Alternative reproductive strategies in black-winged territorial males of *Paraphlebia zoe* (Odonata, Thaumatoneuridae)

Anais Rivas-Torres Corresp., [1] , **Rosa Ana Sánchez-Guillén** [2] , **Adolfo Cordero-Rivera** [1]

[1] ECOEVO Lab, Departamento de Ecoloxía e Bioloxía Animal, Universidade de Vigo, Pontevedra, Galiza, Spain

[2] Department of Ecology and Animal Biology, INECOL, Xalapa, Veracruz, Mexico

Corresponding Author: Anais Rivas-Torres
Email address: anarivas@uvigo.es

Alternative reproductive strategies are commonly associated with male dimorphism. In *Paraphlebia zoe*, a species of damselfly whose males are dimorphic in wing coloration, black-and-white-winged (BW) males defend territories, while hyaline-winged (HW) males usually play the role of satellites. We found that several BW males can sometimes share a territory, and we hypothesized that within this morph there are two alternative tactics: submissive and dominant. We conducted an experiment to test whether dominant and submissive roles are plastic or stable and fixed on each individual. To this end, we manipulated black and white spots of BW males in four treatments: (i) painting over white and black spots without changing their size, (ii) erasing the white spot using black painting, (iii) increasing the black spot and moving the white spot maintaining its size and (iv) control males. Additionally, we investigated the correlation between some phenotypic variables (wing asymmetry, survival and recapture probabilities) and male behaviour (in terms of quality of the territory). We found that the two behavioural roles (submissive and dominant) were not affected by the manipulative experiments, therefore suggesting that they are stable and fixed. Additionally, we found a positive correlation between body size and survival in both sexes, and a positive effect of territory quality and lifespan on mating success. Moreover, the largest and youngest BW males were the most symmetrical. We conclude that *Paraphlebia zoe* holds high behavioural diversity, with two types of strategies in BW males, dominant and submissive. The occurrence of this intra-morph behavioural diversity might depend on demographic factors such as population density and/or the relative frequency of the different morphs.

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2 **Thaumatoneuridae)**

3 Anais Rivas-Torres[1], Rosa Ana Sánchez-Guillén[2] & Adolfo Cordero-Rivera[1]

4 [1]ECOEVO Lab, Departamento de Ecoloxía e Bioloxía Animal, Universidade de Vigo, Pontevedra, Galiza,
5 Spain

6 [2]Department of Ecology and Animal Biology, INECOL, Xalapa, Veracruz, Mexico

7 **Author for correspondence:** Anais Rivas-Torres, **address**: ECOEVO Lab, Universidade de Vigo, Escola de
8 Enxeñaría Forestal, Campus A Xunqueira, 36005 Pontevedra, Galiza, Spain, **telephone number:**
9 0034657885598 **email:** arivasto@gmail.com

10 **Running title:** Alternative reproductive tactics in a dimorphic damselfly.

11 **ABSTRACT**

12 Alternative reproductive strategies are commonly associated with male dimorphism. In *Paraphlebia zoe*,
13 a species of damselfly whose males are dimorphic in wing coloration, black-and-white-winged (BW) males
14 defend territories, while hyaline-winged (HW) males usually play the role of satellites. We found that
15 several BW males can sometimes share a territory, and we hypothesized that within this morph there are
16 two alternative tactics: submissive and dominant. We conducted an experiment to test whether dominant
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18 and white spots of BW males in four treatments: (i) painting over white and black spots without changing
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20 white spot maintaining its size and (iv) control males. Additionally, we investigated the correlation
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22 behaviour (in terms of quality of the territory). We found that the two behavioural roles (submissive and
23 dominant) were not affected by the manipulative experiments, therefore suggesting that they are stable
24 and fixed. Additionally, we found a positive correlation between body size and survival in both sexes, and
25 a positive effect of territory quality and lifespan on mating success. Moreover, the largest and youngest
26 BW males were the most symmetrical. We conclude that *Paraphlebia zoe* holds high behavioural diversity,
27 with two types of strategies in BW males, dominant and submissive. The occurrence of this intra-morph
28 behavioural diversity might depend on demographic factors such as population density and/or the relative
29 frequency of the different morphs.

31   **INTRODUCTION**

32   The existence of alternative reproductive behaviours in individuals of the same sex is widespread in
33   nature. Most of examples of alternative reproductive phenotypes are readily interpreted as alternative
34   tactics within a conditional strategy, *i.e.* monomorphic individuals adopting one strategy or another, based
35   on a condition-dependent trait, such as body size, fat reserves and so on (Gross, 1996). In contrast,
36   alternative strategies linked to genetic polymorphisms are uncommon, and they are usually associated
37   with male polymorphism in insects and other invertebrates. Examples include wing dimorphism in
38   odonates, and size in horned beetles and cuttlefish (Nomakuchi, 1992; Emlen, 1997; Norman, Finn &
39   Tregenza, 1999). In polymorphic species, each morph is usually associated with different behaviours, like
40   two morphs of newts which differed in boldness (Winandy & Denoël, 2015). In harvestmen, a case of
41   trimorphism in chelicerae size has been recently reported, associated with alternative reproductive tactics
42   (Painting et al., 2015).

43   In odonates, colour polymorphism is common in females (Fincke et al., 2005; Van Gossum, Sherratt &
44   Cordero-Rivera, 2008; Sánchez-Guillén et al., 2017). Female-limited colour polymorphism (thorax
45   colouration) is associated with alternative reproductive strategies, normally one female has a male-like
46   coloration and behaviour (androchrome; behaving more aggressively than the gynochrome morphs).
47   However, male-limited colour polymorphism (wing colouration) is a rare phenomenon in damselflies and
48   only found in some families like Calopterygidae (genus *Mnais*; Siva-Jothy and Tsubaki 1989; Plaistow and
49   Tsubaki 2000), Platystictidae (Gonzalez-Soriano, Novelo-Gutierrez & Verdugo-Garza, 1982), Synlestidae
50   (Samways, 2006) and in the genera *Thaumatoneura* and *Paraphlebia*, (Garrison, von Ellenrieder, & Louton,
51   2010; Paulson, 2016). In *Diastatops obscura* (Libellulidae), there are three types of males: territorial males
52   near the riverbank (the best territories), territorial males in the middle of the river, and satellites in the
53   riverbank vegetation, who do not defend territories (Bañuelos Irusta & Araújo, 2007). Territories can be
54   even shared by several males, like in *Libellula luctuosa*, and are surrounded by non-territorial satellite
55   males (Moore, 1987).

56   The damselfly *Paraphlebia zoe* Selys *in* Hagen, 1861, is a polymorphic species, with two male colour
57   morphs, one with coloured wings, with a black spot and a white stripe (BW), while the other morph shows
58   hyaline wings (HW), similar to females. In *Megaloprepus caerulatus*, a monomorphic species whose males
59   have a similar wing pattern to BW *P. zoe males*, it has been found that white wing bands of males are
60   correlated with territory residence and they might be a signal of male condition, because they are based
61   on wax (Schultz & Fincke, 2009; Xu & Fincke, 2015). In *P. zoe*, each morph has been associated with a
62   specific reproductive strategy. BW males are more territorial and aggressive than HW males, secure more
63   matings and copulate for shorter times (Romo-Beltrán, Macías-Ordóñez & Córdoba-Aguilar, 2009). This
64   species is therefore a typical example of genetic polymorphism associated with alternative reproductive
65   strategies, presumably maintained by frequency-dependent selection (Gross, 1996). Some BW males that
66   do not defend a territory have been previously found in *P. zoe* (Romo-Beltrán, Macías-Ordóñez &
67   Córdoba-Aguilar, 2009), and are considered as satellite males. Our preliminary observations suggested
68   that BW territorial males can behave as *dominants*, particularly when their territory is close to the water
69   or as *submissive*, when they occupy a territory away from the water, in a similar way as the behaviour
70   described for *D. obscura* (Bañuelos Irusta & Araújo, 2007). Dominant BW males are highly territorial and
71   highly aggressive against submissive males, probably giving them resource advantages (Baker, 1983), and
72   submissive males are less aggressive, usually avoiding confrontation with dominants, but nevertheless
73   defend their territory against satellites. *Paraphlebia zoe* does not show precopulatory courtship (Wong-
74   Muñoz et al., 2013), consequently, females could be choosing territory quality instead of male quality.

75 Previous studies have indicated that longevity and body size are among the main correlates of male
76 reproductive success in damselflies (e.g. Banks & Thompson, 1987; Cordero, 1995). The main aim of our
77 study was to determine whether dominant and submissive roles of BW males are related to phenotypic
78 characters, in particular body size, wing asymmetry and size of the wing pigmentation (black spot and a
79 white stripe), and how this behavioural polymorphism relates to reproductive success. To this end, we
80 first, using mark-recapture methods, estimated survivorship rates and the effect of body size on survival
81 of BW males (dominant and submissive). Second, fluctuating asymmetry (Forbes, Leung & Schalk, 1997;
82 Beck & Pruett-Jones, 2002) has been widely used as a correlate of genetic quality, because it is presumed
83 that, for traits with bilateral expression, small deviations between sides are due to the inability of the
84 organism to buffer environmental stressors (Leung & Forbes, 1997a). In odonates, some contrasting
85 results about the effect of asymmetry on reproductive success have been found. Harvey & Walsh (1993)
86 found a negative effect, while others did not find any effect (Leung & Forbes, 1997b; Koga et al., 1998;
87 Carchini et al., 2001). We therefore analysed the effect of male wing spot asymmetry on mating success
88 of BW males (taking into account territory quality and male strategy). Third, some studies have suggested
89 that male mating success might be more related to the ability to be in the right place at the right time,
90 which is expected to be related with the capacity to maintain the territory (Switzer, 2002). For this reason,
91 we studied mating behaviour and evaluated which factors affect copulation duration, including male
92 phenotype, time of day and temperature (e.g. Cordero, 1990), because these variables might affect
93 territory tenancy and hence reproductive success. Finally, we designed a manipulative experiment to test
94 whether dominant and submissive BW male roles are plastic or fixed over time. Based on previous studies
95 with odonates that have found that more pigmented males have higher success (e.g. Alex Córdoba-
96 Aguilar, 2002) we hypothesized that increasing the black-wing spot of the BW submissive males would
97 change their status towards dominance. This prediction is based on the idea that males adapt their
98 aggressiveness to the result of previous interactions, so that other males would tend to become
99 submissive in confrontations with a male with an enlarged black spot, and the manipulated male would
100 increase its aggressiveness (Senar & Camerino, 1998). However, increasing the black spot size of the BW
101 dominant males would not affect their status, because they are already dominant. For the white spot,
102 there is no information about its function in this species. Therefore, if we conceal the white spot, we could
103 either expect that BW dominant males change their status to submissive if this spot is related to
104 aggressiveness (Schultz & Fincke, 2009; Xu & Fincke, 2015), or that they maintain the same dominance,
105 if the spot is not related to dominance. In the case of submissive BW males, concealing their white spot
106 would not affect their behaviour under the assumption that the white spot is not related to dominance.

107 **METHODS**

108 ***Morphometrics and asymmetry***

109 *Paraphlebia zoe* was studied in Teocelo, Veracruz, Mexico (19°40'42'' N, 96°98'28'' W) in a creek
110 depression in a runoff water habitat, from 11 June to 25 July, 2017. Fieldwork was carried out from 9:00
111 to 16:30, every day if the weather allowed it (*i.e.* if there were no major showers), by two observers who
112 recorded date and time of capture, male morph and body size, measured to the nearest 0.1 mm using a
113 caliper. Males and females were captured with an entomological net and marked with a small number on
114 the left anterior wing, using a black *Staedleter* permanent lumocolor pen, a method that does not affect
115 the survival of the damselflies (Munguía-Steyer, Córdoba-Aguilar & Romo-Beltrán, 2010). The number was
116 situated far from the wing spots (see Figure 1), to minimize the possible effect of this mark on behaviour.

117 During our fieldwork period, HW males were extremely rare or absent, and were therefore not included
118 in the study. For BW males, behavioural status was divided into two categories: territorial males, defined

119 as those individuals who stayed in the same place for more than two days and returned to the same perch
120 site after participating in a fight in flight with a conspecific male, while individuals who did not meet this
121 criterion were considered as non-territorial BW (satellite) males (Romo-Beltrán, Macías-Ordóñez &
122 Córdoba-Aguilar, 2009). Within the BW territorial males, we found two subcategories: the dominant
123 territorial males and the submissive males. The subcategories of the BW males were assigned observing
124 them during 3 days, using 10-min focal observations each day. The male which won more than 60% of the
125 interactions in which he was involved, was labelled as the dominant, whereas the submissive male was
126 the one that won less than 50% of the interactions (Figure 2). Moreover, the histogram of figure 2 shows
127 that there is no overlap between dominant and submissive males, and therefore they can be
128 unambiguously identified. When a focal individual was observed perching outside the area of territories,
129 it was considered to have switched to submissive. However, for focal males not observed during a day,
130 we maintained their originally assigned status because they could be feeding, or making a break in their
131 reproductive activities.

132 Body size was measured as length from the head to the end of the abdomen (including cerci) to the
133 nearest 0.1 mm with a caliper. After that, each BW male was photographed with the wings spread for
134 asymmetry measurements. The software Image J (Schneider, Rasband & Eliceiri, 2012) was used to
135 measure area of the black and white spots from BW males as proxies of spot size. To control for trait size,
136 asymmetry was calculated as the absolute value of the difference between right and left sides, divided by
137 the average value of both sides (Cuervo, 2000). Four estimates of asymmetry were obtained for each BW
138 male (one for each black and white spot), and we calculated the total asymmetry by adding up the four
139 partial estimates. To distinguish measurement error from actual asymmetry, each individual was
140 measured twice and the variance due to replicate and wing size was estimated following Crawley (2007).
141 A sample of ten males, marked and photographed as young individuals and recaptured after 15 to 37 days,
142 were photographed again to study ontogenetic changes in spot size. If spot size is related to genetic
143 quality, and is not condition-dependent, we expect spot size to remain invariable over time. This could
144 not be compared among dominant and submissive roles because the number of young individuals that
145 were recaptured was too low.

146 ***Estimation of survival rates***

147 To estimate survival (Phi) and recapture (p) probabilities we analysed the recapture histories of marked
148 animals using the software MARK 8.1 (White & Burnham, 1999). Sex, time and their interaction were
149 included as factors in the models (Lebreton et al., 1992). First, we tested the fit of the full time-dependent
150 Cormack-Jolly-Seber model by groups (model {Phi(g*t) p(g*t)}, where *g* is sex and *t* is time) using program
151 RELEASE. The results indicated highly significant lack of fit, due to heterogeneity in males (TEST2+TEST3,
152 males χ^2_{87}=204.25, p<0.001; females χ^2_{31}=8.31, p=1). We therefore increased the number of groups to
153 account for BW and HW males. This model with three groups was again not appropriate due to
154 heterogeneity in the group of BW males (TEST2+TEST3, BW males χ^2_{75}=176.59, p<0.001; HW males
155 χ^2_{15}=2.81, p=1; females χ^2_{31}=9.72, p=1). Finally, we subdivided BW males into two behavioural categories
156 (dominant and submissive), and found that the model fitted all the groups, except for dominant BW males,
157 which still showed lack of fit (TEST2+TEST3, dominant BW males χ^2_{43}=70.85, p=0.005). Nevertheless, the
158 overall fit was acceptable (TEST2+TEST3, four groups χ^2_{146}=145.46, p=0.497), and we started with this
159 model, given that no other phenotypic variables could be used to subdivide the group of dominant BW
160 males.

161 Then, we estimated the variance inflation factor (c-hat; needed to correct for overdispersion) using two
162 procedures: by dividing the c-hat obtained from model {Phi(g*t) p(g*t)} by the mean c-hat of the bootstrap

163 simulations in MARK, and by dividing the mean deviance of the saturated model by the mean deviance of
164 the bootstrap simulations. The first method yielded an estimation of c-hat=1, and the second c-hat= 1.007.
165 We used the second value (more conservative) to adjust parameter estimates and standard errors. In a
166 first step, we ran models without individual covariates, to select the most supported model, as the one
167 that minimizes the quasi-likelihood version of the Akaike's Information Criterion adjusted for small sample
168 sizes (QAICc). In a second step, body length was included as an individual covariate.

169 ***Reproductive behaviour***

170 During the first 10 days of fieldwork, we conducted focal observations to estimate the limits of the
171 territories and the alternative tactics (dominant and submissive; see Results) that BW territorial males
172 showed. In territorial damselflies, males tend to occupy first high quality areas, and therefore the amount
173 of fighting for territories increases with the number of males (Switzer, 2002). In *P. zoe*, little is known
174 about which areas offer the best resources, but males concentrate in the areas closer to the water, where
175 most matings are observed. We assume that males choose the best territories first (those close to the
176 water), and territory quality could be estimated as the average number of males observed in a territory
177 over the three days of focal observations. Copulations were timed to the nearest second. We studied 16
178 territories, whose limits were defined by the flight path that the territorial male used for patrolling
179 (following Romo-Beltrán, Macías-Ordóñez, & Córdoba-Aguilar, 2009). Two observers, from 9:30 to 16:00,
180 carried out focal observations. The duration of each focal observation was 10 min per territory. In these
181 observations, we registered the identity of males, BW alternative tactics and reproductive success
182 (number of copulations and copulation duration).

183 ***Dominant and submissive roles: plastic or fixed?***

184 We conducted a manipulative experiment to test whether wing spot size is related to the
185 dominant/submissive roles. To this end, we manipulated black and white spots in four treatments: (i)
186 painting over white and black spots without changing their size (control 1), (ii) unmanipulated males
187 (control 2), (iii) erasing the white spot using black painting (EWS), (iv) increasing the black spot and moving
188 the white spot maintaining its size (IBS) (Figure 1). We used a black Staedtler® permanent Lumocolor pen
189 and a white Edding® 751 paint marker**.** Each male was followed for three days after manipulation to
190 establish the territorial male subcategory (*i.e.* dominant or submissive) as described above (Romo-Beltrán,
191 Macías-Ordóñez, & Córdoba-Aguilar, 2009). The response variable was change of status, coded as 0 if the
192 male maintained the previous state (dominant or submissive) and as 1 when he changed status or was
193 found far from the territory. This variable was analysed with a GLM with Bernoulli distribution and logit
194 link, entering as explanatory variables the treatment and the initial status. We compared the change of
195 status between day 0 and the following three days, in separate GLMs.

196 The number of males that copulated once, twice, and so on, followed a negative binomial distribution
197 (Goodness of fit test, χ^2_2=0.004, p=0.998). Therefore, we used a GLM with a negative binomial distribution
198 and a log link function (with the dispersion parameter estimated from the residual deviance) to test the
199 effect of longevity, body length, territory quality, spot size (mean of black and white spots of fore- and
200 hindwings entered separately), asymmetry and male strategy (dominant or submissive) on the number of
201 matings obtained by each BW male.

202 Air temperature was obtained from a datalogger situated in the shade, which took a measure every 5 min,
203 to consider this variable in further analyses, as it is known to influence copula duration in odonates
204 (Michiels, 1992). We found that copulation duration did not follow a normal distribution, but was

205 normalized using a Box-Cox transformation with lambda=-0.6. Using a GLM with normal errors, we tested
206 the effect of time of start, temperature, asymmetry, body length, territory quality, age and status
207 (dominant/submissive) on copulation duration.

208 Statistical tests were carried out using xLSTAT 2018 software (www.xlstat.com) and Genstat 18.1 software
209 (GenStat, 2015). Mean values are presented with their standard error and sample size.

210 **RESULTS**

211 Overall, we observed 931 interactions between BW males. On average BW males considered dominant
212 won 11.05 ± 0.77 disputes (mean ± SE) and lost 1.17 ± 0.15, whereas BW males assigned as submissive
213 won 0.81 ± 0.14 and lost 9.7 ± 0.67 interactions. Figure 2 shows that there were clearly two groups of
214 males (*i.e.* submissives and dominants) without any intermediate category.

215 *Morphometrics and asymmetry*

216 Over the period of study, we marked 212 males and 111 females. Table 1 shows the number of BW and
217 HW males, females and their recapture rates. The average size (area) of black spots varied between 0.44
218 and 1.14 cm^2, and white spots between 0.08 and 0.40 cm^2 (Table 2). The analysis of the size of the spots
219 in young males that were recaptured after 15-37 days, indicates that spot area diminished with age (Figure
220 S1). The slope of the regression between initial spot size and final spot size was compared to 1, the
221 expectation if the spots do not change over ontogeny. With the exception of the white spot of the fore
222 wings, the slope was significantly lower than 1 (Figure S1), indicating that their size diminished with age.

223 The mean asymmetry was 0.341±0.015 (N=168). There were no significant differences between dominant
224 and submissive males in asymmetry or size of the spots (Table 2). There was a significant negative
225 relationship between body length and total asymmetry (Pearson r=- 0.278, p<0.0001; Figure 3).

226 *Estimation of survival rates*

227 Among BW males, dominant males were resighted a mean of six times in contrast to three times for the
228 submissive males. HW males and females were resighted 1-2 times (Table 1). The analysis of daily survival
229 and recapture probabilities using MARK indicated that the most supported model was {Phi(g) p(g*t)},
230 implying an effect of the group (three types of males and females) on survival and a variable recapture
231 probability due to the effect of the group, the time and their interaction (Table S1). Introducing body
232 length as an individual covariate improved the statistical support for the model (Table S1). We fitted
233 models with common and different intercepts for the covariate, and also a model with a quadratic term
234 of body length, to test for stabilizing selection. Results indicated that the model with a common intercept
235 and without the quadratic term is the most supported (model {Phi(g*length) p(g*t)}-common intercept},
236 table S1). The best three models, all included daily variation of recapture rates and the effect of the group,
237 and their interaction. We estimated survival probabilities using the model averaging option of Mark (Table
238 1, and present the recapture rates of the first model with the term p(g), to allow a comparison between
239 groups.

240 The effect of the individual covariate, body length, was positive on survival rate in all types of individuals
241 (Figure 4). Hence, larger individuals had increased survivorship, even among non-territorial HW males and
242 females.

243 *Reproductive behaviour*

244 BW males (dominant and submissive) were identified and their reproductive activity in terms of number
245 of matings, sperm translocation and copulation duration was registered.

246 Sperm translocation occurred in precopulatory tandem, and had a duration of 19.3±0.4 (53), with a range
247 from 12 to 25 sec. Copulation duration oscillated between 3 and 16 minutes, with an average of 6.6±0.5
248 min (N=49 matings, all BW males), and only occasionally copulation was interrupted by short breaks.
249 Copulation duration was not correlated with any of the variables measured using bi-variate correlations
250 (results not shown; Spearman r; variables tested: asymmetry, body length, quality of territory (number of
251 individuals in the territory), temperature and age). Using a GLM with normal errors (see Methods), we
252 found that copulation duration was not different between dominant and submissive males, and the only
253 marginally significant variable was temperature, which had a negative effect (estimate=-0.039±0.020,
254 p=0.066; Table S2).

255 We analysed lifetime mating success of marked males. This analysis suggests that longevity had a positive
256 effect on mating success (estimate: 0.042±0.011, t_{158}= 3.90, p<0.001; Figure 5). Territory quality also had
257 a positive effect (estimate: 0.232±0.057, t_{158}= 4.07, p<0.001; Figure 6) and BW-submissive strategy had a
258 negative effect compared to BW-dominant strategy (estimate: -1.040±0.225, t_{158}= -4.62, p<0.001). The
259 other variables were not significant (see Supplementary Table S3).

260 ***Dominant and submissive roles: plastic or fixed?***

261 The sample of 79 BW males, whose spots were manipulated (Figure 1) to test whether spot size (black
262 and white) had an effect on their mating strategy, were observed during three days after manipulation.
263 Comparing day 0 to day 3, the experimental treatments had no significant effects, suggesting that the
264 strategy was not affected by spot size manipulation (Table 3). However, in two comparisons (day 0 to day
265 1, and day 0 to day 2) the initial status had a negative significant effect, i.e. animals with dominant status
266 were more likely to become submissive over time than the opposite (Table 3).
267

268 **DISCUSSION**

269 Our results indicate that BW males can behave as dominant or submissive. We found evidence for a
270 positive effect of territory quality (measured as the number of males occupying the area over time) and
271 lifespan on mating success, and that male morph strategy and sex affected the probability of recapture,
272 and larger individuals had higher survival. However, black wing spots asymmetry was not correlated with
273 the reproductive strategy of BW males, and the experimental manipulation of the black and white wing
274 spots did not affect male dominance. We will discuss these findings in relation to what is known in this
275 species and other territorial animals.

276 BW dominant males were resighted more often than BW submissive males, HW males and females. This
277 is easily explained since BW dominant males are more prone to stay on a territory for long periods,
278 because they are expected to be the best males, the only ones able to defend the territories close to the
279 water (see also Bañuelos Irusta & Araújo, 2007). In many animals, territorial males are usually larger, and
280 defend their territory from other males continuously (e.g. Baker, 1983), a situation commonly found in
281 other territorial damselflies (reviewed by Córdoba-Aguilar & Cordero-Rivera, 2005 and Suhonen, Rantala,

282   & Honkavaara, 2008) and other taxa (e.g. Mathis, 1991). Territory holders behave aggressively and this is
283   expected to be costly. In fact, experimentally increasing the level of aggressiveness with methoprene (an
284   analog of the juvenile hormone) impaired fat reserves and reduced survival in *Calopteryx* damselflies
285   (Contreras-Garduño et al., 2011) and reduced survival in *Argia* (Córdoba-Aguilar & Munguía-Steyer, 2015).
286   Being large and being territorial can be therefore costly, and the expectation is that only males of high
287   quality are able to defend their territory for long periods of time (Tsubaki & Ono, 1987). In our case, larger
288   individuals had higher survival rates not only in the two BW male morph strategies, but also in HW males
289   and females (Figure 3). This contrasts with previous results on the same population, that only found a
290   positive effect of size on survival in females but not in males (Munguía-Steyer, Córdoba-Aguilar & Romo-
291   Beltrán, 2010). The general trade-off between territory defence and survival, under the assumption that
292   territory holding is costly (Blanckenhorn, 2000), did not hold in our experiment, suggesting again that BW
293   dominant males were of high quality. In other damselfly species, larger males presented higher
294   survivorship (e.g. *Heteragrion cooki*: Rivas-Torres, et.al, 2017; *Polythore mutata*; Cordero-Rivera et al,
295   unpublished), and similar results were also found in other taxa, such as the mosquito *Aedes aegypti*
296   (Maciel-De Freitas, et.al, 2007). Large size is favoured in adult odonates, but probably not in larvae,
297   contributing to the stasis in body size observed over evolutionary time (Waller & Svensson, 2017).

298   We did not find differences in the asymmetry of the black wing spots between BW dominant and BW
299   submissive males. Nonetheless, our results indicated that larger males (independently of their
300   reproductive strategy) were more symmetric. Therefore, asymmetry *per se* does not seem to affect the
301   ability of males to behave in a dominant way, but perhaps could affect indirectly *via* the effect of the body
302   size. Furthermore, those males marked when young and recaptured as mature, indicated that spot size
303   diminished with age, a result in agreement with previous findings in other wing-pigmented damselflies
304   (*Mnais*: Sanmartín-Villar, 2017; *Polythore*: Sanmartín-Villar & Cordero-Rivera, 2016). Whether these
305   changes are adaptive, as apparently occurs with changes in coloration with age in other taxa (Dreiss &
306   Roulin, 2010; Lopez-Idiaquez et al., 2016) remains to be studied. It seems, therefore, that black wing spots
307   in *P. zoe* are important for agonistic interactions, and that over their life, males lose part of their signals
308   of quality. The expectation is that old males will be unable to hold territories when confronted by young
309   freshly coloured males (reviewed by Suhonen et al., 2008).

310   Our observations on mating behaviour and copula duration are consistent with other studies on the genus
311   *Paraphlebia*, with the exception that in *P. zoe* copulation was usually not interrupted, a fact commonly
312   observed in *P. quinta*, where it was interpreted as evidence for sperm ejection by females (González-
313   Soriano & Córdoba-Aguilar, 2003). We found that copulation is brief for odonates, with an average of 7
314   minutes, a value almost identical to previous studies of the same species (Wong-Muñoz et al., 2013), and
315   of similar duration for dominant and submissive males. During our fieldwork period, HW males were very
316   rare, but previous studies showed that HW males copulate for longer (Wong-Muñoz et al., 2013). Figure
317   5 shows that mating success was positively related to longevity, a result that is general in many odonates
318   (Fincke, Waage & Koenig, 1997; Koenig, 2008) and other animals (e.g. Madsen & Shine, 1992). Given the
319   unpredictable nature of weather, particularly in some regions, animals able to live for long periods are
320   likely to be more successful (Cordero, 1995), and in our species this correlates with a large body size. The
321   fact that previous studies have also found a positive effect of body size on male success in *P. zoe* (Bello-
322   Bedoy et al., 2015) is an argument for the necessity to demonstrate these effects in more than one study.
323   Contrasting results between studies could be due to variable selection regimes among years, which is a
324   reason to replicate research (Kelly, 2006) and increase our confidence on the generality of results.

325   Another factor that correlates with mating success is territory quality (Figure 6). In our case, the territory
326   quality was estimated as the number of males that occupied the area over time, although only one of

327   them was the dominant. Note that we assumed that males are able to identify the best territories (but
328   see below). Moreover, the higher the number of BW submissive males that surrounded a dominant BW
329   male, the more successful the dominant BW male was, suggesting that submissive BW males do not
330   represent a real threat for the dominant BW male, or at least the presence of submissive BW males does
331   not completely counterbalance whatever factors are affecting mating success of the BW dominant male.
332   Submissive BW males probably behave more as sneakers, which would make this system particularly
333   interesting as HW males may also behave as territorials, despite its more common satellite strategy, as
334   found by Romo-Beltrán et al (2009). These authors found that some territories were consistently more
335   attractive for females than others, which is similar to our findings (Figure 6). They suggested that males
336   did not recognize the best territories because in their study male turnover did not correlate with the
337   number of matings observed in each area (Romo-Beltrán, Macías-Ordóñez & Córdoba-Aguilar, 2009).
338   Nevertheless, this could depend on the season: when density is low, some territories would be vacant,
339   and males could in these cases perform better by occupying a vacant site than by trying to fight for an
340   already occupied territory. Being able to find and defend the best territories, i.e., those that attract a
341   higher number of females, seems to be the key for success in *P. zoe* males, and territorial defence is
342   apparently related to fat reserves (Romo-Beltrán, Macías-Ordóñez & Córdoba-Aguilar, 2009).

343   Contrarily to our predictions, we found that manipulating black and white wing spot size did not change
344   behavioural status in BW males; submissive males remained submissive, even after an enlargement of
345   their black spot. In agreement with this, we did not find differences in the black and white wing spot size
346   between dominant and submissive males (Table 2), and the size of the black and white wing spots did not
347   correlate with mating success. In birds, increasing the size of the spots, changed the aggressive behaviour
348   of manipulated males (Senar, 2006). Our reasoning was that wing spot size would be relevant in intra-
349   sexual selection (Romo-Beltrán, Macías-Ordóñez & Córdoba-Aguilar, 2009), but apparently the effect, if
350   any, was negligible. The only change detected was a tendency for dominant males to lose their status over
351   time (Table 3), but without relation to the experiment. It is possible that in species whose males do not
352   court, as *P. zoe*, females have to rely on cues that are not related with the attractiveness of the males (like
353   wing spots) and follow rules related with the resources offered by the territories, which in this species are
354   basically the best sites to oviposit.

355   **CONCLUSIONS**

356   Our findings add further arguments to the recognition of ethodiversity as a basic element of biodiversity
357   (Cordero-Rivera, 2017). We have found that *Paraphlebia zoe*, a species with male dimorphism (BW and
358   HW morphs) associated with alternative reproductive tactics, holds high behavioural diversity, because at
359   least three types of strategies, dominant, submissive and satellite, are concealed in males. This intra-
360   morph behavioural diversity might be related to male phenotype and environmental factors, such as
361   population density or different proportions of BW:HW males in different periods of the reproductive
362   season (Wong-Muñoz et al., 2013), which may affect male reproductive behaviour in damselflies
363   (Cordero-Rivera & Andrés, 2002). Performing similar manipulative experiments with the HW males when
364   they are in sufficient density would be of great relevance to understand the relationship between male
365   morph and dominance. Furthermore, future studies should take into account the UV wavelength of the
366   black and white bands, which in other species have been found to relate to territoriality (Xu & Fincke,
367   2015).

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524

The number of individuals marked and recaptured in each category, with their body length.

The number of individuals marked and recaptured in each category, with their body length. Survival rate was estimated by model averaging over the three most supported models (Table S1). Recapture rate was different for each day and morph. Here we present the estimates obtained from model {Phi(g, length) p(g)} (where g is group and t refers to time; see Table S1), to allow a comparison between groups. BW= black-winged male; HW= hyaline winged male. Mean±SE

2   The number of individuals marked and recaptured in each category, with their body length. Survival rate
3   was estimated by model averaging over the three most supported models (Table S1). Recapture rate was
4   different for each day and morph. Here we present the estimates obtained from model {Phi(g, length)
5   p(g)} (where g is group and t refers to time; see Table S1), to allow a comparison between groups. BW=
6   black-winged male; HW= hyaline winged male. Mean±SE

Variable	BW dominant	BW submissive	HW	Females
Number marked	54	133	25	111
Recaptured (%)	44 (81.5)	61 (45.9)	7 (28.0)	22 (19.8)
Number of recaptures	6.3±0.7	2.8±0.3	1.9±0.4	1.3±0.1
Body length (cm)	48.9±0.2	48.1±0.2	43.7±0.3	41.8±0.2
Daily survival rate	0.926±0.019	0.825±0.022	0.917±0.029	0.888±0.038
Daily recapture rate	0.558±0.024	0.408±0.024	0.197±0.046	0.062±0.015

Descriptive statistics of asymmetry and spot size (cm^2) for BW males of *Paraphlebia zoe*, in function of their mating strategy (D= dominant, S= submissive).

Descriptive statistics of asymmetry and spot size (cm^2) for BW males of *Paraphlebia zoe*, in function of their mating strategy (D= dominant, S= submissive). P-value refers to the comparison between dominant and submissive males using an ANOVA.

1 Descriptive statistics of asymmetry and spot size (cm²) for BW males of *Paraphlebia zoe*, in function of
2 their mating strategy (D= dominant, S= submissive). P-value refers to the comparison between dominant
3 and submissive males using an ANOVA.

Variable	Sample size	Minimum	Maximum	Mean	Std. deviation	p-value
Asymmetry | D	55	0.035	0.722	0.316	0.159	0.257
Asymmetry | S	113	0.066	1.066	0.353	0.211	
Fore-black right | D	55	0.556	0.901	0.730	0.077	0.974
Fore-black right | S	113	0.525	1.013	0.730	0.086	
Fore-black left | D	55	0.547	0.909	0.741	0.087	0.859
Fore-black left | S	113	0.472	1.144	0.744	0.098	
Back-black right | D	55	0.509	0.905	0.685	0.087	0.664
Back-black right | S	113	0.452	0.926	0.679	0.088	
Back-black left | D	55	0.497	0.878	0.693	0.089	0.562
Back-black left | S	113	0.436	0.900	0.684	0.090	
Fore-white right | D	55	0.136	0.309	0.215	0.041	0.651
Fore-white right | S	113	0.135	0.395	0.212	0.042	
Fore-white left | D	55	0.132	0.298	0.216	0.040	0.957
Fore-white left | S	113	0.097	0.357	0.216	0.044	
Back-white right | D	55	0.086	0.289	0.157	0.037	0.245
Back-white right | S	113	0.083	0.266	0.151	0.033	
Back-white left | D	55	0.088	0.227	0.153	0.035	0.851
Back-white left | S	113	0.082	0.270	0.152	0.035	

Results of the experiment of manipulation of black and white spot size of BW males of *Paraphlebia zoe*.

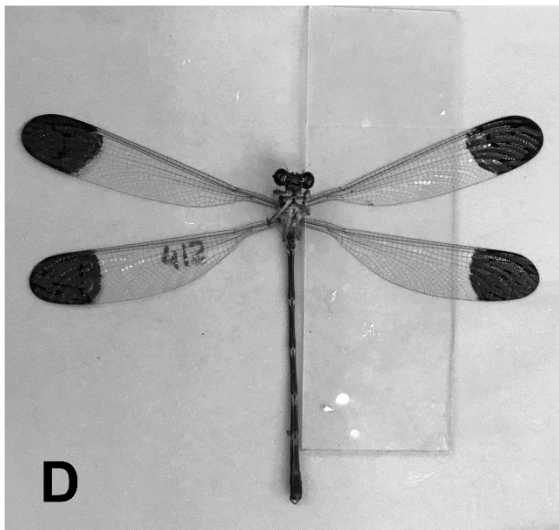
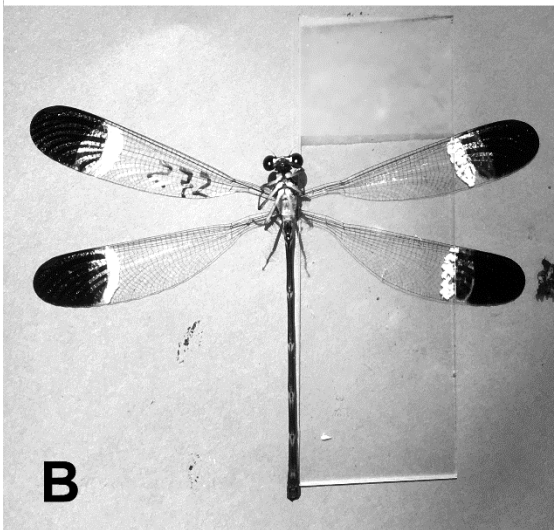
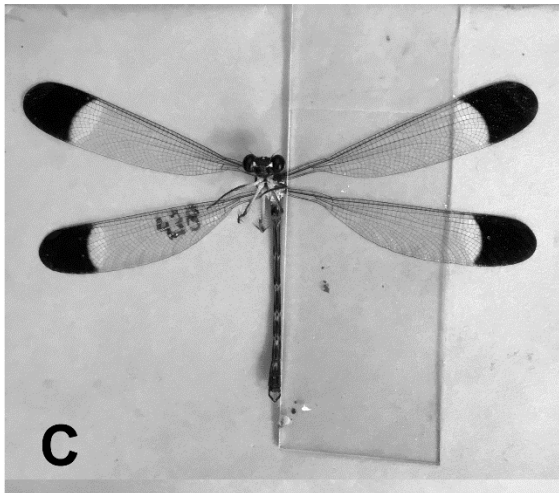
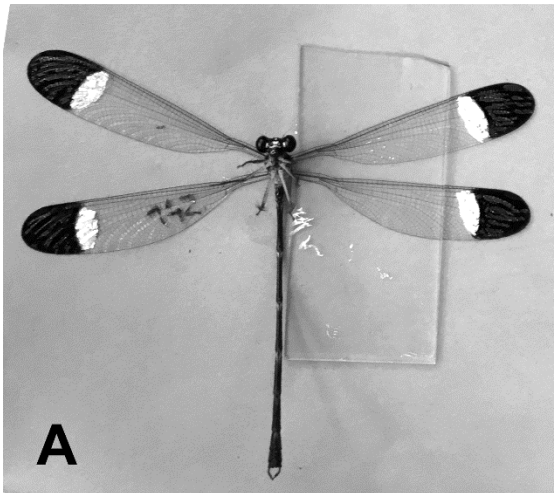
Results of the experiment of manipulation of black and white spot size of BW males of *Paraphlebia zoe*. Values are parameter estimates (±SE) after a GLM with Bernoulli distribution and logit link, where the response variate is "change of status", coded as 1 if changed or 0 if not. Treatments include (i) painting over white and black spots without changing their size (control 1), (ii) unmanipulated control males (control 2), (iii) erasing the white spot using black painting (EWS), (iv) increasing the black spot (IBS) and moving the white spot maintaining its size (reference level for the comparisons). Strategy refers to the initial reproductive strategy of the males, dominant (D) or submissive (S). Spot size manipulation significantly affected only whether males were dominant or submissive, and only for Day 0 versus Day 1 and Day 0 versus Day 2, as indicated by values of p<0.05 in **bold**.

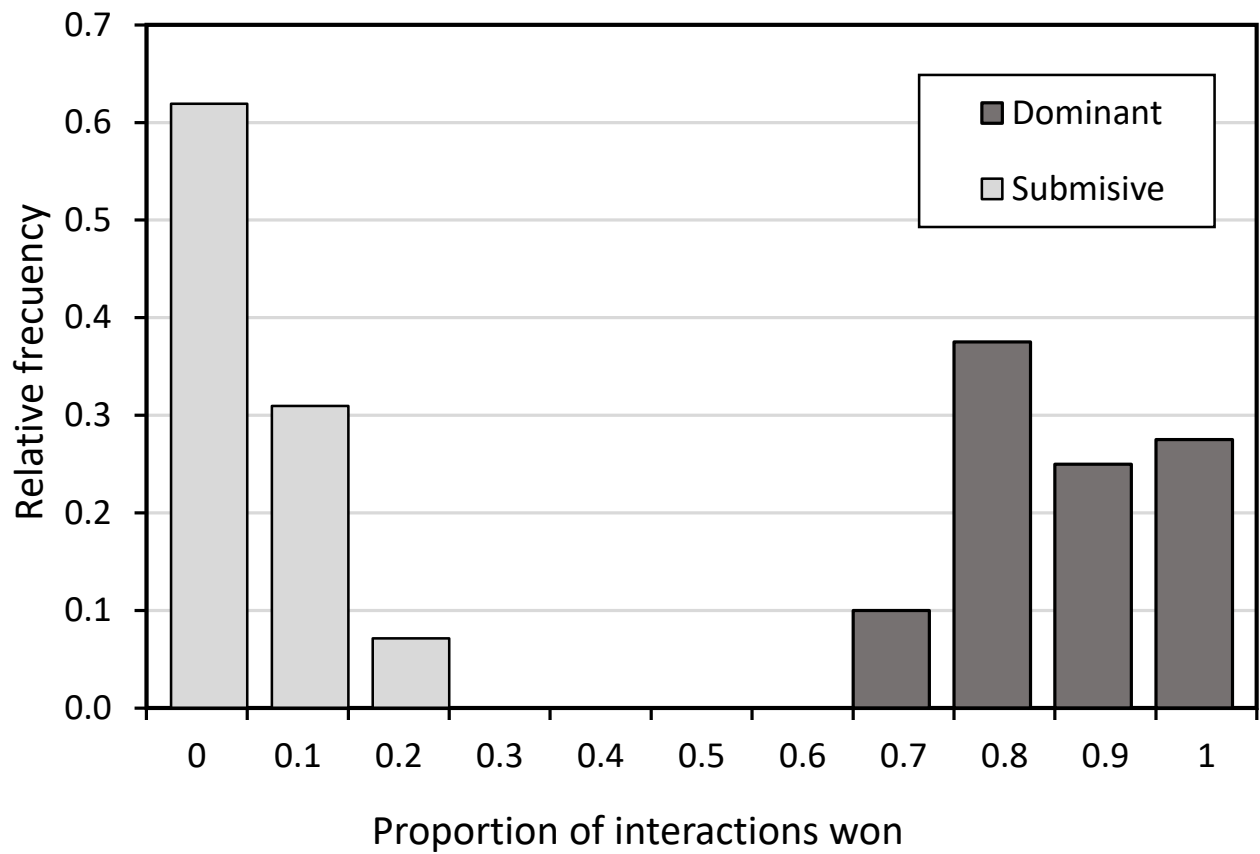
1   Results of the experiment of manipulation of black and white spot size of BW males of *Paraphlebia zoe*. Values are parameter estimates (±SE) after
2   a GLM with Bernoulli distribution and logit link, where the response variate is "change of status", coded as 1 if changed or 0 if not. Treatments
3   include (i) painting over white and black spots without changing their size (control 1), (ii) unmanipulated control males (control 2), (iii) erasing the
4   white spot using black painting (EWS), (iv) increasing the black spot (IBS) and moving the white spot maintaining its size (reference level for the
5   comparisons). Strategy refers to the initial reproductive strategy of the males, dominant (D) or submissive (S). Spot size manipulation significantly
6   affected only whether males were dominant or submissive, and only for Day 0 versus Day 1 and Day 0 versus Day 2, as indicated by values of
7    $p<0.05$ in **bold**.

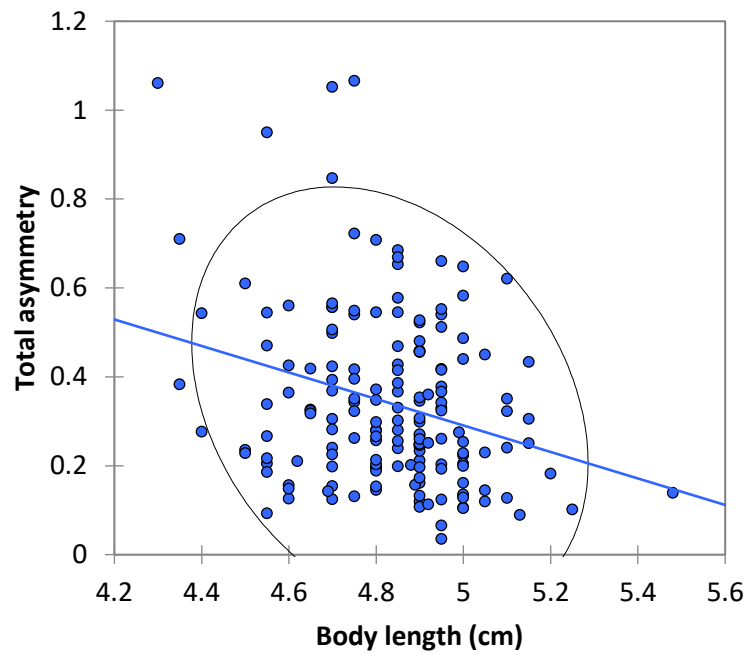
Factor	Comparison between days					
	0 to 1	0 to 2	0 to 3	1 to 2	1 to 3	2 to 3
control 1 (compared to IBS)	-1.07±1.00	-0.67±1.00	-0.51±0.68	-0.10±1.45	-0.13±0.70	-0.06±0.79
control 2 (compared to IBS)	-0.99±1.00	0.39±0.88	-0.63±0.71	1.59±1.17	0.00±0.71	-1.57±1.17
EWS (compared to IBS)	-0.39±0.89	0.71±0.86	-0.93±0.74	0.76±1.27	-0.92±0.81	-1.57±1.17
Strategy (S compared to D)	**-1.80±0.83**[a]	**-1.69±0.71**[b]	-0.89±0.52	-0.68±0.79	-0.71±0.53	0.02±0.70

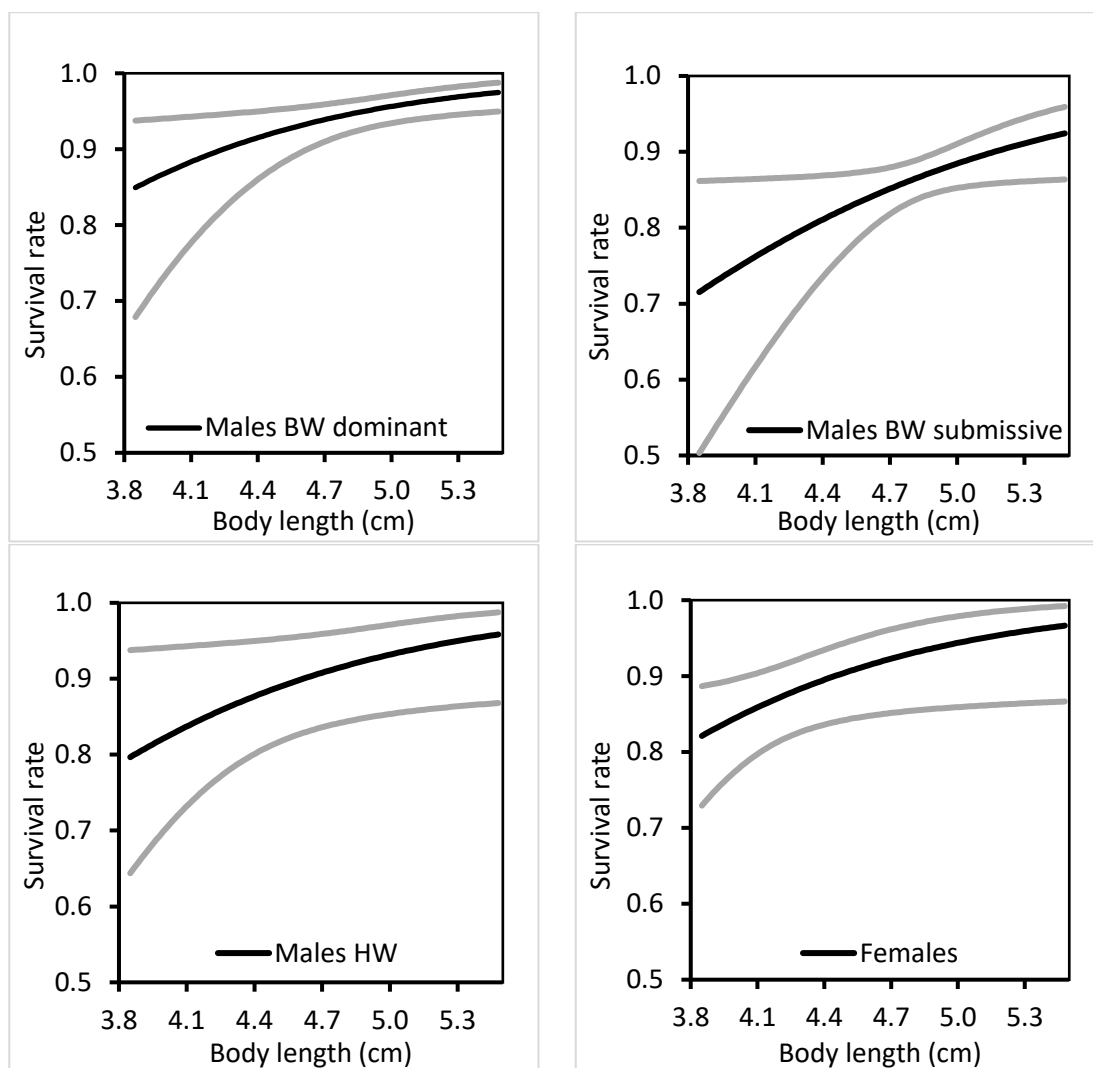
9   [a] p=0.030, [b] p=0.01

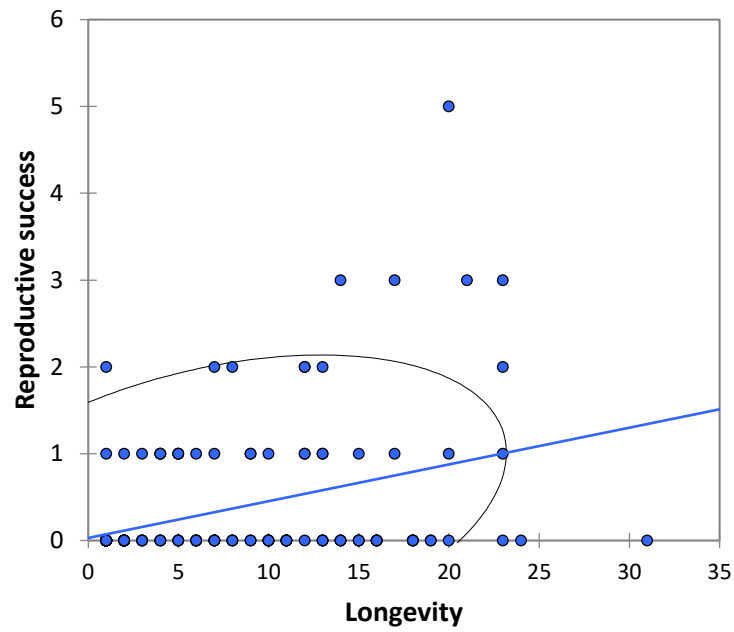
The four manipulative experiments.

(A) Control 1; painting over white and black spots. (B) Control 2; unmanipulated males. (C) IBS; increasing the black spot and moving the white spot maintaining its size. (D) EWS; erasing the white spot using black painting.

Histogram of the proportion of interactions won in BW males of *P. zoe.*

We considered dominant males, these that won more than 60% of the interactions, and submissive males these that won less than 50% of the interactions. In black, dominant BW males. In grey, submissive BW males.

The relationship between body length and total asymmetry for BW males of *P. zoe.*

The line represents the regression equation and the ellipse the 95% confidence interval (Pearson r= -0.167, p= 0.283).

The relationship between body length and survival rate for territorial (BW), non-territorial (HW) and females of *Paraphlebia zoe*.

The black line represents the estimate and the grey lines the confidence intervals. In all cases, larger individuals survived better.

The relationship between longevity and reproductive success (number of matings) for BW males of *P. zoe.*

The line represents the regression equation and the ellipse the 95% confidence interval (Pearson r= 0.39, p<0.001).

The relationship between the quality of territory (number of individuals in the territory) and reproductive success (number of matings) for BW males of *P. zoe.*

The line represents the regression equation and the ellipse the 95% confidence interval (Pearson r= 0.29, p<0.001).