

# Wing Pigmentation in Males of a Territorial Damsselfly: Alternative Reproductive Tactics, Allometry and Mating Success

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**Abstract** Alternative reproductive tactics (ARTs) evolve to maximise fitness by favouring alternative phenotypes when high variance in relative fitness occurs amongst individuals. In the damsselfly *Hetaerina vulnerata* males occur as either territorial or nonterritorial, depending on whether males acquire and defend an area to which females are attracted for copulation. Territorial males are usually larger, more pigmented and more successful in obtaining copulations than nonterritorial males. Several studies further suggest that territorial males are in overall better condition than nonterritorial ones. Other studies have investigated whether wing pigmentation, a sexual trait in damsselflies, scales hyperallometrically with body size, and asked whether this pattern is related to fitness—nonetheless, a clear answer to this question remains elusive. Here we investigate whether i) territorial and nonterritorial males differed in body size and wing pigmentation; ii) body size, wing pigmentation and/or male status (male ART) predicted male mating success; and iii) the allometry of wing pigmentation in territorial and nonterritorial males, and amongst mated and unmated males. We first found that territorial and nonterritorial males did not differ in body size. Second,

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contrary to what occurs in other damselflies, territorial and nonterritorial males exhibited similar amounts of wing pigmentation. Third, only territory tenure, but not body size or wing pigmentation, predicted male mating success. Finally, with the exception of the relationship exhibited by mated males, which exhibited isometry, wing pigmentation was hyperallometric in all groups of males tested. The latter result suggests that hyperallometry of the sexual trait in this damselfly may not be selectively advantageous.

**Keywords** Alternative reproductive tactics · sexually selected traits · mating success · territoriality · allometry

## Introduction

Darwin (1871) recognised that certain individuals have an advantage over others of the same sex and species in terms of mating. Thus, it is likely that within a single population certain individuals attain a higher number of mates than others. In order to overcome this asymmetry in mating success, alternative reproductive tactics (ARTs) evolve. ARTs maximise the fitness of individuals (Taborsky et al. 2008; Taborsky and Brockmann 2010) by favouring alternative phenotypes with distinct morphological, behavioural, and/or physiological traits when high variance in relative fitness occurs amongst them (Shuster and Wade 2003). For example, in some scarab beetles (*Onthophagus* sp.), larger-than-average males develop horns and guard the entrance to the tunnel where the female is contained; conversely, smaller males do not develop horns and dig side tunnels that are used to reach and copulate with the females (Emlen 1997). Typically, when certain males monopolise access to females by establishing and defending an area to which females are attracted (i.e., territory), other males adopt different ARTs (Thornhill and Alcock 1983), which are characterised by non-aggressive behaviour, cryptic morphologies and quick and furtive copulations with females (Gross 1996). In many animal taxa, territorial males have higher encounter rates with females than wandering males who are not territorial and/or actively search for females (reviewed by Andersson 1994). Nonetheless, establishing and defending a territory is very costly in terms of energy (Taborsky et al. 2008; see below), thus only those males in overall better conditions will be able to withstand the costs associated with territorial defence, whereas other males will adopt an alternative and less expensive mating tactic (e.g., nonterritoriality; Taborsky and Brockmann 2010). For instance, in the damselfly *Mnais costalis*, males occur in two morphs: orange-winged, territorial males (OW), and clear-winged, nonterritorial males (CW) (Tsubaki et al. 1997; Plaistow and Tsubaki 2000). OW males are larger than CW males and have higher daily mating rates (Plaistow and Tsubaki 2000); however, the former have a shorter lifespan than the latter. Such disparity in survival arises given the energetic costs associated with territoriality (e.g., Plaistow and Siva-Jothy 1996): when males adopt this tactic, they will sustain a higher number of fights than nonterritorial ones (Nomakuchi et al. 1984; Serrano-Meneses et al. 2007). These agonistic encounters may last from a few seconds to hours, and only those males with higher amounts of metabolic fat will be able to remain territorial (Marden and Waage 1990; Plaistow and Siva-Jothy 1996; Koskimäki et al. 2004; Contreras-Garduño et al. 2006a; Serrano-Meneses et al. 2007).

In other odonates, male mating success is further improved by the amount of male wing pigmentation (WP) (reviewed by Córdoba-Aguilar and Cordero-Rivera 2005). Studies in *Hetaerina* and *Calopteryx* species show that males with more WP are more likely to win contests over territories (Grether 1996a; Siva-Jothy 1999; Córdoba-Aguilar 2002; Contreras-Garduño et al. 2006a; Serrano-Meneses et al. 2007). Pigmentation and fat reserves in *H. americana* are in fact closely correlated (Contreras-Garduño et al. 2006a; Serrano-Meneses et al. 2007), since WP is known to signal the energy status of males (Contreras-Garduño et al. 2006a). Thus, males with higher amounts of WP are likely to communicate a larger availability of metabolic fat. Albeit an ornament such as WP entails costs to its bearers: it reduces the survival of males by increasing both their conspicuousness to prey (Grether and Grey 1996) and to predators (Grether 1997; Svensson and Friberg 2007).

A common pattern in the scaling relationship between sexual traits and body size is hyperallometry (the relative greater increase in sexual traits' expression, when modelled as a function of body size; e. g., Kodric-Brown et al. 2006) (but see Bonduriansky 2007). This allometric pattern is detected when the slope ( $\beta$ ) between the sexual trait of interest and body size is  $>1$  (provided that both variables are in the same units of measurement, or are dimensionless; Warton et al. 2006; Sokal and Rohlf 2012). The evolution of such pattern is generally thought to be driven by directional sexual selection acting on the trait in question (Kodric-Brown et al. 2006) (but see Bonduriansky and Day 2003 and Bonduriansky 2007 for contrasting empirical and theoretical evidence) and it is commonly modelled in terms of resource-allocation trade-offs (Bonduriansky and Day 2003; Kodric-Brown et al. 2006), so that individuals are expected to invest heavily in structures that enhance mating success (Kodric-Brown et al. 2006) compared to other traits, such as body size. In a study that investigated the allometry of WP in two *Hetaerina* species (Odonata: Calopterygidae), *H. americana* and *H. vulnerata* (Álvarez et al. 2013), it was found that WP scales hyperallometrically with body size in territorial and nonterritorial males. Similarly, Bello-Bedoy et al. (2015) found a hyperallometric pattern in the WP of *H. americana*, albeit ARTs were not identified. Nonetheless, although hyperallometry of sex traits is relatively common, little is known on the adaptive significance of such pattern (but see Bello-Bedoy et al. 2015).

Here we investigated the determinants of male mating success in the territorial damselfly *Hetaerina vulnerata*, an insect with non-fixed reproductive tactics. Males of *Hetaerina* damselflies exhibit a red, pigmented spot at the base of the wings, which is a sexual trait maintained via male-male competition (Grether 1996a, b; Contreras-Garduño et al. 2006a, 2008). Typically, males establish territories along the shore of rivers or streams to which females are attracted (e.g., Serrano-Meneses et al. 2007), although a fraction of males fails to establish territories and adopt a nonterritorial tactic. By applying these considerations and using data from two field seasons, the objectives of our study were to investigate whether i) body size and WP were different amongst territorial and nonterritorial males; ii) WP, body size and/or male status (male ART) predicted male mating success; and iii) the allometry of WP was different amongst territorial and nonterritorial males, and amongst mated and unmated males.

## Materials and Methods

We studied adult males from a natural population of *Hetaerina vulnerata* located in San Tadeo Huiloapan (19° 23' 53" N, 98° 15' 51" W), Tlaxcala, Mexico, in two different seasons. The first season was carried out from June 4th to July 7th, 2011, and the second one from May 17th to June 10th, 2013. Both seasons encompass the reproductive season of the species in the population studied. Unmarked males were caught on a daily basis (except during rainy days, when damselflies are not active) using aerial entomological nets. Once a male was caught, it was marked with an indelible marker on the right anterior wing with a unique combination of three digits (for a similar procedure see Serrano-Meneses et al. 2007), which were easily readable through binoculars (Pentax Papilio 8.5x21 mm). All males were photographed from a constant distance ( $\approx 30$  cm) with a digital camera (Canon Powershot SX 100 IS) against a gray card (neutral gray, 18 % reflectance) placed next to a scale in mm. We then used the software ImageJ 1.47 t (National Institutes of Health, Maryland, USA) to measure wing length (our *proxy* for body size; the right anterior wing, from the insertion of the wing to the thorax to the tip of the wing) and the length of the pigmented patch (WP; from the insertion of the wing to the thorax to the pigmented patch's distal end, following an imaginary straight line traced over the posterior cubital vein; see Álvarez et al. 2013 for a similar procedure) from these photographs.

## Determination of Age, Male Reproductive Tactics and Mating Success

We performed surveys on a daily basis from 11:00 to 14:00 h every day (Central Standard Time), which is the time when *H. vulnerata* males are most active. During the surveys we recorded the identity (three-digit combinations) of each male along the study site and noted (i) the age of males, and (ii) whether they followed a territorial or nonterritorial tactic (henceforth male status). First, the age of a given male was estimated from morphological cues (see Córdoba-Aguilar 1994): (1) juvenile mature individuals have a bright, intense body colouration and highly transparent wings; (2) mature individuals show less brightness and intensity in body colouration and have less transparent wings; (3) old individuals have dark body colouration and the tips of their wings are usually torn or missing. In our analyses we only included individuals from age classes 1 and 2, since most individuals belonging to age class 3 exhibit nonterritorial mating strategies (M. A. S.-M. pers. obs.). It is difficult to determine whether individuals belonging to age class 3 defended territories at earlier stages of their lives, which would add further uncertainty to our results, should these be included in analyses. Second, territorial males (T), on the one hand, defend a given area against conspecifics and remain faithful to the area for at least 1 day. Nonterritorial males (NT), on the other hand, are not particularly attached to any area and instead wander along the stream, and are commonly chased away by territory owners (see similar rationale in Serrano-Meneses et al. 2007). Also, during the surveys, we determined mating success by direct observations. Thus, whenever a male was observed in copulation, we noted the male's identity. When a copulating male was unmarked, we captured the pair and marked and measured the male. Male mating success, however, was only determined during 2013. Given that the number of times *Hetaerina* males mate during a day is very low (see daily mating rates in *H. americana* reported by Serrano-Meneses et al. 2007) in our analyses we used mating success as a binary variable (see below).

## Statistical Analyses

Before carrying out statistical tests, we assessed the frequency distributions of all continuous variables using Q-Q plots. In the case of the data analysed using major axis regressions, we tested for the normality of residuals via the *plot* function implemented in the R (version 3.1.1; R Development Core Team 2014) package ‘smatr’ (Warton et al. 2006, 2012), which did not depart from normality in any case. We therefore analysed our data using General Linear Models (GLMs); in the models we tested all first order interaction terms and further removed statistically non-significant terms by backward elimination, starting from saturated models. When an interaction term was significant, it was retained in the model. With the exception of the models in which we investigate the determinants of mating success (see below) here we show only the reduced models, however, all models are available from the corresponding author upon request.

We investigated differences in *body size* between *male status* (1, 2; territorial, nonterritorial males; respectively) and *seasons* (2011, 2013) using a GLM. In this analysis, *body size* was used as the independent variable and *male status* and *seasons* were used as factors. We then tested for differences in *WP* in two ways. First, we used *WP* as an independent variable, and *male status* and *seasons* as factors. Note that in this analysis the allometric relationship between *WP* and *body size* (see Álvarez et al. 2013) was not accounted for, given that we were interested in testing for differences in absolute values of *WP* between *male status* and *seasons*. Second, we constructed a model to account for the allometric relationship between *WP* and *body size*. In our model, *WP* was modelled as a function of *male status* and *seasons* (factors) and *body size* (covariate). This procedure allowed us to test whether T and NT males differed in relative *WP*, by considering *seasons*. Given that in this model the interaction term *body size\*seasons* was significant (see Results), we tested the allometry of *WP* separately for 2011 and 2013 (see below).

To investigate the determinants of mating success, we built two binomial Generalised Linear Models, given that two of the variables of interest (*body size* and *WP*) were correlated ( $r_{131}=0.594$ ,  $P=0.001$ ). Therefore, in order to avoid any biases arising from collinearity, we tested their effects on mating success separately. Model 1 included *mating success* as a binary, response variable (1, 0; mated, unmated; respectively), and *body size* and *male status* as main effects. Model 2 included *mating success* as a response variable, and *WP* and *male status* as main effects. The *logit* canonical link function was used, given the error structure specified for the GLMs.

Lastly, we investigated the scaling relationship between *WP* and *body size* in (i) T and NT males, and (ii) in mated and unmated males by fitting six major axis regressions (MA regression; model II regression; Sokal and Rohlf 2012) to our  $\log_{10}$  transformed data. We used MA regressions to estimate allometric slopes because this method has several advantages over others, such as ordinary least squares regression and reduced MA. The advantages of MA have been discussed elsewhere (e.g., Fairbairn 1997; Warton et al. 2006; Sokal and Rohlf 2012; Álvarez et al. 2013). We tested the allometry of *WP* between T and NT males separately for 2011 and 2013 for two reasons. First, we were interested in testing for intra seasonal variation in *WP* allometry, and second, in whether *WP* relates differently to wing length between seasons (see Results).

MA regressions were performed in R, version 3.1.1 (R Development Core Team 2014), using the ‘smatr’ package, which calculates allometric slopes between two variables, as well as their 95 % confidence intervals (CIs; upper CI – lower CI). ‘smatr’ further implements a procedure that allows to test whether the slope from a statistically significant MA regression differs from a given slope value (‘slope.test’). The procedure is described in Warton et al. (2006). A slope was considered to be significantly different from 1 if the confidence intervals excluded  $\beta=1$ , and the associated  $P$  value was  $\leq 0.050$ .

All statistical analyses and figures were produced in R.

## Results

### Body Size and WP in Relation to Male Status and Seasons

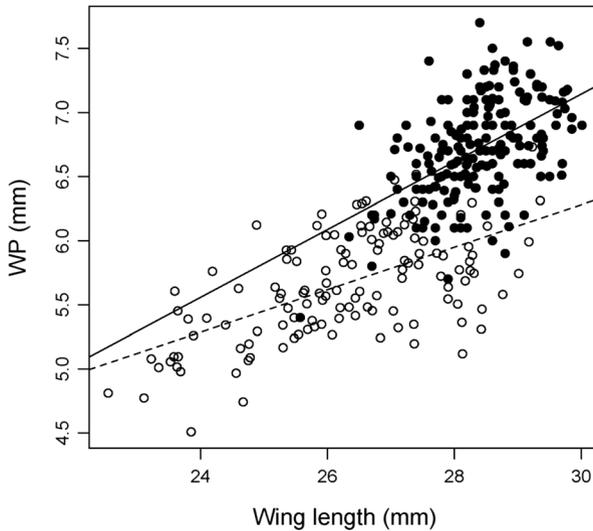
T males were not larger than NT males (GLMs;  $\beta=0.039$ , S.E. = 0.128,  $t=0.309$ ,  $P=0.757$ ); however, males collected in 2011 were on average larger than those collected in 2013 ( $\beta=-1.038$ , S.E. = 0.063,  $t=16.405$ ,  $P=0.001$ ). Similarly, in an analysis in which we investigated differences in absolute values of WP, we found that T males were not more pigmented than NT males ( $\beta=-0.007$ , S.E. = 0.046,  $t=0.171$ ,  $P=0.864$ ), but males collected in 2011 were more pigmented than those collected in 2013 ( $\beta=-0.522$ , S.E. = 0.022,  $t=22.947$ ,  $P=0.001$ ). Also, in an analysis in which we accounted for the effect of body size on WP, we found that T and NT males had similar amounts of WP ( $\beta=-0.009$ , S.E. = 0.038,  $t=0.255$ ,  $P=0.798$ ), albeit in this analysis, WP related differently to body size amongst seasons (seasons,  $\beta=1.042$ , S.E. = 0.497,  $t=2.095$ ,  $P=0.036$ ; body size,  $\beta=0.990$ , S.E. = 0.360,  $t=2.747$ ,  $P=0.006$ ; seasons\*body size,  $\beta=-0.049$ , S.E. = 0.017,  $t=2.742$ ,  $P=0.006$ ; Fig. 1).

### Determinants of Male Mating Success

The two models in which we investigated the potential determinants of male mating success suggest that only male status (territory tenure) predicts whether males are able to obtain copulations, since body size and WP do not contribute significantly to the models (Model 1: male status:  $\beta=-1.283$ , S.E. = 0.502,  $Z=-2.552$ ,  $P=0.011$ ; body size:  $\beta=-0.044$ , S.E. = 0.153,  $Z=-0.291$ ,  $P=0.771$ ; Model 2: male status:  $\beta=-1.294$ , S.E. = 0.503,  $Z=-2.573$ ,  $P=0.010$ ; WP:  $\beta=0.061$ , S.E. = 0.539,  $Z=0.113$ ,  $P=0.910$ ).

### Allometry of WP

Table 1 summarises the calculated MA slopes between WP and body size for T and NT males, as well as for mated and unmated males. With the exception of the relationship exhibited by mated males, WP scaled hyperallometrically with body size in all groups tested. In 2011, T and NT males exhibited similar hyperallometric slopes (Fig. 2a), whereas T males showed a steeper slope than NT males in 2013 (Fig. 2b). When we compared the allometry of WP of mated vs unmated males we found no significant differences. Although the calculated slope for mated males seems higher than the slope



**Fig. 1** Wing pigmentation (WP) in relation to male body size (wing length) in *Hetaerina vulnerata*. The closed dots and the continuous line describe the relationship for males collected in 2011, whilst the open dots and the dashed line detone the relationship for males collected in 2013

of unmated males at first sight (Table 1; Fig. 3), the CIs of such slope are highly variable (lower – upper CIs; 0.967 – 11.116). Note that out of 27 mated males, 6 were NT males.

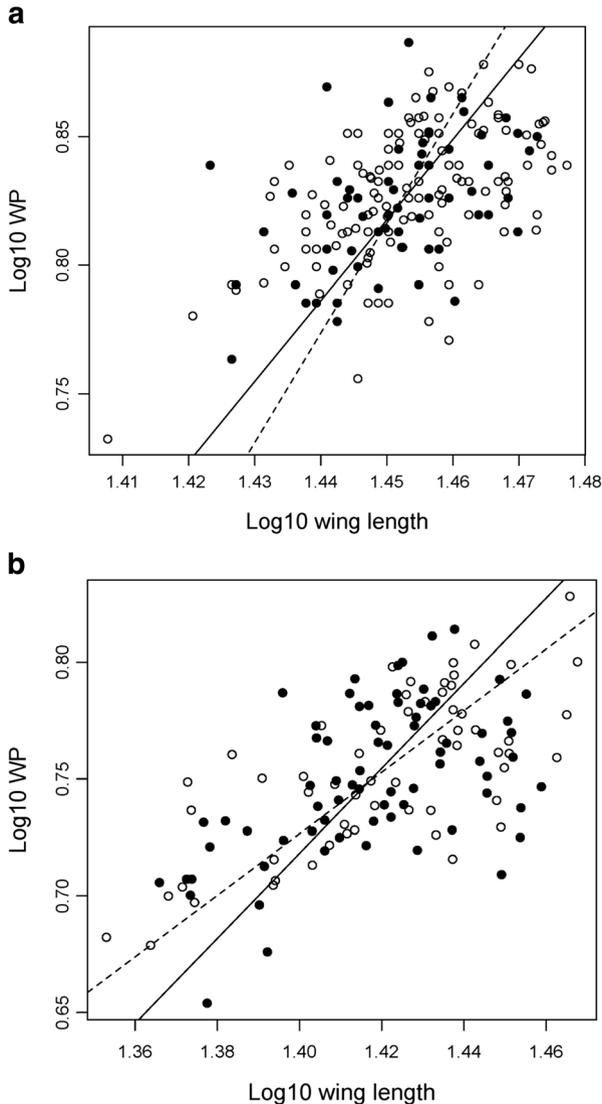
### Discussion

Males of *Hetaerina vulnerata* exhibit two non-genetically distinct ARTs: T males, that establish and defend areas along rivers or streams; and NT males, that wander along sections of such habitats but do not establish or defend territories. T and NT males of

**Table 1** Slopes, 95 % confidence intervals (CIs),  $R^2$  and  $P$  values obtained from MA regressions (see Materials and methods) fitted between WP and body size ( $\log_{10}$  transformed values) of territorial (T) and nonterritorial (NT) and mated (Mated) and unmated (Unmated) males of *Hetaerina vulnerata*

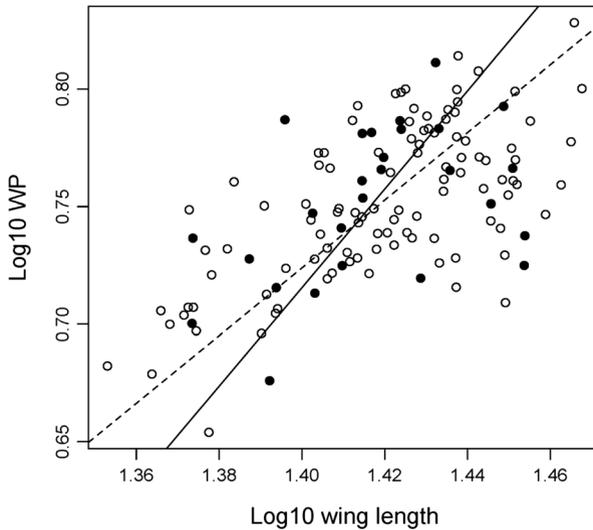
Model	Male status	Slope	Lower CI- Upper CI	$R^2$	$P$ value	Slope test $P$ value
Season 2011	T	3.136	2.524–4.085	0.330	0.001	0.201
	NT	4.262	2.720–9.162	0.188	0.001	
Season 2013	T	1.819	1.262–2.871	0.270	0.001	0.032
	NT	1.317	1.006–0.761	0.481	0.001	
Mating success	Mated	2.093	0.968–11.116	0.194	0.022	0.327
	Unmated	1.439	1.149–1.834	0.416	0.001	

Slope comparison  $P$  value refers to a procedure which tests whether two MA slopes are significantly different (see Warton et al. 2006). Sample sizes are 144 territorial and 61 nonterritorial males in 2011, 73 territorial and 60 nonterritorial males in 2013, and 27 mated and 106 unmated males



**Fig. 2** Wing pigmentation (WP) in relation to male body size (wing length) in individuals collected during **a** 2011 and **b** 2013. The *closed dots* and the *continuous line* describe the relationship for territorial males, whilst the *open dots* and the *dashed line* denote the relationship for nonterritorial males. The data were  $\log_{10}$  transformed prior to analyses (see [Materials and methods](#))

this species are not present in different discrete morphs, and according to our results, there were no evident morphological differences between these males. We found that T and NT males had similar body sizes (for similar findings see Lefevre and Muehter 2004; Serrano-Meneses et al. 2007). This contradicts a number of studies, which have reported that T males are generally larger than NT males (for studies in *Hetaerina* see Raihani et al. 2008; Álvarez et al. 2013; for studies in other odonates see Tsubaki et al. 1997; Beck and Pruett-Jones 2002; Koskimäki et al. 2009; Romo-Beltrán et al. 2009).



**Fig. 3** Wing pigmentation (WP) in relation to male body size (wing length) in mated and unmated males. Mated males were observed copulating at least once, whereas unmated males were never observed *in copula*. The *closed dots* and the *continuous line* describe the relationship for mated males, whilst the *open dots* and the *dashed line* denote the relationship for unmated males. The data were  $\log_{10}$  transformed prior to analyses (see [Materials and methods](#))

Large size in T males amongst Zygopteran males is expected because it may enable them to store a larger amount of fat reserves, which are necessary for territorial defence (e.g., Serrano-Meneses et al. 2007; Raihani et al. 2008). For NT males, small body size may be more advantageous given the lower flying costs per unit time associated with small body size. Such males may be able to allocate more time to searching for potential mates rather than defending a territory or foraging ('Ghiselin-Reiss' small male hypothesis; Blanckenhorn et al. 1995). Nonetheless, body size selection is known to operate primarily on NT males at the clasping stage of the mating sequence (Grether 1996a). When attempting to mate, males commonly try to clasp females by pinning them against a surface (such as the ground or surrounding vegetation; Grether 1996a). Although males cannot force females to copulate (Corbet 1963), they can hold them long enough for them to accept the *copula*. Also, large male body size may be advantageous in intrasexual competition, given that it is common to find several males trying to mate with the same female simultaneously (Grether 1996a). Under both circumstances, larger-than-average body size in NT males may be selectively advantageous because it may allow large males to attain a considerable number of copulations, which in turn may explain why NT males are as large as T males. Note that this pattern was maintained in both seasons studied, albeit males studied in 2011 were larger than those studied in 2013. The latter finding is not uncommon in studies of Odonata that consider data from different seasons. Size at emergence is greatly influenced by the duration of development (Crowley and Johansson 2002; Strobbe and Stoks 2004), so that the larvae of species with flexible developmental times emerging early in the reproductive season may bear smaller sizes compared to those emerging later in the season. This pattern is known to occur in the closely related *H. americana*, whose

males are known to emerge at smaller sizes during the winter months, reaching a peak in the months of July–October (Córdoba-Aguilar et al. 2009). The first individuals of *H. vulnerata* emerge during early April in our study site, and they are last seen up until mid December (M. A. S.-M. pers. obs.). Our results may thus reflect the fact that males from the 2011 season were collected later (June–July) than those collected in 2013 (May–June). The former may have had more time to develop and reach larger sizes than the latter, but further experimental studies are needed to support this hypothesis.

Both T and NT males had similar amounts of WP. This finding is similar to other studies in damselflies (e.g., Tynkkynen et al. 2006) that contradict what is commonly found in Zygoptera, given that T males are usually more pigmented than NT males (e.g., Grether 1996a; Siva-Jothy 1999; Córdoba-Aguilar 2002; Contreras-Garduño et al. 2006a; Córdoba-Aguilar et al. 2007). WP, as it is expected for sexual traits, is costly to produce, so that only males in overall high conditions are expected to exaggerate its expression (Andersson 1994). In *Hetaerina* damselflies, WP is known to convey information on the resource-holding ability of its bearers: males with large amounts of fat reserves have large amounts of WP (Contreras-Garduño et al. 2008) so that only males with such amounts of WP would be expected to defend a territory. Furthermore, it is likely that high amounts of WP correlate with immune defence components (Contreras-Garduño et al. 2006b; Córdoba-Aguilar et al. 2009; but see González-Santoyo et al. 2010; Rantala et al. 2011); therefore, males with higher amounts of WP will deal with pathogen infestation more efficiently. Both relationships are usually put forward to explain why T males bear larger pigmented patches than NT males. Our results, however, suggest that T and NT males are able to invest similarly in WP, to the extent that both types of males exhibit similar amounts of WP (but see below).

The morphological characteristics of males (body size, WP) did not predict mating success, but territory tenure did. That is, T males were more likely to copulate than NT males. This is fully consistent with results from other studies carried out in territorial odonates (reviewed by Suhonen et al. 2008) which highlight the fact that territoriality greatly increases male mating success. It is interesting that it was not possible to separate the morphologies of T and NT males using “conventional” statistical tests, given that when we investigated the allometry of WP, we found that for T males studied in 2013, WP increased faster per body size unit, compared to NT males. This means that at least during one season, T males were able to invest more in WP than NT males. This pattern has been a standing topic of discussion and the platform of studies that investigate the adaptive significance of hyperallometry of sexual traits (e.g., Bello-Bedoy et al. 2015). In our study we also investigated whether mated males had higher allometric slopes than unmated ones. We found that both males exhibited similar allometric slopes, with mated males exhibiting more variability in the expression of WP. This suggests that males that are able to mate do not exhibit higher allometric slopes, like it would be expected if hyperallometry of sexual traits were adaptive (via enhanced mating success). These results may have three explanations. First, we obtained a relatively small sample size of mated males ( $N=27$  males). Second, we are very likely to have missed a significant number of copulations and the identities of the males, given the difficulty to detect matings by direct observations (i.e., an unknown number of copulations remained undetected; see Cordero Rivera and Egido Pérez 1998). Finally, it may be the result of including both T and NT males in a single analysis. It has to be realised that although T males attain a significantly larger number

of copulations, NT males still manage to obtain mates. Note that our test of the relationship between allometry and mating success is an indirect one. A direct test would, for instance, require a modification of the regression equation included in methods such as General Linear Models or Generalised Linear Mixed Models, given that in order to properly estimate allometry, the fact that the  $X$  variable is measured with error must be taken into account (see Álvarez et al. 2013 for a discussion on the topic). Therefore our results and those of other studies that have attempted to link hyperallometry of sexual traits to fitness (e.g., Bello-Bedoy et al. 2015) (but that have failed to carry out direct tests) should be interpreted with care.

Very commonly, in studies of odonates, NT males are expected to have lower condition than T males (reviewed by Córdoba-Aguilar and Cordero-Rivera 2005), but we argue that there must still be a positive correlation between WP and condition in these animals. This may be possible, given that they are able to produce the same amount of WP than T males. This suggests that although NT males are often assumed to do “the best of a bad job” because of their inability to acquire and defend a territory (Forsyth and Montgomerie 1987; Córdoba-Aguilar and Cordero-Rivera 2005), their “job” seems to be as good as that of T males (Tsubaki et al. 1997), specially in species in which lifetime reproductive success does not differ between morphs (e.g., Tsubaki et al. 1997). However, to our knowledge, no study has investigated differences in lifetime reproductive success amongst T and NT males in *Hetaerina* damselflies. Such studies would allow us to grasp a better understanding of the forces that shape the evolution of ARTs and their distinct morphologies and behaviour in taxa with non-fixed tactics.

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**Conflict of Interest** The authors declare that they have no conflict of interest.

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