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Static allometry of a threat device that is not a weapon: wing spots in male *Heterandrium fallax* (Hymenoptera Agaonidae)

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Males of the agaonid wasp *Heterandrium fallax* have wing spots that they display during aggressive encounters near the ostioles of syconia of the fig *Ficus pertusa*, apparently in competition for the opportunity to copulate with emerging females. In accord with predictions of the "functional allometry hypothesis" for the allometry of structures that are under sexual selection as threat devices and that do not function as weapons, larger males tended to have proportionally larger wing spots. Some smaller males lacked spots, and smaller males were less likely to be collected near female emergence sites or to show antennal damage that probably results from male fights.

KEY WORDS: fig wasp, positive allometry, scaling, threat signal.

INTRODUCTION

Static allometry is a method for quantifying an animal's investment in different morphological structures relative to its overall body size. A classic technique (Huxley 1972) has been to use log-log graphs of the size of a structure against an indicator of the size of the animal's body, utilizing individuals of the same species and at the same developmental stage: a slope > 1.0 indicates that larger individuals have proportionally larger structures ("positive allometry"); a slope < 1.0 indicates that smaller individuals have proportionally larger structures ("negative allometry"). Many previous studies have associated positive allometry with sexual selection on (Huxley 1972; Green 2000; Kelly 2005; Kodric-Brown et al. 2006; O'Brien et al. 2018), and Kodric-Brown et al. concluded from their review of > 150 species that positive allometry is "nearly universal". It is now clear, however, that there are many exceptions; in fact, exceptions

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may actually be the rule (Bondurianski & Day 2003; Bondurianski 2007; Eberhard 2009). A recently proposed "functional allometry hypothesis" attempted to explain these contradictions (Eberhard et al. 2018; Rodriguez & Eberhard 2019). Sexual selection was hypothesized to favor different slopes for structures that have different functions: selection on a structure to function as a weapon was predicted to select, in different species, for both positive and negative allometry, with positive allometry being more frequent. Selection on a structure to function as a threat device was predicted to select consistently for positive allometry. And selection on a structure to function as a courtship device was predicted to select for mix of slopes in different species, with negative allometry being especially common for courtship devices that contact the female.

Testing the functional allometry hypothesis has been difficult, however. Many traits perform more than a single function and thus do not have clear predictions: for instance, behavioral observations indicate that many and perhaps nearly all weapons are also used as threat devices; and in some cases they also appear to be used in courtship. Morphological traits that have been demonstrated to have only a single function under sexual selection, and that can thus be used to test the predictions regarding allometry of the functional allometry hypothesis, are not common. In part this lack of data is because behavioral studies that are sufficiently complete (that include both male-female and male–male interactions) to confidently establish that a particular structure performs only a single sexually selected function are lacking for most of the species for which measurements of the allometry are available.

This study constitutes a new test of the functional allometry hypothesis, using the chalcidoid fig wasp *Heterandrium fallax*, in which males (but not females) have dark spots on their wings. Wing markings are widespread in some families of flies, and also occur sporadically in several families of chalcidoid wasps (Peck et al. 1964; Noyes & Hayat 1984; Bouček 1993). Patterned wings are known to be used in intraspecific aggressive and courtship displays in some flies (e.g. Aluja et al. 1999; Han 1999 on tephitids; Eberhard 2002 on a sepsid), but there is apparently little known regarding their functions in chalcidoids. This paper describes the aggressive behavior of male *H. fallax* and the allometry their wing spots. Male behavior suggests that the spots function as intraspecific threat devices in battles for access to females, but not as weapons or as courtship devices. These behavioral details allow us to test a prediction of the functional allometry hypothesis: the wing spots of male *H. fallax* should show relatively steep allometric slopes – i.e. steeper than those of other body parts, and an overall positive allometry.

MATERIALS AND METHODS

Field observations were made in mornings in May 1988, May 1989, and Nov.–Dec. 1990 when one of us (W.G. Eberhard) climbed into three approximately 10 m tall trees of *Ficus pertusa* HBK at about 1500 m el. above San Antonio de Escazu, San José Province, Costa Rica. Trees with wasps bore a few very mature syconia (dark red) and many younger syconia (nearly as large but light pink with dark pink spots). Male wasps resting on syconia (see below) and those walking on leaves were collected separately in 1989 and 1990 (relatively more time was spent searching on syconia in 1990). Wasps on syconia were captured by enclosing the entire syconium in a small jar; those on leaves were captured between moistened fingertips. It was easier to search for wasps on syconia than on leaves, and a few wasps on leaves escaped capture attempts. The total numbers of wasps collected at the two types of site were clearly influenced by relative collecting effort and

effectiveness), but the difficulties capturing individuals with clear and spotted wings were probably similar, so the data can be used to estimate the relative frequencies with which wasps with different wing markings occurred at each type of site.

We measured several traits that behavioral observations suggested might be under sexual selection (wing length, wing width, and the sizes of apical and basal wing spots; Fig. 1), and several other non-sexual "control" traits including thorax length, head width, and gaster length under an 80 × dissecting microscope. Pieces of coverslips were used to hold specimens in appropriate positions so that all trait-defining landmarks were level. Not all variables were measured for all specimens, so sample sizes vary (details in Tables 1–3). Because there was some uncertainty regarding species names, we checked to confirm that the males collected in 1989 were nearly identical in size with those collected in 1990 (Table 1) before combining the two samples in some analyses. Because it was uncertain how long the figs had been mature and had had wasps emerging from them in the 2 years in which collections were made, we performed separate analyses of antennal damage and the correlations between body size and collection site for the 2 years; unless otherwise specified, the analyses described below refer to the combined samples.

We emphasize allometric regressions on thorax length as an indicator of body size, rather than on head width (because the males probably fight using their mandibles) or on gaster length (because segments can telescope inside each other). We used OLS rather than RMA regressions (see Al-Wathiqui & Rodríguez 2011; Kilmer & Rodríguez 2017). In calculation of allometric slopes, the magnitude of the error in the measurement of the estimate of body size – the "x-axis" is of special concern. We did not estimate measurement error because all measures were taken by one author (W.G. Eberhard) who has extensive experience in aligning structures to bring into sharp focus the landmarks that define the traits. We typically attain measurement errors of under 5–1% (i.e. measurement repeatabilities of $r = 0.95$–0.99; unpubl.), which would at most lead to negligible slope underestimation (Kilmer & Rodríguez 2017). Means are reported followed by one standard deviation (SD) and the standard error (SE).
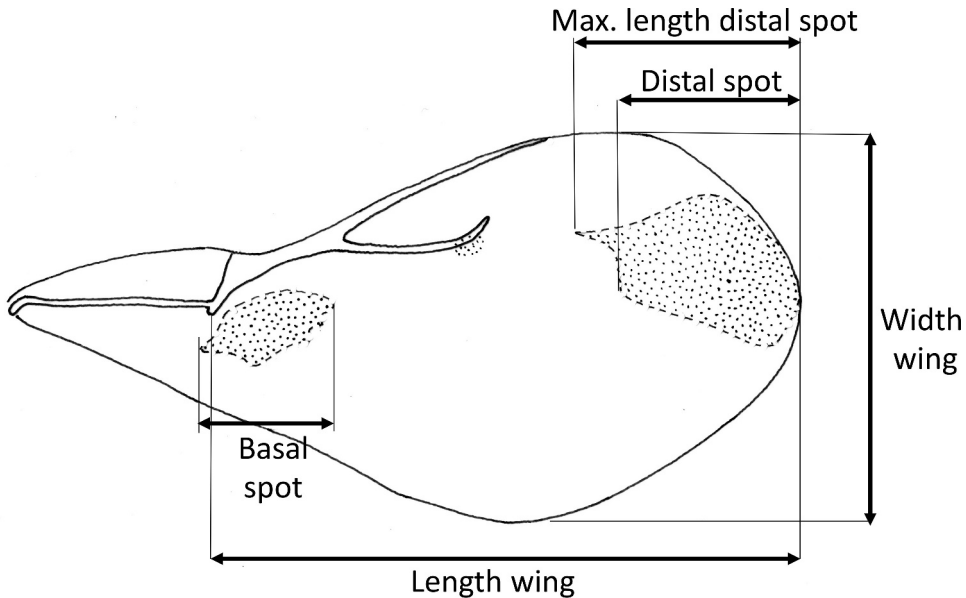

Fig. 1. — Dimensions that were measured in wings of male *Heterandrium fallax*.

Table 1.

The mean dimensions (in mm) of the structures that were measured (see Fig. 1) in male *Heterandrium fallax* in 2 years and their hypothesized functions in the regression analyses. Those collected in 1989 were almost identical in size with those collected in 1990 (the maximum length of the apical wing spot and the length of the basal wing spot were not measured in 1989). In each case we report: mean (**SD**, **SE**).

Trait function	Trait	1989 ($n = 68$)	1990 ($n = 139$)	Totals
Control	Thorax length	0.75 (0.07, 0.008)	0.75 (0.07, 0.006)	0.74 (0.12, 0.008)
	Head width	0.49 (0.03, 0.004)	0.47 (0.04, 0.003)	0.48 (0.04, 0.003)
	Gaster length	0.96 (0.09, 0.011)	0.96 (0.07, 0.006)	0.96 (0.09, 0.006)
	Wing length	1.33 (0.14, 0.017)	1.28 (0.14, 0.012)	1.30 (0.14, 0.010)
	Wing width	0.72 (0.07, 0.008)	0.73 (0.06, 0.005)	0.73 (0.07, 0.005)
Threat	Apical wing spot length	0.37 (0.10, 0.012)	0.37 (0.08, 0.007)	0.37 (0.09, 0.006)
	Apical wing spot max. length	–	0.38 (0.11, 0.009)	0.38 (0.11, 0.008)
	Basal wing spot length	–	0.21 (0.05, 0.004)	0.21 (0.05, 0.004)

Besides raw differences and significance tests, we also report estimates of the effect size of the differences we found (Nakagawa & Cuthill 2007) using "r", a dimensionless variable that ranges from 0–1 (i.e. as a correlation coefficient) and by convention indicates small (< 0.3), medium (0.3–0.5) and large (> 0.5) differences (Nakagawa & Cuthill 2007).

W. Ramírez identified the trees. Z. Bouček kindly identified (and published on) wasp specimens collected in 1990 (Bouček 1993). Because he also identified a second species of *Heterandrium* (*H. brevicaude*) in a collection of wasps made in the same trees in a subsequent year (1991, when no behavioral observations were made and no wasps were collected), it is possible that we observed or measured individuals of more than one species of *Heterandrium*. The similar behavior and nearly identical values of measurements of wasps from 1989 and 1990 argue against this possibility, however. Voucher wasp specimens are deposited in the British Museum of Natural History, the US National Museum, and the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.

RESULTS

Behavior in the field

Two small masses of struggling wasps were collected that fell onto the observer's arm high in the tree. Each had a single female surrounded by 3–4 males. One additional pair was collected "in copula", also after they had fallen onto the observer. Females were easily distinguished from males by their long ovipositors. These were

the only observations of females, and the behavioral descriptions that follow concern only males.

Wasps were common on both syconia and nearby leaves. Wasps on leaves seemed to spend most of their time walking, making only occasional short flights. They did not interact with other wasps that they encountered, and flew off immediately when approached by another individual. Walking wasps often moved onto a syconium, but usually left almost immediately. In contrast, some less mobile males remained on a single syconium for periods of up to at least 30 min. All but one of the syconia occupied by these less mobile males were immature; the exception was very mature. Up to five wasps occupied a single syconium; often at least one rested on the lip of the ostiole (the opening at the tip through which new adult wasps emerged), facing the opening.

Males on the same syconium often fought. Typically one individual (the "resident") was nearer the ostiole than the others. When another wasp approached, the resident turned to face him and then moved toward him. On at least 50 occasions the resident opened his wings to make approximately 90° angles with his body and made a short darting movement (less than half a body length) toward the invader while simultaneously performing a short burst of wing vibration. Darting movements may have sometimes included rapidly repeated forward and backward movements, but this detail was not certain. The resident usually only attacked other males when they approached the ostiole. On three different syconia occupied by multiple males, it proved possible to follow the behavior of the "resident" (the individual first seen near the ostiole); the resident consistently initiated and won aggressive encounters.

Usually the wasp being threatened turned and walked away. On more than 20 occasions, however, a male stood his ground, turned toward the resident, and spread his wings as he darted forward; the two combatants darted at each other head-to-head, probably at least sometimes biting each other's antenna (it was not possible to discern this detail directly; it was deduced from antennal damage – see below). The males' wings were directed slightly anteriorly and twisted so that their ventral surfaces were directed anteriorly; the anterior portions of the males' bodies were raised slightly from the substrate. After the two wasps grappled for up to 2–3 sec, one wasp retreated; in one case the loser appeared to be thrown from the surface of the syconium by his opponent.

Mature females (presumably *H. fallax*) emerged in the next 24 hr from one of eight syconia on which at least one male was present in 1989; no females emerged from 33 other syconia that lacked males. Morphologically similar females also emerged from defended syconia in 1990.

The wasps collected on leaves in 1989 did not differ significantly in thorax length from those collected on syconia, but wasps collected on leaves in 1990 were significantly smaller than those collected on syconia (Table 2). Those collected in groups struggling around a female in 1990 were similar in size to those collected on syconia (Table 2).

Antennal damage

Of 62 males collected in 1989, 35% lacked at least one antennal segment; a similar fraction of males collected in 1990 also lacked at least one antennal segment (25% of 143; $\chi^2 = 2.27$, $P = 0.13$). The numbers of missing segments were similar in the

Table 2.

Sizes of male *H. fallax* wasps collected on syconia and leaves in *F. pertusa* trees. We compared these sites with Student *t* Tests for each year. In each case we report: mean (SD, SE, n).

Year	On syconia	On leaves	In groups on a female	*t*
1989	0.75 (0.09, 0.021, 19)	0.76 (0.06, 0.009, 46)		0.28 (*P* = 0.78)
1990	0.77 (0.06, 0.007, 76)	0.71 (0.07, 0.010, 46)	0.77 (0.05, 0.019, 7)	4.48 (*P* = 1.1×10^{-5})
Totals	0.77 (0.07, 0.007, 95)	0.74 (0.07, 0.007, 92)	0.77 (0.05, 0.019, 7)	3.01 (*P* = 0.003)

2 years, averaging 4.2 (SD = 2.7; SE = 0.58; n = 22) per damaged antenna in 1989; and 5.3 (SD = 2.2; SE = 0.37; n = 36) in 1990. Of 57 males with damaged antenna, 18% lacked segments in both antenna. The males collected in 1990 with damaged antenna were larger (mean thorax length = 0.78 mm; SD = 0.06; SE = 0.010; n = 36) than those with undamaged antenna (mean thorax length = 0.74 mm; SD = 0.07; SE = 0.007; n = 107) (t = 2.44, one-tailed P = 0.008). The difference in 1989 was not significant (males with damaged antenna: thorax length = 0.76 mm; SD = 0.08; SE = 0.017; n = 22; males with undamaged antenna: thorax length = 0.75 mm; SD = 0.07; SE = 0.011; n = 40). But when the 2 years were combined, males with antennal damage were slightly larger (thorax length = 0.77 mm; SD = 0.07; SE = 0.009; n = 58) than males without antennal damage (thorax length = 0.75 mm; SD = 0.07; SE = 0.006; n = 147) (t = 2.05, one-tailed P = 0.02). These are relatively small differences (r = 0.06, 0.25, and 0.13 for 1989, 1990, and the 2 years combined, respectively), with males with damaged antenna being on average only 1–5% larger than males with undamaged antenna. However, such small differences in linear measures of body size would be associated with more substantial differences in mass (the cubes of the two thorax lengths for 1990 are 0.474 and 0.405; the smaller is only 85% of the larger), and could have important consequences in fights (Eberhard et al. 2018). There was no significant difference in the likelihood of antennal damage comparing wasps captured on leaves as opposed to those captured on syconia.

Sizes and allometric relations

The sizes of apical and basal spots on male wings showed two trends associated with body size. First, the males that lacked apical spots were relatively small (Figs 2–4); the thorax lengths of males with apical spots (mean = 0.77 mm; SD = 0.06; SE = 0.005; n = 165) were significantly larger than those of males lacking an apical spot (0.65 mm; SD = 0.05; SE = 0.009; n = 31) (t = 17.0, one-tailed P << 0.0001). This is a large linear difference (effect size: r = 0.60), with males having an apical spot being on average 18% larger than males lacking it; the difference in mass would be even larger. Less than half (33%) of the males that lacked an apical spot also lacked a basal spot.

Second, among those males with an apical wing spot, the lengths of both the apical and the basal spot were proportionally larger in larger males. The allometric

Table 3.

Allometric slopes (obtained from log-log ordinary least squares regressions) of different structures in male *Heterandrium fallax* (for each slope estimate: n = 165; all slopes were significantly different from 0 (in all cases $P \ll 0.0001$).

Body size estimate	Trait function	Trait	Slope ± SE	r
Thorax length	Control	Head width	0.61 ± 0.03	0.81
		Gaster length	0.55 ± 0.06	0.56
		Wing length	0.89 ± 0.05	0.80
		Wing width	0.78 ± 0.04	0.79
	Threat	Apical spot length	1.63 ± 0.27	0.43
		Apical spot max. length	1.98 ± 0.46	0.43
		Basal spot length	1.77 ± 0.19	0.64
Head width	Control	Gaster length	0.71 ± 0.08	0.56
		Wing length	1.35 ± 0.04	0.91
		Wing width	1.00 ± 0.05	0.81
		Apical spot length	2.82 ± 0.34	0.54
	Threat	Apical spot max. length	2.87 ± 0.59	0.46
		Basal spot length	2.26 ± 0.26	0.61

slopes of the threat traits (both measures of the apical spot and the basal wing spot) were substantially steeper (mean slope = 1.79; SD = 0.18; SE = 0.10; n = 3 traits) than the slopes of the other "control" traits not thought to be under sexual selection (all slopes < 1.0; mean = 0.71; SD = 0.71; SE = 0.36; n = 4 traits) (Table 3) (1-way ANOVA: $F_{1,5}$ = 74.9, P = 0.0003). This is a large difference (effect size: r = 0.60), with threat traits having on average 2.5-fold steeper slopes than control traits. The difference in slopes remained highly significant when we excluded "total apical spot" from the test to avoid two measures of the same trait ($F_{1,4}$ = 63.6, P = 0.0013). Alternatively, distinguishing three trait types (threat vs wing length vs control traits) also detected a significant difference ($F_{2,4}$ = 59.7, P = 0.0011), but wing length was not distinct from the control traits in a post-hoc Tukey test.

The spots themselves seemed to be paler in some individuals with relatively small spots, but we did not measure this variable.

DISCUSSION

Wing spot function: the "threat device" hypothesis

Several types of evidence support the "threat function" hypothesis that the male wing spots serve exclusively as threats in aggressive interactions between males. Wing-spreading behavior consistently occurred during preliminary aggressive interactions, and the apical wing spots, which generally extended to the tips of the wings (Fig. 2), would make a male's spread wings be more visually obvious to his opponent. Twisting
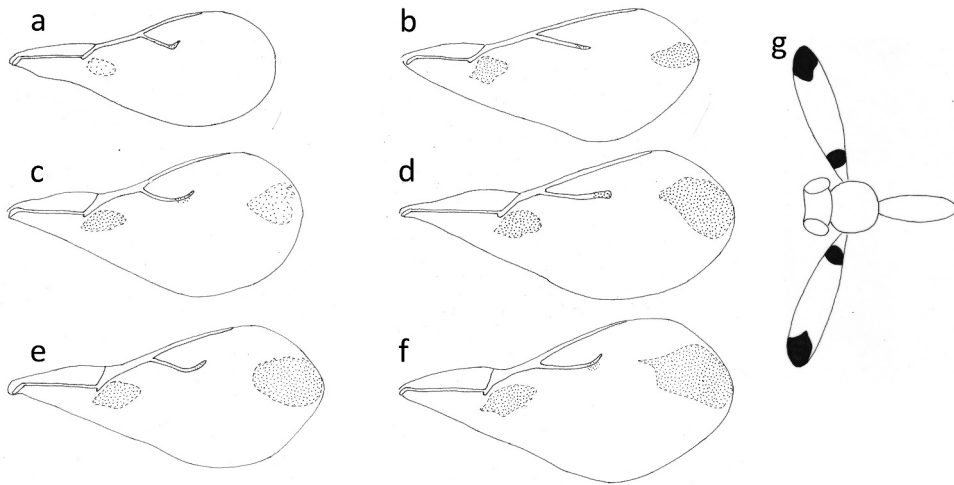
Fig. 2. — A sampler of wing spots in male *Heterandrium fallax*, presented in order of wing size (a) to (f), and a sketch of typical wing positions during an intense threat (g).

the wings so their ventral surfaces were directed toward the opponent (as also occurs during aggressive wing displays in the sepsid fly *Palaeoepsis dentatiformis*; Eberhard 2002) would further increase the rival male's visual perception of the wing spots. Wing length correlated strongly with the thorax length (Table 3), so the distance between the tips of the male's apical spots when he spread his wings would provide a good indication of his size and thus presumably of his fighting ability; selection could thus favor male use of an opponent's apical wing spots to gauge his rival's fighting ability.

The threat hypothesis for wing spot function is also supported by other data: the absence of spots in smaller males; the lower tendency for small males to be found on syconia, where fights occurred; and the lower rate of antennal damage in smaller males. These observations imply that males that fight less often tend to lack spots. The lack of wing spots in females is also in accord with the threat function hypothesis. The widespread damage to male antenna indicates that accurate assessment of a rival male's fighting ability, the presumed function of responding to wing spot stimuli, could be important in avoiding injuries in fights. In sum, several lines of evidence support the threat function hypothesis.

Details of the allometry of the wings and the wing spots suggest additional complexity, however. Wing length did not scale nearly as steeply on thorax length as would have been expected if wing length itself were evolving under sexual selection as an aggressive signal; the slope was sharply lower than that for apical spot length. This argues against the hypothesis that the distance between wing spots is the cue used in aggressive interactions that has favored the steep allometric slopes of apical spots. Perhaps the apical spots originated to emphasize the length of the wing, and subsequently wasps evolved to use the sizes of the spots themselves as cues, leading to selection for proportionately large spots in larger individuals. The fact that in high intensity head-to-head confrontations the males directed their wings slightly anteriorly and tilted them to orient the spots more nearly perpendicular to the rival's sight is in accord with this idea: this position would increase the apparent length and width of

the wing spots as perceived by the rival male. The possibility that greater wing length hinders the male's ability to fly could also have been important in sexual selection altering the spots more than the wing length.

The basal wing spots also showed strong positive allometry, despite their inappropriate design for visually emphasizing the wing's overall length, again suggesting selection on the spots themselves as cues. It is possible, however, that basal spots emphasized the width of the male's body, which would correlate with his overall size and fighting ability. Nothing is known regarding exactly what rival males see during battles, so these ideas are only speculations at the moment.

The observations in this study do not directly address the possibility that the wing spots of male *H. fallax* were used to court females. Males positioned themselves appropriately to intercept females emerging from the ostiole, and all fights occurred near ostioles; but no female was observed emerging in the field. At least on the syconia where multiple males were waiting near the ostiole when the female emerged, such courtship display seems unlikely, because a male would probably have to climb directly onto a female as she emerged to avoid being thwarted by other males. The groups of males found struggling on single females show that multiple-male battles over females occur, and thus also argue against the likelihood of such displays.

The observations of Bronstein (1986) of the behavior of *Heterandrium* sp. (under the name *Aepocerus* sp.) on the same species of tree, *Ficus pertusa*, in Monteverde, Costa Rica may be pertinent. Given the species identity of the tree and the general ecological similarities between the San Antonio and Monteverde sites (Harris 1973), she may have observed the same wasp species. At least five named species of *Heterandrium* occur in Costa Rica (Bouček 1993), however, so this is not certain. Her observations of behavior and morphology closely resemble those described above; she distinguished two male morphs, smaller, "clear-winged" individuals, and larger, "spot-winged" individuals; the spot-winged males appeared to defend fig syconia where females were about to emerge, flashing their wings at each other; and clear-winged individuals seemed to be more likely to occur on leaves and twigs rather than on syconia (no quantitative data were given for any of these differences, however). Bronstein (1986) demonstrated that syconia on which males were present were more likely to contain adult female *H.* sp. (= *Aepocerus* sp.) than were unoccupied syconia. Males of the Old World fig wasp genus *Odontofroggatia* also wait at the ostiole to mate with emerging females (Galil & Copeland 1981).

Allometry of wing spots

The conclusion that wing spots probably function as threat devices (above), combined with the fact that they were not used as weapons (and indeed, they seem physically incapable of inflicting damage) and the low likelihood that they are courtship devices, imply that they are appropriate structures for testing the prediction of the functional allometry hypothesis (Eberhard et al. 2018; Rodríguez & Eberhard 2019) that threat devices will show positive allometry. This prediction was confirmed. Both apical and basal wing spots showed strong positive allometry, with slopes substantially greater than those of control traits (Table 3).
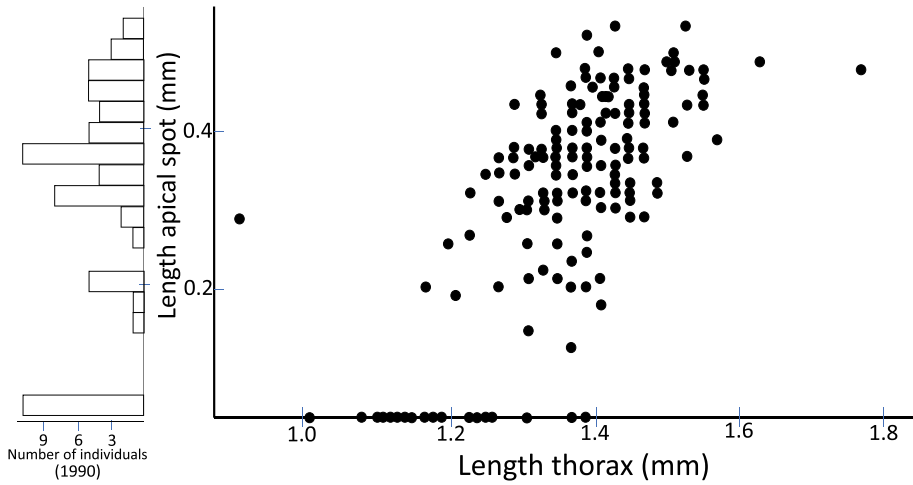
Fig. 3. — Relationship between thorax length and apical wing spot length in 206 male *Heterandrium fallax* (males from 1989 and 1990 combined); the bar graph at the left illustrates the bimodal distribution of apical wing spot lengths. Males lacking an apical wing spot ("0" length) tended to be smaller.
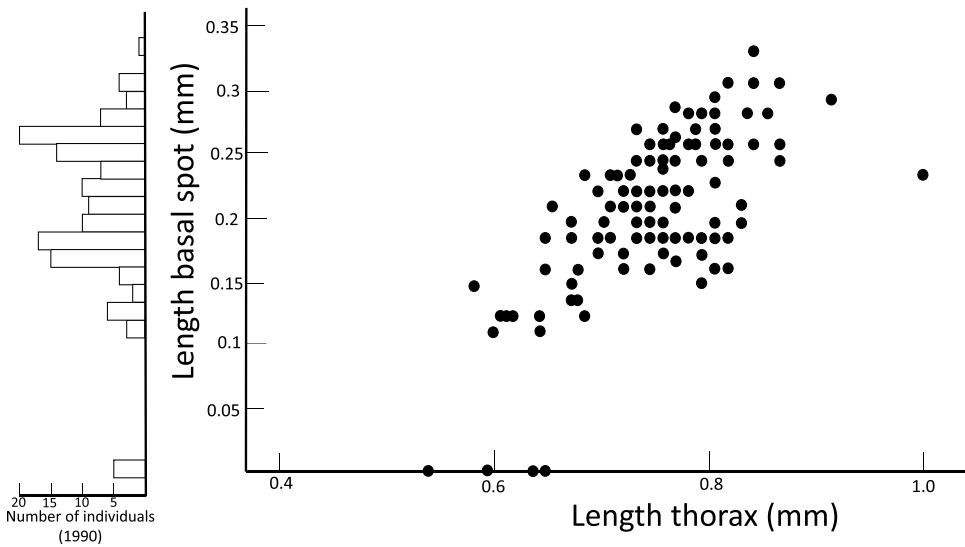

Fig. 4. — Relationship between thorax length and basal wing spot length in 104 male *Heterandrium fallax* males collected in 1990.

Male dimorphism

The bimodal distribution of the sizes of apical spots (graph at the left in Fig. 3), the differences in the sizes of wasps found on syconia vs leaves, and the differences in the antennal damage that probably results from aggressive interactions, indicate

that the differences in wing spots may be associated with behavioral differences. The smaller male morphs in other male-dimorphic insect species also differ behaviorally in being less aggressive or occurring less often at sites where aggression occurs (Eberhard 1982; Thornhill & Alcock 1983; Oliveira et al. 2008; Emlen 2014). The fact that some male *H. fallax* that lacked apical spots nevertheless had basal wing spots indicates, however, that male morphology in this species is not strictly bimodal.

SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at https://doi.org/10.1080/03949370.2021.2024269

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