>Philotrypesis</i> (R ² = 0.47* F = 3.37)		<i>Sycorycteridea</i> (R ² = 0.52 F = 1.28)	
	β	t	β	t
Average head width	4.05	2.36*	1.15	0.28
Fig diameter	-0.02	-1.40	-0.01	-0.22
LEI	-0.02	-0.85	-0.07	-1.12
Morph ratio	-0.49	-1.09	-0.48	-0.67
Wasp sex ratio	-0.32	-0.90	-0.93	-1.61

*P < 0.05.

Murray’s score. Seventy-one (39.0%) *Philotrypesis* males and 11 (26.2%) *Sycorycteridea* males had antenna injured. Moreover, 12 *Philotrypesis* males and two *Sycorycteridea* males have seen their injury level increased using our scoring method (from minor to severe). The new injury scores were significantly higher than Murray’s scores for *Philotrypesis* (Wilcoxon signed rank test: V = 2556, P = 3.548e-15) and for *Sycoscapteridea* (Wilcoxon signed rank test: V = 66, P = 0.001586).

Male exit

Most of the male fig wasps exited within 2 h after the first wasp had emerged from the fig. No difference in the proportion of exited males was observed between the two non-pollinating species ($\chi^2_1 = 0.00$, NS; Table 5). However, the two species differed in terms of the injury scores of exited males. First, the average injury scores of exited and philopatric *Philotrypesis* males were 3.1 (range: 0–8) and 4.2 (range: 0–18), respectively, indicating significant variation between the two groups (Wilcoxon rank sum test: W = 4329.5, P = 0.001145). The test for *Sycorycteridea* values was not significant (Wilcoxon rank sum test: W = 229.5, P = 0.1595): 1.33 (range: 0–5) for exited males and 2.33 (range: 0–11) for philopatric males. Moreover, the severe injury proportion was lower for exited males than for philopatric males among *Philotrypesis* males ($\chi^2_1 = 6.25$, P < 0.05) but not among the *Sycorycteridea* males ($\chi^2_1 = 0.00$, NS).

The multiple linear regression model contained five variables (average head width, fig diameter, LEI, morph ratio, and sex ratio) was significant, showing that the five variables collectively explain the exit rate. In addition, the average *Philotrypesis* male head width was the main contributor of the model (Table 6).

Discussion

Our results show that the males of each of the two studied species had two clearly defined morphs. The *Philotrypesis* males could not be categorized according to their size only because some of the atypical males were smaller than the largest typical male: The shapes of the heads and mandibles were the discriminative morphological features. The shapes of the head and the mandibles were also discriminative for the morphs of the *Sycorycteridea* males but these males could also be segregated according to their size only. Such dimorphism (discontinuous distribution of male size) has never been observed before in male fig wasps. Moreover, injuries were found in every morph of both species, and it seems that belonging to a specific morph does not affect the probability of injury. Nevertheless, morph type may affect the severity of injury; no decapitated males belonging to the atypical *Philotrypesis* or large *Sycorycteridea* morphs were found in this study. However, the absence of decapitated males could be a random effect of the sampling as only the little number of atypical *Philotrypesis* has been found.

In contrast to other *Philotrypesis* species (Cook et al. 1997; Jousselin et al. 2004), no winged males have been found in *P. taida*. The dimorphism of the *Philotrypesis* morphs in the present study is similar to that of congeneric species living on *F. septica* in Australia (Cook and Bean 2006) and *F. rubiginosa* (Moore et al. 2009). In other words, in the three *Philotrypesis* species whose morphometries have been analyzed, atypical males have longer mandibles than typical males (for a given head size). The main difference between the Taiwanese species and Australian species is that the Australian *Philotrypesis* morphs are more clearly separated by their head and mandible morphometry (Cook and Bean 2006; Moore et al. 2009) (Fig. 2a). To the best of our knowledge, no other study has described the morphometry of the *Philotrypesis* male morphs.

The *Sycorycteridea* morphs in this study were uniquely morphometrically defined; no continuous distribution of mandible length or head width was noted, in contrast to Australian *Sycosapter* species living on *F. macrophylla* (Bean and Cook 2001) or *F. rubiginosa* (Moore et al. 2008). Genera *Sycorycteridea* and *Sycosapter* are closely related but phylogenetically distinct (Segar et al. 2012). Dimorphism seems to be expressed differently among the genera of a single hymenopteran group, with three distinct morphometric manners to be dimorphic according to Cook and Bean (2006). Our study added a fourth manner among *Sycorycteridea* morphs, namely discrete size-dependent dimorphism. The diversity of the allometric dimorphism has also been documented in other insect genera such as *Onthophagus* dung beetles (Emlen et al. 2005), *Oxyporus* rove beetles (Hanley 2001), and hymenopteran insects (Danforth and Desjardins 1999).

The injury frequencies (IF) of *P. taida* and *S. taipeiensis* in this study are the highest ever documented in any non-pollinating fig wasp species (88% and 62% for *Philotrypesis* and *Sycorycteridea* respectively). In congeneric species, very few fight winners were injured, whereas 22% of *Philotrypesis* losers and 73% of *Sycorycteridea* losers were injured (Moore et al. 2008). As examples for other genera, in *Walkerella*, the IF was approximately 17% (Wang et al. 2010), and in *Idarnes* wasps, it was approximately 40% (Pereira and Prado 2008). In our study, morph type had no effect on IF for either of the

studied species; however, for another species of *Philotrypesis* for a given mandible size, atypical males were less injured (Moore et al. 2009). The IF of non-pollinating wasps living in *F. benguetensis* figs is higher than that of other species; thus, environmental factors might be key for determining the intensity of fights. Indeed, IF is often affected by the number of conspecific males (Murray 1987; Pereira and Prado 2005, 2008; Wang et al. 2010), fight duration (Moore et al. 2008, 2009), fig diameter (Pereira and Prado 2005, 2008), male size (Moore et al. 2008; Pereira and Prado 2008), and number of females (Pereira and Prado 2008). Furthermore, injuries can occur only after a certain number of males have hatched (Wang et al. 2010). On the basis of our data, we cannot discriminate between hypothetical explanatory factors. The severe injury frequency (SIF) values of *P. taida* and *S. taipeiensis* in this study are within the ranges presented in the literature; SIF was low (1–3%) in *Idarnes* wasps (Pereira and Prado 2008), approximately 25% in *Sycoscapter* wasps (Bean and Cook 2001), and approximately 44% in *Sycoscapter* fight losers (Moore et al. 2008). Also, 11% of *Philotrypesis* losers—four times less than the SIF of our studied *Philotrypesis* species—were severely injured (Moore et al. 2008). This difference may be due to the changes we made to Murray's injury score (1987), increasing the value of damaged antennae.

Although studies on the dispersal (exit from a natal fig) of non-pollinating wingless male fig wasps are extremely limited, the few published studies have revealed a wide range of exit rates; 27%–71% of males of non-pollinating fig wasp species living in *F. ingens* figs exit their native figs (Greeff and Ferguson 1999), as do 17% of *Sycoscapter australis* (Bean and Cook 2001) and 29% of *Walkerella* sp. ex. *F. benjamina* male wasps (Wang et al. 2010). The exit rate of the *Philotrypesis* males from *F. benguetensis* (31%) is very close to that of *Philotrypesis* (35%) from *F. ingens* (Greeff and Ferguson 1999). In addition, species from the Sycoryctini tribe exhibit a wide range of exit rates: 17% for *Sycoscapter australis* on *F. macrophylla* in Australia (Bean and Cook 2001), 45% for *Sycorycteridea* sp. 1 on *F. benguetensis* in Taiwan; and 71% for *Sycoryctes* sp. on *F. ingens* in South Africa (Greeff and Ferguson 1999). These numbers reveal highly variable exit rates among studied species in the literature, and even among species living in the same figs (*F. benguetensis* and *F. ingens* wasps). This feature may be a strong indicator that exit rate is not primarily driven by environmental factors but by genetic or maternal factors. Even in a single wasp species, different morphs can have very distinct exit rates; almost all typical *P. taida* typical males exit figs, whereas very few of atypical male ones do. This situation is similar to that of the non-pollinating wasp species *Otitesella longicauda*, which has two morphs. The dispersing morph (called *digitata*) always exits figs, whereas the other morph (called *religiosa*) almost never leaves its natal fig (Greeff and Ferguson 1999). The exit rates of different morphs in a single species do not always differ extremely; for example, in contrast to the *Otitesella rotunda* *digitata* and *religiosa* morphs having an exit rates of 70% and 27%, respectively, the small and large *Sycorycteridea* sp. 1 have exit rates of 58% and 42%, respectively, and the black and pale morphs of *Walkerella* sp. ex. *F. benjamina* have low exit rates of 36% and 23%, respectively (Wang et al. 2010). Differences in exit rates between intraspecific morphs show

that dispersal is likely not influenced by environmental cues but by maternal choices, and these choices may be influenced by environmental factors. Nevertheless, some exit rate values fit the morphological adaptations of the males, such as the digitata males (attracted to light and strong legs) and black *Walkerella* males (darker males may better resist to dehydration). However, the smaller morphs of *P. taida* and *S. taipeiensis* exited most frequently; for *Philotrypesis*, it may be that the largest males of the typical morph exited (i.e., the head width is the only significant factor to explain the exit rate). The fact of smaller morphs exiting more frequently is somewhat counterintuitive because figs of *F. benguetensis* are patrolled by numerous ants (Lin et al. 2016) and are, on average, more frequently and more severely injured (for *Philotrypesis*) than the larger morphs; thus, their chances of successful dispersal are low. Smaller males may exit as an alternative strategy to avoid more competitive fighting males inside figs, and because figs can be closely clustered together (Suppl. material 2: Fig. S2), exited males may find females in neighboring figs. Finally, it seems that males with severe injuries are less inclined to exit figs than are males with minor injuries.

Considering the high probability of being captured by ants (Lin et al. 2016), the cost of dispersal seems very high; however, because a fig regularly contains few mothers (in three *Sycosapter* species) and because 10%–22% of females are born in figs without conspecific males (Cook et al. 2017), mating in one's non-natal fig would be extremely rewarding from a genetic perspective. The dispersal strategy could be adopted by less successful fighting males, but not by the smallest males.

Conclusion

The findings of this study confirm the type of dimorphism that has been described in other *Philotrypesis* species and reveal a new dimorphism type in the Sycoryctinae sub-family. Some intermorph values found in this study could be used as insights for behavioral differences between morphs related to aspects such as fighting or exiting figs. Our research provides basic information that could lead to behavioral studies of these males and the environmental factors that may affect the choices of fig wasp mothers to produce any morph at an oviposition site.

Acknowledgments

The authors thank Prof. Tzeng Hsy-Yu from National Chung Hsing University for generous guidance on study methods. The authors would also like to express deepest appreciation to Prof. Hsu Yu-Ying and Prof. Yang Jeng-Tze from National Taiwan Normal University and National Chung Hsing University, respectively, for their valuable suggestion and discussion. This research is supported by National Science Council of Taiwan (99-2923-B-002-001-MY3).

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Supplementary material 1

Table S1. Thirty sampled figs were haphazardly collected from *Ficus benguetensis* trees within five natural habitats of Taiwan

Authors: Da-Mien Wong, Anthony Bain, Shiuh-Feng Shiao, Lien-Siang Chou

Data type: species data

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Supplementary material 2

Figures

Authors: Da-Mien Wong, Anthony Bain, Shiuh-Feng Shiao, Lien-Siang Chou

Data type: multimedia

Explanation note: **Figure S1.** The heads from two *Philotrypesis taida* individuals. **Figure S2.** Cluster of *Ficus benguetensis* figs in the National Taiwan University campus, Taipei, Taiwan.

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