Armament under direct sexual selection does not exhibit positive allometry in an earwig

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The allometric scaling relationships of armaments and ornaments have been subject to extensive debate. A large body of empirical evidence suggests that sexually selected traits typically exhibit positive static allometry, where the large individuals express proportionally larger traits. Recent theory suggests that this need not be the case. We confirm this prediction using the earwig *Euborellia brunneri* as a model species—unusually, the male armament in this species does not exhibit positive allometry. We experimentally assessed the strength of direct and indirect selection on armament length and morphology and on body size and weight. In a 3-stage experiment, we first permitted females to choose between 2 males and assigned 1 male as the preferred and the other the nonpreferred male. We then allowed the same pair of males to establish a dominance hierarchy in fighting trials. Last, to evaluate the implications of female choice, we conducted mating trials where half the females were mated to their preferred male and half with their nonpreferred male. We found that male armament length and body weight were under direct sexual selection through intrasexual competition. In contrast, female mate preferences did not relate to any measured male trait. Finally, mating behavior was not related to male preference status or armament length. Thus, armament size is sexually selected through intrasexual competition although it does not exhibit positive allometry. Our finding suggests that researchers should be cautious when inferring the absence of sexual selection in traits that do not exhibit positive allometry. 

Key words: allometry, armament, combat, Dermaptera, female choice, sexual selection.

In theory, sexual selection favors exaggeration of ornaments or armaments (sensu Berglund) until opposed by natural selection or other constraints (Darwin 1871; Gould 1989; Andersson 1994). Similarly, sexual selection is thought to affect the scaling relationship that these traits have with body size, usually called the traits’ static allometry (Gould 1966). Generally, sexually selected traits exhibit positive static allometry, where larger, higher quality individuals bear relatively larger traits (Petrie 1988, 1992; Green 1992; and Simmons and Tomkins 1996). This pattern is often explained through the greater marginal fitness returns that high-quality individuals derive when investing in sexually selected traits, for instance, through nonlinear increases in benefits such as signal efficacy (Getty 1998). Larger individuals may also have relatively more resources to invest through lower relative costs of parasitism (Green 1992) or predation (Petrie 1992). Although positive allometry is found in naturally selected traits such as the wing-span in birds (Nudds 2007), this appears to be relatively rare (Eberhard 2002), whereas examples among sexually selected traits are numerous (Kordic-Brown et al. 2006). Indeed, the presence or absence of positive allometry is sometimes considered a means to distinguish between sexually and naturally selected traits (Green 2000).

The close link between sexual selection, trait exaggeration, and allometry is illustrated by a study on the allometry of male earwig forceps, a conspicuous armament under intrasexual (Briceno and Schuch 1988; Moore and Wilson 1993; Forslund 2003) and a signal under intersexual selection (Tomkins and Simmons 1998). Among 42 species, Simmons and Tomkins (1996) found overall positive allometry in forcep length and that the degree of allometry related to the magnitude of trait exaggeration. However, allometric slopes were highly variable, even between congeneric species, and 1 species (*Labidura truncata*) exhibited negative allometry (Simmons and Tomkins 1996). This raises the question about the cause of variability in and deviations from positive allometry. In theory, this may arise either through an absence of sexual selection on the trait or through a failure of sexual selection to bring about a positive allometric relationship. Because the variance appears independent of phylogeny, an explanation relying on constraints is unlikely. An alternative interpretation was proposed by Bonduriansky and Day (2003). Using an allocation trade-off model, they found that sexual selection may in fact produce a range of allometric patterns—including negative allometry—depending on the precise nature of net selection on body and trait sizes. Their theoretical predictions have gained increasing empirical support. For example, Pomfret and Knell (2006) found that strong positive allometry in stag beetle mandible size decreases with increasing body size. Negative allometry is frequently detected in genitalia and claspers and is often explained through stabilizing “one-size-fits-all” sexual selection (Eberhard et al. 1998; Hosken et al. 2005). In some Diptera, legs and laterally expanded heads that have additional functions as weapons or intrasexual signals scale isometrically or exhibit negative allometry (Eberhard 2002; Bonduriansky 2006). Naturally selected functions of sexually selected traits may constrain their exaggeration and limit modification of their scaling relationships.

Here, we confirm that, in contrast to many other earwigs, male armament size in *Euborellia brunneri* does not exhibit positive allometry. Following the traditional paradigm (Green 2000), we would predict that forceps morphology is not subject to sexual selection. We investigate this prediction in 3 ways. First, we assess whether forceps morphology is used as a cue in precopulatory female mate choice. Second, we assess the effect of 3 dimorphic aspects of forceps morphology on outcomes of male–male competition. Last, we determine whether mating behavior is affected by cryptically expressed female preferences or morphology of male forceps.
MATERIALS AND METHODS

Experimental animals came from a captive population at the University of Melbourne, originally sourced and frequently supplemented with animals from a natural population at Point Wilson (Victoria, Australia). All experiments were conducted in February 2006. We used 34 female and 35 male nonvirgin adult E. brunneri that were either field-collected or the offspring of field-collected females. Morphology did not vary with origin (weight: $t = -0.83$, degrees of freedom [df] = 33, $P = 0.41$; forceps’ length: $t = 1.52$, df = 33, $P = 0.14$). Animals were kept at 24–26 °C under a 12:12 light:dark light regime and housed individually in transparent plastic containers (diameter = 6 cm, height = 3.5 cm). They were provided a water-soaked cotton wool ball and ad libitum with dry cat food (Whiskas, Melton Mowbray, UK), which was slightly moistened with a 1% propionic acid solution to inhibit fungal growth. Females had no access to males for at least 1 month prior to experimentation to ensure sperm depletion. Under laboratory conditions, female Euborellia sustain eggs production until death (Lemos et al. 2003).

**Female choice and male–male competition**

To investigate inter- and intrasexual selection on male forceps morphology, we conducted a 2-stage experiment to first determine female mate preferences and then explore male fighting behavior.

We first selected pairs of males matched in participation in any previous trials. These males were then introduced at opposite ends of individual 3-compartment choice arena (Figure 1) separated by a black mesh screen. The screen allows chemical and tactile communication but prevents copulation. Females interact normally with males through the screen and exhibit the natural progression from reciprocal antennation to soliciting copulation by presenting their abdomens. Once both males were behaviorally active, we placed a single female in the center compartment. During 10-min choice trials after introduction, the cumulative amount of time a female spent in direct contact with the mesh screen of each male was recorded. We then used this time to determine his attractiveness to the female. A male was considered preferred if the female spent 50% more time with him than with his competitor. Three trials where no male was preferred were excluded. Two trials in which females spent no time with either male were also excluded. Choice trials were conducted under red light. Between trials, choice arenas were thoroughly cleaned with soapy water and alcohol and then allowed to dry.

We then investigated male intrasexual selection on male forceps morphology by forcing each pair of males to contest a single resource in the form of a small shelter. Immediately after their choice trial, we transferred each pair of males to a plastic container (diameter = 60 mm, height = 35 mm) with a single shelter (20 × 20 mm) constructed from red Perspex and with moist sand at its base. We placed each container under a bright light source to stimulate males to contest for access to the shelter to escape the light. Males quickly resolved exclusive ownership of the shelter through fights. Possession was, on occasion, challenged once but was seldom contested thereafter. Occasionally, males settled ownership prior to discovery of the shelter. In all instances, the occupant of the shelter after 5 min provided a clear and unambiguous measure of dominance.

We conducted 60 trials in total. All females were tested twice and males 4 times, unless excluded because of death or inactivity. We never paired males with familiar rivals or females from previous trials. Females were never related to any of the males they chose between. Individuals were isolated for at least 24 h in the same conditions as above prior to being used in a further trial. To test whether female choice and male–male competition outcomes were nonrandom across males, we compared their frequency distribution with predicted frequencies based on the binomial distribution with equal probabilities of winning and losing. Only males that had participated in 4 trials were considered in this analysis.

**Mating behavior and preference status**

To investigate whether female preference for a particular male was reflected in her mating behavior, after the male–male competition trials, we paired 10 females with their preferred male and 15 females were paired with their nonpreferred male from the female choice trials. Each pair was introduced into a standard culturing container and their behavior recorded every minute for 24 h using time-lapse photography (Logitech QuickCam VC). Euborellia brunneri assume a typical mating position where the male and female are aligned facing opposite directions with contact between male and female subgenital plates. Copulation in E. brunneri is relatively short (median: 9.0 min, 95% confidence interval: 2.0–84.1 min). Thus, to reduce the possibility of scoring failed copulation attempts, the pair was defined as copulating when 2 subsequent images showed the pair in the copulation position. This procedure did not bias the results (single-image matings: preferred males = 90/400; nonpreferred males = 53/245; $\chi^2 = 2.33$, $P = 0.12$). An independent observer, unaware of the mating treatment, scored the number and duration of copulations for each pair from the resulting images. One male in each treatment group died during the mating trials, and both were partially cannibalized. These trials were excluded from further analysis.

**Analysis**

**Allometry**

We used Huxley’s (1932) power function, $y = bx^a$, where $x$ represents body size and $y$ trait size, to express the scaling relationship of forceps size and other traits included in the models below. Trait allometry was quantified by deriving exponent $a$ by regressing the natural logarithm of the size of each trait against the natural logarithm of body size and obtaining the slope. Maximum thoracic width was preferred over weight as an index of body size as it is invariant after eclosion, and its measurement and unit are similar to those of forceps length. Body weight, measured prior to experimentation, was also cube root transformed to match thoracic width in dimensionality. For consistency with existing literature, slopes were...
Selection on morphology of forceps

In the analysis of fighting outcomes and female preferences, we included 3 aspects of male forceps morphology that define their sexual dimorphism: length, curvature, and asymmetry. After experimentation, animals were frozen and kept in 70% ethanol. All traits were measured from digital photos (camera: Moticam 480, Motic China Group Co. Ltd, Xiamen, China; software: ImageJ 1.37). For imaging, we partially emulated objects in putty to control the plane photographed. Forceps’ length was measured over the lateral arc as the distance between 2 landmarks at the apex and base of each forcep (Figure 2) after dissection. The measurement was taken after digitally straightening the arch in photos (“straighten curved objects” plugin: Kocsis et al. 1991). Curvature was calculated by taking the ratio between forceps length and diagonal length (Figure 2). As male forceps in E. branneri exhibit consistent directional asymmetry (see below), length and curvature were measured for right and left forceps. All measurements were repeatable (right forceps length: 0.98; left forceps length: 0.93; right diagonal length: 0.98; left diagonal length: 0.94; thoracic width: 0.81; for all, N = 15 males, P < 0.05) (Lessells and Boag 1987). Asymmetry was expressed as both the differences between right and left forceps length and right and left curvature. Principal component analysis was performed to reduce dimensionality (SPSS version 12.0.0). This analysis explained more than 90% of the total variation and yielded 3 components with eigenvalues exceeding 1 that related to asymmetry, length, and curvature.

In addition to these 3 orthogonal variables, we included a fixed and a condition-dependent measure of body size: maximum thoracic width and body weight prior to experimentation. Weight was measured prior to experimentation on a balance (Mettler Toledo Inc., Greifensee, Switzerland) to 0.01 mg and was cube root transformed to match other variables in dimensionality. Analyses were conducted with relative data for 1 randomly chosen male from each pair.

To measure selection on forceps morphology and other traits, we employed models for cross-sectional multivariate selection on correlated traits (Lande and Arnold 1983) as adapted for binary data by Janzen and Stern (1998). This approach determines whether selection on a trait is direct or indirect through correlation with other traits. Our choice of variables allowed us to attribute indirect selection on body size to forceps characters or vice versa while retaining resolution between forceps characters. We employed generalized linear mixed models with logit link function in GenStat (version 10.1.0.72) to analyze the likelihood of winning choice and competition trials. To account for reuse of individuals, female identity was included as a random term in the analysis of female choice and male identity was similarly included in analyses of both choice and competition outcomes. The partial regression coefficients from these analyses correspond to logistic selection coefficients α, which describe only direct selection on a trait. The observed selection differentials s, products of both direct and indirect selection on traits, were obtained through multiplication of the phenotypic covariance matrix with the vector of approximated linear selection gradients, which in turn are calculated by correcting logistic selection coefficients using average gradient of the estimated selection surface (for details on the method, see Janzen and Stern 1998). All original variables, and hence resultant coefficients and errors, were standardized.

We tested the effect of preference status and male body size and forceps traits on 2 aspects of mating behavior. Cumulative copulation duration and copulation count were analyzed using general linear method with male preference status as a factor and the above male morphological characters as covariates. Reduced models, where terms with probabilities greater than 0.1 were sequentially dropped, are presented to avoid collinearity.

RESULTS

Morphology and allometry

As is typical with earwigs, females were larger than males. The degree of sexual size dimorphism (SSD) in our experimental animals was 14% for thoracic width (male: 1.76 ± 0.02 mm; female: 2.00 ± 0.02 mm; F_{1,73} = 74.19, P < 0.001). Females weighed 52% more than males (male: 41.15 ± 1.39 mg; female: 62.86 ± 2.25 mg; F_{1,66} = 66.44, P < 0.001). Male forceps were asymmetric, both in length (right: x ± standard error [SE] = 2.66 ± 0.03 mm; left: 2.46 ± 0.19 mm; F_{1,68} = 17.72, P < 0.001) and curvature (right: 1.23 ± 0.03; left: 1.16 ± 0.03; F_{1,68} = 144.94, P < 0.001). Male forceps length exhibits relatively little variation (coefficient of variation, right: 7.4%; left: 8.7%) and is unimodally normally distributed (Kolmogorov–Smirnov test, right: Z = 0.633, P = 0.82; left: Z = 0.71, P = 0.70).

Male forceps length exhibited either negative allometry or isometry depending on the regression model used (Figure 3, Table 1). A similar pattern emerged for the cube root of body weight (Table 1). Regressions of right and left forceps...
Female choice and male–male competition

The distribution of male performances over consecutive choice trials did not differ from a predicted distribution where probabilities of winning or losing were equal (chi-square test: $\chi^2 = 0.886, P = 0.93$; Table 2). In contrast, the distribution of outcomes of subsequent fighting trials was nonrandom (chi-square test: $\chi^2 = 18.58, P < 0.001$; Table 2), with consistent winners and losers overrepresented. We determined, for each trial, whether the outcomes for female mate choice and male competition corresponded. There was no consistency between the outcome of choice and competition trials (32 corresponding vs. 22 conflicting; $\chi^2 = 1.85, P = 0.17$). When limiting the comparison to cases where females had visited both males, to ensure an informed choice, this pattern persisted (22 corresponding vs. 12 conflicting; $\chi^2 = 2.94, P = 0.09$).

Table 1

<table>
<thead>
<tr>
<th>Trait</th>
<th>OLS slope</th>
<th>RMA slope</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forcipe length</td>
<td>Right</td>
<td>0.91 ± 0.09, NS</td>
<td>1.14, NS</td>
</tr>
<tr>
<td></td>
<td>Left</td>
<td>0.76 ± 0.09$^*$</td>
<td>1.03, NS</td>
</tr>
<tr>
<td>Forcipe curvature</td>
<td>Right</td>
<td>$-0.08 ± 0.06$**</td>
<td>0.25$^*$</td>
</tr>
<tr>
<td></td>
<td>Left</td>
<td>$-0.16 ± 0.06$**</td>
<td>0.31$^*$</td>
</tr>
<tr>
<td>Forcipe asymmetry</td>
<td>Length</td>
<td>0.15 ± 0.06$^*$</td>
<td>0.52$^*$</td>
</tr>
<tr>
<td></td>
<td>Curvature</td>
<td>$0.08 ± 0.06$**</td>
<td>0.37$^*$</td>
</tr>
<tr>
<td>Weight$^{1/3}$</td>
<td></td>
<td>0.60 ± 0.13$^*$</td>
<td>0.95, NS</td>
</tr>
</tbody>
</table>

Slopes were calculated on loge transformed variables using least squares (OLS) regression and RMA regression. Slopes were tested against isometry. NS, not significant.

* Significance tested following Warton et al. (2006).

** Significant at the 0.05 level.

DISCUSSION

Our data suggest that male armament size is under direct sexual selection in E. brunneri but that it does not exhibit the characteristics often considered typical for such traits. Male forcep length did not exhibit positive allometry and displayed relatively little variation for a sexually selected trait (Alatalo et al. 1988; Pomiankowski and Møller 1995). The level of exaggeration of forcep length in male E. brunneri is relatively small for earwigs, and it falls well below the interspecific allometric regression line for this taxon (Simmons and Tomkins 1996) despite the fact that there is direct selection for greater forcep length through male–male competition. These findings appear paradoxical in light of traditional views on the effect of sexual selection on trait allometry (Green 1992; Petrie 1992; Kodric-Brown et al. 2006).

Earwig forceps provide a classic example of a conspicuous armament that generally exhibits positive allometry (Simmons and Tomkins 1996). During fights, males face away from each other and use their forceps to try to pinch their rival or establish a lock around their abdomen. Larger forceps may promote establishing a lock or facilitate locking larger rivals. The role of the forceps in E. brunneri, like those of many antlers
Table 2

Observed and predicted frequency distributions of males over the 5 possible outcomes of 4 consecutive male–male competition and female choice trials

<table>
<thead>
<tr>
<th>Outcome</th>
<th>Female choice</th>
<th>Male competition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Predicted</td>
</tr>
<tr>
<td>Won all 4</td>
<td>2</td>
<td>1.25</td>
</tr>
<tr>
<td>3 wins–1 loss</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>2 wins–2 losses</td>
<td>9</td>
<td>7.5</td>
</tr>
<tr>
<td>1 win–3 losses</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Lost all 4</td>
<td>1</td>
<td>1.25</td>
</tr>
</tbody>
</table>

and horns, may not be limited to a sexual context. In addition, forceps may have a range of naturally selected uses, including defense against predators (Eisner 1960) and foraging (Bennett 1904), which each may influence the morphology and allometry. Exactly why further elaboration of forceps is limited in male E. brunneri is unknown.

Forceps morphology in E. brunneri is relatively simple. More complex, nonlinear allometric patterns, like sigmoid or discontinuous scaling, occur in a number of earwig species (Emlen and Nijhout 2000). For example, in some populations, Forficula auricularia exhibits a male dimorphism in forcep length (Bateson and Brindley 1892) associated with alternative reproductive strategies and selection regimes (Forslund 2003). Whereas F. auricularia is gregarious and experiences relatively high encounter rates (Tomkins and Brown 2004), Euborellia is nongregarious (Sauphanor and Sureau 1993), and adults in our source population are rarely found in groups greater than 3 (van Lieshout E, unpublished data). Group size affects allometry in other taxa, for instance, male horn length among bovid species (Bro-Jørgensen 2007). Low interaction rates reduce the occurrence of male–male competition and may hence limit further elaboration of weapons if they confer a cost to their bearer (e.g., stag beetle mandibles, Knell et al. 2004).

Considering the advantage of larger forceps for combatant males, selection may favor females to prefer this trait. However, forceps’ length did not affect either precopulatory between-male choice or subsequent decisions about mating duration and frequency with particular males. These results provide an interesting contrast to those of F. auricularia (Tomkins and Simmons 1998), where males with elongated forceps were more likely to gain copulations. Female E. brunneri may be unable to detect any differences between males in forcep size due to a lack of sufficient variation. Forcep length in male F. auricularia exhibits greater variation (Forslund 2000) and a male dimorphism (Bateson and Brindley 1892). The lack of correspondence between choice and competition outcomes may alternatively be explained through redundancy of intersexual selection in the face of strong intrasexual selection. Although structures with a dual function are frequently reported (Berglund et al. 1996), an effective male competitive process can eliminate the need for females to express preferences with regard to armaments (e.g., lekking or scramble competition systems) or deny females’ choice among its losers (Wong and Candolin 2005). Finally, costs to females’ fitness associated with male dominance may annul its benefits and associated preferences (Qvarnström and Forsgren 1998). No such costs in earwigs have been identified. Persistent suitors are occasionally cannibalized by female E. brunneri, and neither dominant nor subordinate males provide parental care (van Lieshout E, personal observation).

Our analysis showed that, although no other dimorphic aspects of forceps morphology experienced direct, precopulatory selection, forcep curvature underwent negative indirect selection. Because the variables describing forceps traits were orthogonal, this must be due to correlated selection with body weight. Interestingly, males with lesser forcep curvature mated for longer and more frequently, presumably providing a fertilization advantage. Female cooperation is required to initiate copulation in earwigs (Radesater and Halldorsdottir 1993a), and females also control termination by simply walking away (van Lieshout E, personal observation). If patterns of copulation are indeed female driven, it suggests that females use curvature as a cue to derive information about males. Typically, on introduction, a male and a female antennate reciprocally. The male then turns around and draws closer to engage copulation. The female may briefly antennate the male forceps now facing her before either turning around to establish a coupling or walking away. During copulation, the forceps are not used. Greater curvature of forceps in males is ubiquitous among Forficulina, even in more “primitive” genera (e.g., Echinodesmus, Giles 1963), and appears an adaptation for the role of forceps in male intrasexual competition. However, the effect of curvature on other fitness components and potential trade-offs with fighting success remain to be investigated.

Table 3

Standardized directional selection differentials (s) and logistic selection gradients (β ± SE) and associated statistics for 5 male traits in male–male competition and female mate choice experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Character</th>
<th>s</th>
<th>β ± SE</th>
<th>Wald</th>
<th>df</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male competition</td>
<td>Forcep asymmetry</td>
<td>−0.03</td>
<td>0.25 ± 0.29</td>
<td>0.74</td>
<td>1</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Forcep length</td>
<td>0.69*</td>
<td>1.03 ± 0.41</td>
<td>6.24</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Forcep curvature</td>
<td>−0.36</td>
<td>−0.32 ± 0.35</td>
<td>0.81</td>
<td>1</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>Thoracic width</td>
<td>0.44*</td>
<td>−0.77 ± 0.42</td>
<td>3.40</td>
<td>1</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Weight</td>
<td>0.72*</td>
<td>1.31 ± 0.52</td>
<td>6.36</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Female mate choice</td>
<td>Forcep asymmetry</td>
<td>−0.30</td>
<td>−0.29 ± 0.26</td>
<td>1.30</td>
<td>1</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Forcep length</td>
<td>0.23</td>
<td>0.33 ± 0.31</td>
<td>1.15</td>
<td>1</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>Forcep curvature</td>
<td>0.15</td>
<td>0.11 ± 0.28</td>
<td>0.16</td>
<td>1</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Thoracic width</td>
<td>−0.06</td>
<td>−0.10 ± 0.32</td>
<td>0.09</td>
<td>1</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Weight</td>
<td>0.02</td>
<td>−0.08 ± 0.37</td>
<td>0.04</td>
<td>1</td>
<td>0.83</td>
</tr>
</tbody>
</table>

All variables are relative values, where loge transformed and weight was cube root transformed.

* Significance tested using Spearman rank correlations of relative fitness with the traits, Holm–Bonferroni corrected.

** Significant at the 0.05 level.

*** Significant at the 0.001 level.
Our results show precopulatory mate preferences to be inconsistent among females. This result is unlikely to be due to our experimental design as females exhibited normal assessment and solicitation behavior toward males in the female choice experiment. Instead, female preferences could be individual, for instance, based on genetic complementariness (Landry et al. 2001). However, because male preference status did not influence subsequent mating behavior, it appears more likely that the role of precopulatory female mate choice is limited. Females may instead exert “indirect choice” by relying on male intrasexual competition if dominance is the measure of male quality (Wong and Candolin 2005) or may express preferences during or after copulation. The latter option seems plausible given the elaborate structure of the spermatheca within the genus (Kamimura 2000).

More strongly than forcep length, relative body weight affected the outcome of male–male competition. Green (1992) suggested that the balance between selection on body and trait sizes determines the resultant scaling relationship. However, central to any nonisometric scaling relationship is the differential fitness payoff of investment based on relative body size. The trade-off model of Bonduriansky and Day (2003) specifies a more complex interactive relationship between selection on body size and armaments, which incorporates viability selection, that dictates the manner of scaling.

Despite the selection for greater body weight in males, we showed that *E. brunneri* exhibit a pronounced female-biased SSD in body weight. This paradox is not uncommon in invertebrates (e.g., Farshad and Crompton 1981) and also occurs in vertebrates (e.g., Stuart-Smith et al. 2007). What ultimately maintains relatively small male size in *E. brunneri* is unclear. Balancing selection may come from a host of costs associated with large male body size (Blanckenhorn 2000). In *F. auricularia*, it has been suggested that smaller males may emerge earlier due to reduced developmental time (Radesater and Halldorsdottir 1993b), presumably conferring a benefit in scramble competition.

This study is not the first to demonstrate that sexually selected characters need not exhibit positive allometry. Although the great number of cases of negative allometry in genitalia are explained through stabilizing one-size-fits-all selection (Eberhard et al. 1998), Bertin and Fairbairn (2007) showed that these patterns can exist despite directional sexual selection. House and Simmons (2003) suggested that the amount of variation in traits under directional sexual selection, the principle determinant of allometric slopes, may be limited by natural selection. Such constraints potentially explain the absence of positive allometry in sexually selected traits that serve locomotion or other naturally selected functions (e.g., leg length, head dimensions, and antenna length: Eberhard 2002; Bonduriansky 2006; ornamental feather size: Cuervo and Møller 2001). This study illustrates a case where a conspicuous armament, which generally exhibits positive allometry and ample variation in related species, fails to conform despite direct sexual selection. Future studies of armament or ornament allometry would benefit from determining net selection by assessing viability consequences of investment.

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