



Is allometry of sexual traits adaptive? A field test with territorial damselflies

RAFAEL BELLO-BEDOY¹, ISAAC GONZÁLEZ-SANTOYO²,
MARTÍN ALEJANDRO SERRANO-MENESES³, DAVID VRECH⁴, MIGUEL RIVAS²,
ROBERTO MUNGUÍA-STEYER^{5*} and ALEX CÓRDOBA-AGUILAR^{2**}

¹Facultad de Ciencias, Universidad Autónoma de Baja California, Km. 103 Carretera Tijuana – Ensenada, Pedregal Playitas, 22860 Ensenada, Baja California, Mexico

²Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. Postal 70-275, Ciudad Universitaria, 04510, Mexico, D.F., Mexico

³Laboratorio de Biología Evolutiva, Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-Puebla Km. 1.5, 90062, Tlaxcala, Mexico

⁴Laboratorio de Biología Reproductiva y Evolución, Cátedra de Diversidad Animal, Departamento de Ecología y Diversidad I, Universidad Nacional de Córdoba, Vélez Sarsfield 299 (5000), Córdoba, Argentina

⁵Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes de Iztacala, 54090, Tlalnepantla, Estado de México, Mexico

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Recent studies have linked static allometry of sexual traits to selective advantages, in terms of sexual selection. An underlying, yet untested, assumption is that the allometry of sexual traits confers higher mating success and/or survival. Here, we investigated whether the allometry of two sexual traits is related to male mating success and survival in two species of damselflies: wing size in *Paraphlebia zoe* and the red-pigmented wing spot in *Hetaerina americana*. We used large field-based data sets of marked-recaptured animals, in which we recorded male mating success and survival. Both sexual traits exhibited hyperallometric patterns; however, allometry was not linked to either mating success or survival. These results indicate that, at least during the period of sexual competition, allometry does not seem to be adaptive. Although our results may only apply to our damselfly study subjects (which nevertheless would require further tests in different seasons and/or study sites), our findings should encourage researchers to evaluate at least whether the assumed adaptiveness of sexual trait allometry holds for their study animals. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, ●●, ●●–●●.

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INTRODUCTION

The evolution of sexual traits is the result of both sexual and natural selective pressures (Hall, 2011). Knowledge of the relative contribution of these forces in shaping sexual traits has remained central in evolutionary studies. According to an indicators

mechanisms hypothesis, it is expected that if sexual traits are indicators of condition (thereby correlating positively with survival), the expression of such traits will be favoured via mating competition success, up to a point where viability costs constrain their further evolution (Endler, 1986; Breed & Moore, 2012).

Given that sexual traits often exhibit allometric patterns, researchers of the area usually estimate the static allometry (i.e. the relative growth of a trait in relation to body size across individuals of the same species, in the same life stage) of such traits (e.g.

*Corresponding author. E-mail: rmunguia.steyer@gmail.com

**Corresponding author.

E-mail: acordoba@ieecologia.unam.mx

Bonduriansky, 2007; Eberhard, Rodriguez & Polihronakis, 2009). The emerging results of such studies show that hyperallometry (e.g. the case of extremely elaborated ornaments; e.g. Kodric-Brown, Sibly & Brown, 2006) and hypo-allometry (i.e. the case of genital traits; e.g. Eberhard *et al.*, 1998) are more common in nature than are isometric patterns (see the arguments against this rationale in Bonduriansky, 2007). These resulting allometric patterns have been widely discussed and modelled in terms of resource-allocation trade-offs (e.g. Bonduriansky & Day, 2003; Lindström, Metcalfe & Royle, 2005; Kodric-Brown *et al.*, 2006). Organisms are expected to show a particular type of sexual-trait allometry, given certain fitness pay-offs (e.g. Green, 1992). Nonetheless, independently of whatever allometric pattern arises and its explanation, the underlying assumption is that a particular allometric pattern is linked to fitness.

According to this, one would expect, for example, that whatever the allometric pattern of a sexual trait, it would be favoured via mating success and/or survival and counterbalanced by the survival costs imposed on extremely elaborated phenotypes. Attempts to test this are scarce and mainly limited to correlates between sexual trait allometry and mating success (e.g. LeBas, Hockham & Ritchie, 2004; Yang & Wang, 2004; Harvey & Gange, 2006; Herrell *et al.*, 2010) but with no attempt to relate the allometry of sexual traits to survival. Why are these attempts important? If the allometry of a sexual trait does not show a relationship with either mating success or survival, the findings of other previous studies could then be interpreted as patterns of morphological correlates that may not necessarily be adaptive.

Here, we investigated a link between sexual trait allometry and mating success and survival. To this end we used two species of territorial damselflies and correlated their sexual traits with mating success and survival: wing size for *Paraphlebia zoe* and a red pigmented wing spot in *Hetaerina americana*. For *P. zoe*, despite previous analyses (Romo-Beltrán, Macías-Ordóñez & Córdoba-Aguilar, 2009), we here provide evidence suggesting that wing size is a predictor of mating success for males and therefore such a trait is treated here as sexually selected. For *H. americana*, male mating success is explained by the size of a red spot located on the wing bases of adult males (Grether, 1996; Serrano-Meneses *et al.*, 2007). Thus, by tracking marked animals in the field, we aimed to answer the question: is the allometry of wing length of *P. zoe* and/or wing spot of *H. americana* related to male mating success and survival? Our findings are discussed in the light of recent analyses of sexual trait allometry and sexual selection.

MATERIAL AND METHODS

STUDY SPECIES

Similarly to other odonates, *P. zoe* and *H. americana* spend their first life stage as larvae, after which they emerge as adults. The newly emerged adult will have its sexual traits fully fixed after a few minutes, which is the case for wing size in *P. zoe*, or after a week, which is the case for wing spot in *H. americana* (A. Córdoba-Aguilar's unpubl. data; also see Córdoba-Aguilar, 1993 for supporting evidence in a sister species, *Hetaerina cruentata*). After several weeks, males will then compete for matings (all authors' unpubl. data). *Paraphlebia zoe* exhibits two alternative male phenotypes: black-winged and hyaline-winged (henceforth referred to as black males and hyaline males, respectively; Romo-Beltrán *et al.*, 2009). Black-winged males are more likely to defend territories, have a larger body size and wing length, and a higher thoracic muscular fat-mass volume than hyaline-winged males (Romo-Beltrán *et al.*, 2009; Munguía-Steyer, Córdoba-Aguilar & Romo-Beltrán, 2010). *Hetaerina americana* males also show alternative mating tactics, which are dependent on the male condition (which is, in turn, reflected on the size of the wing spot) (Grether, 1996; Contreras-Garduño, Lanz-Mendoza & Córdoba-Aguilar, 2007; Serrano-Meneses *et al.*, 2007): territorial males tend to exhibit larger wing spot sizes, higher fat reserves, and higher mass volume than nonterritorial males (Contreras-Garduño *et al.*, 2007; Serrano-Meneses *et al.*, 2007).

DATA COLLECTION

Marking, morphometrics, and determination of mating success in P. zoe

Paraphlebia zoe was studied in Teocelo, Veracruz, Mexico (19°40'42" N, 96°98'28" W) from 7 May to 15 October, 2010. Although we used the data set of Romo-Beltrán *et al.* (2009) for survival estimates (see the next subsection), we had to have a different data set for mating success because wing size and male morph frequency change as the mating season progresses (all authors' unpubl. data) and this was not considered by Romo-Beltrán *et al.* (2009). Marking was carried out by two people who recorded male morph, forewing and body size, and date of capture. Measurements were taken to the nearest 0.01 mm using a digital vernier. Forewing was measured from its insertion to the thorax to the distal region, whereas body size was taken from the head tip to the end of the abdomen. After marking, the animals were immediately returned to their original capture sites. In total, 168 black males and 72 hyaline males were marked. Focal observations by two observers on

randomly selected males were carried out from 10:00 to 14:00 h. The duration of each focal observation was 30 min. In these observations, we registered the identity of males, male morph, number of copulations, and date of observation.

Estimation of survival rates in P. zoe

Field work was carried out in the same location where mating success was recorded but from 17 May to 3 September, 2004, which is the data base used by Romo-Beltrán *et al.* (2009). Individual adult males and females were marked by two people on a daily basis with a visible three-digit number on the left forewing using an indelible black marker. After marking, the animals were immediately returned to their original capture sites. During marking, the right forewing and total body length were measured to the nearest 0.01 mm using a digital vernier. Forewing and body size were measured as indicated for mating success in 2010. The marked population was monitored via 43 mark–recapture sampling sessions (each session was carried out on a different day) during the entire field season. Time intervals between sampling sessions were usually 2 days (30 sessions) although on some occasions there were 3- (four times), 4- (three times), and 5- (five times) day intervals. Such irregularity was caused by rain. In such weather, the animals perch in inaccessible sites (e.g. treetops) where they cannot be detected or their individual numbers cannot be recorded. We marked 191 individuals, of which 79 were female, 66 were hyaline males, and 125 were black males. Of animals that were recaptured at least once, 33.48% were females, 59.06% were black males, and 42.42% were hyaline males.

Marking, morphometrics, and determination of mating success in H. americana

Fieldwork was carried out in Tehuixtla, Morelos, Mexico (18°32'56" N, 99°16'23" W) from 12 November 2003 to 27 February 2004. In total, 239 animals were marked on a daily basis with an indelible black marker on the right forewing using an individual combination of three digits. Such identification was readable at a distance of several metres using binoculars. During marking by two people, a digital vernier was used to measure body length (from the head to the tip of the abdomen) and wing length (right forewing, from the site of insertion to the thorax to the distal tip). As well as marking and measuring, a photograph of their four wings was obtained at a constant distance using a digital camera (Olympus 765 UZ). These photographs were used to obtain an average measurement of the area of the wing that the spot covered. To this end, spot and wing areas were estimated using ImageJ 1.34 s (National

Institutes of Health, <http://imagej.nih.gov/ij/>). After marking, the animals were immediately released in their original capture sites. Male behaviour (of either territorial or nonterritorial males) was recorded daily between 10:00 h and 15:00 h by two observers. Each male was observed for 15 min by scan sampling in which we recorded copulation occurrence. It has been shown that this time duration gives reliable information about mating success in this species (Serrano-Meneses *et al.*, 2007) and in others of the same genus (Córdoba-Aguilar *et al.*, 2009). Although it is likely that we missed a number of matings, the fact that our mating-success data resemble those of the same (and also related) species, despite being recorded at a different time (i.e. Córdoba-Aguilar *et al.*, 2009), provides indirect evidence that our data are reliable.

Estimation of survival rates in H. americana

To estimate survival rates we observed a population located in the Tetlama river, Morelos, Mexico (18°45'55" N, 99°14'45" W), from 25 September to 28 December, 2010, with daily visits. Males were marked by two people using an individual three-digit combination written on their right forewing with a permanent black marker. Along with marking, the animals were measured (wing spot, same as described above, and wing length) and photographed using a digital camera (Nikon P90 24x). Wing spot area was measured using Adobe Photoshop (version CS2; Adobe Systems Incorporated). This area was then transformed in terms of its percentage area in relation to total wing area. After marking, animals were immediately returned to their original capture sites. In total, 59 individuals were captured and marked, and 46 were recaptured.

STATISTICAL ANALYSIS

P. zoe: mating success and wing length in relation to seasonal date

Using the data from the second season (2010), we investigated whether mating success could be explained by male wing length, by considering season effects as another predictive factor (entered as Julian date). We used a generalized linear mixed model (GLMM) for binomial data (mated = 1, not mated = 0), in which we entered size, male morph, date, and the interaction and male morph × season date as predictor variables, and individual identity as a random variable. This GLMM allowed us to combine the properties of two statistical frameworks: random components and data with binomial distribution. This analysis was carried out in R software lme4 (R Core Development Team, 2012, version 2.15.1).

P. zoe: wing length allometric patterns, mating success, and survival

To detect allometry in the wing length of hyaline and pigmented males in relation to body size (in this case, total body length), we performed model II regressions, specifically three major axis regressions. These regressions are preferred over traditional ordinal least square regressions given that the two morphometric variables are not controlled by us (Warton *et al.*, 2006).

In order to assess whether wing size allometry was linked to the probability of mating, we performed a logistic analysis of covariance (ANCOVA) on the binomial variable of individual mate incidence (mated = 1, not mated = 0) and a covariance on the continuous variable, individual number of mates per male. Both models included mating success (as either a discrete or a continuous variable) as a function of male morph (black or hyaline males), body size/wing length, and the morph type \times body size/wing length interaction. All analyses included the total number of marked males in the study.

We estimated survival parameters for black and hyaline males considering male morph, body length, wing length, and their interactions as predictors. Survival (ϕ) and recapture (p) estimates can be dissociated by maximum likelihood methods from the sequential history of encounters for each individual along time, using capture–recapture models (Lebreton *et al.*, 1992; Williams, Nichols & Conroy, 2002). In our analyses, Cormack–Jolly–Seber (CJS) capture–recapture models included different combinations of the predictor variables for survival and recapture parameters. Goodness of fit was tested, performing 1000 parametric bootstraps in the global model $\phi_{(g+t)} p_{(g+t)}$, by estimating the variance inflation factor (\hat{c}) and dividing the observed deviance by the mean simulated deviance. This model did not include phenotypic characters because suitable tests for models that include individual covariates have not been developed. We performed model selection, ranking the models using the Akaike Information Criterion (AIC) corrected for overdispersion, because the global model $\phi(\text{group} + \text{time}) p(\text{group} + \text{time})$ presented an overdispersion (1.49) far from structural problems (Lebreton *et al.*, 1992).

H. americana: wing spot allometry and its relationship with mating success and survival

To assess whether wing size and wing spot allometry are linked to the probability of mating, we performed generalized linear models with a Poisson distribution. The predictor variables were wing spot area, wing area, and their interaction, and, as a response variable, the number of matings recorded for each male. We performed model selection, assessed the relative

support of the models with different combinations of predictor variables, and used the AIC to rank the support of each model.

We assessed the impact of wing length, the percentage of wing area that covered the wing spot, and their interaction, on survival and recapture probabilities using CJS. Goodness of fit was assessed performing 1000 bootstraps in the global model $\phi(\text{time}) p(\text{time})$ that considers temporal variation in survival and recapture probabilities. We found a slight overdispersion (1.07) and consequently we employed the AIC corrected for overdispersion when performing model selection in the set of candidate models that considered different combinations of predictor variables (Johnson & Omland, 2004).

RESULTS

P. ZOE: MATING SUCCESS AND WING LENGTH IN RELATION TO SEASONAL TIME

Mating success was explained by size (the larger the male, the higher his mating probability), male morph (black males were more likely to mate than hyaline males), and the interaction male morph \times season date (mating probability tends to decrease with season but the effects were different for both morphs: black males were less likely to mate at the end of the season compared with hyaline males) (Table 1).

P. ZOE: WING LENGTH ALLOMETRIC PATTERNS, MATING SUCCESS, AND SURVIVAL

Allometric coefficients indicated hyperallometry: black males $\beta = 1.683$ ($P < 0.001$; 95% CI: 1.379–2.103); and hyaline males $\beta = 1.334$ ($P < 0.001$; 95% CI: 1.051–1.724). Hyperallometry had a marginally nonsignificant effect on mating occurrence [$\chi^2_{\text{Likelihood ratio test}} = 3.65$, degrees of freedom (d.f.) = 1, $P = 0.056$; $N = 239$] and mating success (ANCOVA, $F = 0.350$, d.f. = 1, $P = 0.090$; $N = 239$). Neither male morph \times allometry nor male type \times allometry interactions had a significant effect on mating occurrence (male morph:

Table 1. General linear model of mating success as a function of wing size, male morph, season date, and morph \times season date for *Paraphlebia zoe* males

	Estimate	SE	<i>P</i>
Intercept	−5.483	2.821	0.051
Wing size	1.543	0.739	0.036
Male morph	−2.996	1.031	0.003
Season date	−0.014	0.009	0.120
Male morph \times season date	0.0259	0.009	0.007

SE, standard error.

Table 2. Model selection for effects on survival and recapture probabilities according to time (t), body length (b), wing length (w), group identity (male morph; hyaline or pigmented males), and their interactions, in the damselfly, *Paraphlebia zoe*

Model description					
Survival	Recapture	QAIC	QAIC weight	Par.	Deviance
$\phi(\cdot)$	$p(g + w + g:w + t)$	1428.78	0.429	43	1338.17
$\phi(g)$	$p(g + w + g:w + t)$	1429.03	0.419	44	1335.99
$\phi(g + b + g:b)$	$p(g + w + g:w + t)$	1432.05	0.092	46	1334.54
$\phi(g + w + g:w)$	$p(g + w + g:w + t)$	1433.24	0.051	49	1332.47
$\phi(g)$	$p(g + t)$	1451.05	< 0.001	42	1362.46
$\phi(\cdot)$	$p(g + t)$	1451.15	< 0.001	41	1364.78

QAIC, AIC corrected for overdispersion; Par., number of parameter.

Table 3. Model selection for effects of wing area and wing spot area, and their interaction, on the mating probabilities in males of the damselfly, *Hetaerina americana*

Model description: predictors	d.f.	AIC	Δ AIC	AIC weight
Wing area	2	145.3	0	0.495
Wing area + Wing spot area	3	147.2	1.9	0.189
Null model	1	147.6	2.4	0.151
Wing spot area	2	148.7	3.4	0.090
Wing area * Wing spot area	4	149.1	3.8	0.074

d.f., degrees of freedom.

$\chi^2_{\text{LRT}} = 0.75$, d.f. = 1, $P = 0.400$; male type \times allometry: $\chi^2_{\text{LRT}} = 0.178$, d.f. = 1, $P = 0.18$; $N = 239$) or on the number of copulations attained by males (male morph: ANCOVA, $F = 0.440$, d.f. = 1, $P = 0.5$; male type \times allometry: $F = 0.7$, d.f. = 1, $P = 0.4$; $N = 239$). Mating distribution was as follows. For black males, we recorded 53 matings, of which three males had three matings, eight had two matings, and 28 had one mating, and 129 had no matings. For hyaline males, we registered 18 matings, of which three males had two matings and 12 males had one mating, and 57 males had no matings.

Regarding survival, the most supported models did not include body length, wing length, or their interaction as predictor variables; we therefore concluded that these morphological characters did not influence survival probabilities (Table 2).

H. AMERICANA: WING SPOT ALLOMETRY AND ITS RELATIONSHIP WITH MATING SUCCESS AND SURVIVAL Allometric coefficients indicated that wing spot was hyperallometric ($\beta = 4.3$; 95% CI: 3.4–6.13; $P = 0.05$; $N = 211$). The body size \times wing spot interaction did not have a significant effect on mating occurrence ($\chi^2_{\text{LRT}} = 0.4$, d.f. = 1, $P = 0.500$; $N = 210$) or on the number of copulations attained by males (ANCOVA,

$F = 0.200$, d.f. = 1, $P = 0.200$; $N = 211$). We did not register any mating for 186 males, 13 males had one mating, one male had two matings, and two males had three matings. The most supported model contained wing area as a predictor variable (Table 3). Males with a larger wing area showed a higher probability of mating [deviance = 4.37, d.f. = 1, $p(\chi^2) = 0.037$].

In relation to survival, the three most supported models did not include wing length, wing spot, or their interaction (Table 4). Mean survival daily probability was $\phi = 0.945$ [standard error (SE) = 0.008]. There was a positive relationship between wing spot with recapture probabilities (Table 4), and mean daily recapture probability was $P = 0.420$ (SE = 0.020).

DISCUSSION

We found a hyperallometric pattern for both wing size and wing spot in *P. zoe* and *H. americana*, respectively. This evidence supports the notion that hyperallometries are common in ornamental traits of some species (e.g. Moczek, Bruhl & Krell, 2004; Kodric-Brown *et al.*, 2006; Rodriguez & A-Withiqui, 2012), including *H. americana* (Álvarez *et al.*, 2013). Consistent for both species was that wing size was a good predictor of mating success, which corroborates

Table 4. Model selection for effects of wing length (w) and wing spot (ws), and their interaction, on the survival and recapture probabilities in males of the damselfly *Hetaerina americana* (only the ten most supported models are shown)

Model description					
Survival	Recapture	QAIC	QAIC weight	Par.	Deviance
$\phi(\cdot)$	p(ws)	1109.54	0.283	3	1103.47
$\phi(\cdot)$	p(w + ws)	1110.25	0.197	4	1102.14
$\phi(\cdot)$	p(w + ws + w:ws)	1111.40	0.111	5	1101.23
$\phi(\text{ws})$	p(ws)	1111.46	0.108	4	1103.35
$\phi(\text{ws})$	p(w + ws)	1112.18	0.075	5	1102.02
$\phi(\text{w} + \text{ws})$	p(ws)	1112.86	0.054	5	1102.69
$\phi(\text{ws})$	p(w + ws + w:ws)	1113.34	0.042	6	1101.10
$\phi(\text{w} + \text{ws})$	p(w + ws)	1113.79	0.037	6	1101.55
$\phi(\text{w} + \text{ws} + \text{w:ws})$	p(ws)	1114.21	0.027	6	1101.97
$\phi(\text{w} + \text{ws} + \text{w:ws})$	p(ws + w)	1115.13	0.017	7	1100.82

QAIC, AIC corrected for overdispersion; Par., number of parameter.

previous studies (Romo-Beltrán *et al.*, 2009 for *P. zoe*; Grether 1996 and Serrano-Meneses *et al.*, 2007 for *H. americana*). The relationship holds because of a positive correlation between body size and energetic condition in males (e.g. Serrano-Meneses *et al.*, 2007). Furthermore, our results in *P. zoe* show that morph also has an effect on mating success, which varies along the season. This is complementary to the study of Romo-Beltrán *et al.* (2009). Despite these results, the predicted relationship between allometry and mating success and survival was not detected for both species of damselfly. Thus, our results indicate that the expected relationship of allometry in ornamental traits and mating success assumed by researchers is not general. Also, the lack of relationship between survival rates and allometry does not support that natural selection can be an alternative mechanistic explanation for the static allometry in mature males of our two study species. Interestingly, our survival analysis indicated that *H. americana* males with a larger wing spot were more likely to be recaptured, which is partly explained by the better condition of males with large wing spots (Serrano-Meneses *et al.*, 2007; Contreras-Garduño *et al.*, 2008). However, such recapture patterns have nothing to do with allometry of wing spot. One consideration, however, is that we had just one field season for each of the species studied. Assuming that strength, direction, and form of selection on sexual traits may differ or change in distinct seasons or sites (Cornwallis & Uller, 2009), then it may be that, by chance, selection for hyperallometry was not occurring when we were in the field. The only way to corroborate these results is therefore by accumulating data from other time periods and/or places.

The hyperallometric pattern in our study species is expected for condition-dependent traits (e.g. Cotton, Fowler & Pomiankowski, 2004; Bonduriansky, 2007). Although we do not know whether wing size in *P. zoe* is a condition-dependent trait, this is certainly the case for wing spot size in *H. americana* (Contreras-Garduño *et al.*, 2008; Álvarez *et al.*, 2013). Paradoxically, experiments rearing *H. americana* larvae under different food-availability regimes do not lead to any allometric pattern in recently emerged adult males of *H. americana* (Álvarez *et al.*, 2013). Given that there is no effect of diet but there is still hyperallometry, why then do males show such hyperallometry for their sexual traits? One explanation is that only hyperallometric males are favoured during the maturation period. Before sexual maturity (a period that in our study species may last for approximately 2 weeks; all authors' unpubl. data), odonate males have to face a number of natural selection pressures, including one or a combination of the following: bad weather, scarce food, predators, and parasites (reviewed by Corbet, 1999). Perhaps only males in better condition are able to withstand such pressures and accordingly only hyperallometric individuals are found as mature individuals. However, as our study was initiated after such selection took place, we may have missed an instance in which hyperallometry was positively selected. Notice, however, that even in a situation like this, this explains why we did not find a significant relation between hyperallometry and survival but not with mating success.

Given the widespread occurrence of allometry in nature, ideas of how allometry evolves and is maintained have frequently relied on an adaptive function (e.g. Green, 1992; Petrie, 1992; Kodric-Brown *et al.*,

2006). Particularly for sexual traits, such adaptive ideas suppose that any allometric pattern is favoured via, for example, mating success. For instance, enhanced elaboration of sexually selected structures with respect to body size conveys advantage during direct male–male competition (e.g. Emlen & Nijhout, 2000) and/or exhibition to females (e.g. Andersson, 1994). This assumption has even been taken to the point that positive allometries are used as evidence of sexual selection (e.g. Green, 2000). To our knowledge, tests of whether this holds have not been carried out, so our results should encourage researchers to look for further data. It is, of course, premature to generalize what we found here to other taxa and, at best, our data may only apply to damselflies. Related to this, other studies have found that general allometric patterns present in other taxa do not seem to apply to damselflies. For example, the hypo-allometric pattern for genitalia that has been well described in insects (Eberhard *et al.*, 1998) does not apply to damselflies, even for ‘defensive’ traits that are functionally linked to sperm competition (i.e. removal of rival sperm by the mating male during copulation; Nava-Bolaños, Córdoba-Aguilar & Munguía-Steyer, 2012). In the case of *H. americana*, another study examined whether the two male mating tactics that predominate in this species – territoriality and nonterritoriality – differ in their allometric slopes (Álvarez *et al.*, 2013). This examination is based on the assumption that, unlike nonterritorial males, territorial males should advertise their condition via more investment on wing spot production. Thus, it was expected that the spot in territorial males should show a more elevated slope than that in nonterritorial males. Despite this, the results indicated the opposite: nonterritorial males showed steeper spot allometry than did territorial males (Álvarez *et al.*, 2013). It may simply be that damselflies do not follow allometric rules; nevertheless, given these pieces of research, researchers should now test the presumable relationship between sexual trait allometry and fitness components.

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SHARED DATA

Data are available at: http://figshare.com/articles/_Is_allometry_of_sexual_traits_adaptive_A_field_test_with_territorial_damselflies/1190766