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**Correlated morphological and colour differences among females of the damselfly *Ischnura elegans***

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Running head: Morphological differences in *I. elegans*

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## ABSTRACT

1 1. The female-limited colour polymorphic damselfly *Ischnura elegans* has proven to be an  
2 interesting study organism both as an example of female sexual polymorphism, and in the  
3 context of the evolution of colour polymorphism. The study of colour polymorphism can also  
4 have broader applications as a model of speciation processes.

5

6 2. Previous research suggests that there exist correlations between colour morph and other  
7 phenotypic traits, and that the different female morphs in *I. elegans* may be pursuing  
8 alternative phenotypically integrated strategies. However, previous research on morphological  
9 differences in southern Swedish individuals of this species was only carried out on laboratory-  
10 raised offspring from a single population, leaving open the question of how widespread such  
11 differences are.

12

13 3. We therefore analysed multi-generational data from 12 populations, investigating  
14 morphological differences between the female morphs in the field, differences in the pattern  
15 of phenotypic integration between morphs, and quantified selection on morphological traits.

16

17 4. We found that consistent morphological differences did indeed exist between the morphs  
18 across all study populations, confirming that the previously observed differences were not  
19 simply a laboratory artefact. We also found, somewhat surprisingly, that despite the existence  
20 of sexual dimorphism in body size and shape, patterns of phenotypic integration differed most  
21 between the morphs and not between the sexes. Finally, linear selection gradients showed that  
22 female morphology affected fecundity differently between the morphs.

23

24 5. We discuss the relevance of these results to the male mimicry hypothesis and to the  
25 existence of potential ecological differences between the morphs.

26 INTRODUCTION

27

28 Adaptation to different ecological conditions is well-recognized as both a potential route to  
29 speciation (Schluter, 2000; Nosil *et al.*, 2003; Vines & Schluter, 2006) and as the driver of the  
30 evolution of polymorphism (Galeotti *et al.*, 2003; Leimar, 2005; Ahnesjö & Forsman, 2006).

31 Although ecological polymorphism is better studied to date, interest in sexual polymorphisms,  
32 particularly female-limited sexual polymorphisms, is on the rise (reviewed in Svensson *et al.*,  
33 in press). A recent review also highlighted the importance of studies of colour polymorphisms  
34 as model systems of speciation processes (Gray & McKinnon, 2007). An association between  
35 differences in colour and differences in other traits seems to be a common feature in colour  
36 polymorphic systems, and implies the existence of pleiotropic effects of colour on other traits  
37 such as morphology or behaviour. For example, both male and female colour morphs in the  
38 side-blotched lizard *Uta stansburiana* differ in aggression levels and in immune function  
39 (Svensson *et al.*, 2001; Mills *et al.*, 2008). Similarly, colour morphs of the grasshopper *Tetrix*  
40 *undulata* differ in body size even when reared under identical environmental conditions  
41 (Ahnesjö & Forsman, 2003).

42

43 The colour polymorphic damselfly *Ischnura elegans* has proven to be a useful study species  
44 both in the context of colour polymorphisms in general and of specifically female-limited  
45 sexual polymorphisms. The polymorphism in this species appears to be maintained, in part,  
46 by negative frequency-dependent selection (Svensson *et al.*, 2005) mediated by male mating  
47 harassment (Gosden & Svensson, 2007), and to be related to differences in morphology  
48 (Abbott & Svensson, 2008), development time (Abbott & Svensson, 2005), and patterns of  
49 intersexual genetic correlations (Abbott and Svensson, submitted), at least in the southern  
50 Swedish populations studied in these papers. There also appear to be differences in behaviour

51 between the morphs (Van Gossum *et al.*, 2001a). An interesting twist to this story is the fact  
52 that one of the female morphs is considered a male mimic (Robertson, 1985; Hinnekint, 1987;  
53 Svensson *et al.*, in press), and there is evidence both avoidance of male mimics by males  
54 (Cordero *et al.*, 1998; Hammers & Van Gossum, 2008) which appears to be density-  
55 dependent (Gosden and Svensson, submitted), and of learned mate recognition of common  
56 morphs (Van Gossum *et al.*, 2001b).

57

58 Although previous research has suggested that the female morphs in *Ischnura elegans* differ  
59 in morphology (Abbott & Svensson, 2008; Abbott and Svensson, submitted), these studies  
60 were based on laboratory-raised individuals from a single population. We were also interested  
61 in investigating whether male mimicry could affect selection on morphology and patterns of  
62 phenotypic integration between female morphs. Here, we present results from a more  
63 extensive analysis of multi-generational data from 12 populations, investigating  
64 morphological differences between the morphs in the field. We found that consistent  
65 morphological differences did indeed exist between the morphs across populations, that  
66 morph-specific patterns of phenotypic integration existed between traits, and that fecundity  
67 selection on these morphological traits differed between the morphs. We discuss the relevance  
68 of these results to the male mimicry hypothesis and to potential ecological differences  
69 between the morphs.

70

## 71 METHODS

72

### 73 Study species

74

75 The blue-tailed damselfly, *Ischnura elegans*, is a small species with three female morphs and  
76 monomorphic males (Corbet, 1999). *I. elegans* can be found in ponds set in open landscapes  
77 across Europe from southern Sweden to northern Spain. This species is univoltine in Sweden,  
78 although southern European populations are typically multivoltine (Askew, 1988). One of the  
79 morphs, the Androchrome (A), has similar blue colouration and black melanin patterning as  
80 males, and is considered a male mimic (Robertson, 1985; Hinnekint, 1987; Svensson *et al.*, in  
81 press). The Infuscans (I) morph is generally olive green when mature, but has the same black  
82 melanin patterning as males and Androchromes. The third morph, Infuscans-obsolata (O), is  
83 olive green to brown when mature and generally has less black colouration than the other morphs,  
84 including red (when immature) or brown (when mature) humeral stripes on the sides of the  
85 thorax rather than black humeral stripes (for photographs and illustrations see Svensson *et al.*,  
86 in press).

87

88 The development of the female morphs of *I. elegans* is controlled by a single locus with three  
89 alleles, similar to the closely related species, *I. graellsii* (Cordero, 1990; Sánchez-Guillén *et*  
90 *al.*, 2005). The three alleles form a dominance hierarchy, with the Androchrome allele (A)  
91 dominant to the Infuscans (I) and Infuscans-obsolata (O) alleles and the I-allele dominant to  
92 the O-allele (i.e.  $A > I > O$ , Sánchez-Guillén *et al.*, 2005).

93

94 Data collection

95

96 We visited 12 populations outside Lund, in southern Sweden (Flyinge 30A1, Flyinge 30A3,  
97 Genarp, Gunnesbo, Habo, Hoftorupssjön, Höje å 14, Höje å 6, Höje å 7, Lomma, Vallby  
98 mosse, and Vombs vattenverk) in the years 2002 to 2005. The geographic distance between  
99 these populations ranges from 1.08 to 41.11 km (mean = 14.54km). Our previous work

100 examining molecular population differentiation using AFLP-markers has shown no evidence  
101 of isolation by distance among these populations (Abbott, 2006). The average pairwise degree  
102 of genetic differentiation ( $F_{st}$ ) between these populations is low to moderate and varies  
103 between 0.016 and 0.051 (Abbott *et al.*, 2008), indicating that these populations have  
104 diverged genetically but are not completely independent. Several of these populations have  
105 been relatively recently founded as part of a conservation program (Svensson & Abbott,  
106 2005) and are subject to frequent population extinctions and recolonizations (E. I. Svensson,  
107 personal communication). These two factors possibly explain the observed increase in the  
108 degree of neutral molecular population differentiation over the course of only two generations  
109 (Abbott *et al.*, 2008). These aspects of the genetic population structure of our study  
110 populations suggest that these populations may not yet have reached their evolutionary  
111 equilibria.

112

113 In each population damselflies were regularly collected over each season and five different  
114 morphological measurements taken to the nearest 0.01 mm: total length, abdomen length,  
115 thorax width, wing length, and width of the fourth segment of the abdomen (S4). Significant  
116 narrow-sense heritabilities based on parent-offspring data have been found in four out of these  
117 five traits (mean  $h^2$  forewing length: 0.463, total body length: 0.346, abdomen length: 0.242,  
118 thorax width: 0.173) when individuals have been raised in a common laboratory environment  
119 (Abbott, 2006). The genetic correlations between the traits are positive in all cases (range:  
120 0.025 - 1) and are significant in 8 of the 10 cases (Abbott, 2006). A total of 4937 individuals  
121 are included in the analysis of morphology, 2741 males and 2196 females (1457  
122 Androchromes, 563 Infuscans, and 176 Infuscans-obsoleta).

123



124 Fecundity data was collected as part of a long-term longitudinal investigation of our study  
125 populations (Svensson *et al.*, 2005; Svensson & Abbott, 2005; Gosden & Svensson, 2007;  
126 Gosden & Svensson, 2008; Gosden and Svensson, submitted). Field-caught females found in  
127 copula were set up in plastic oviposition chambers in an indoor laboratory and left for two  
128 days before being released. Eggs were counted on the third day. Sample sizes for the  
129 fecundity data were as follows: 953 Androchromes, 515 Infuscans, and 129 Infuscans-  
130 *obsoleta*. Our fecundity estimate is only a component of the total female lifetime fecundity,  
131 and as such may or may not reflect actual differences in lifetime reproductive success.  
132 However, it is known that fecundity from a single clutch can comprise 10-50% of the life-  
133 time fecundity in female damselflies (Fincke, 1986; Banks & Thompson, 1987; Corbet,  
134 1999), and that inter-clutch intervals can be as short as one day (Banks & Thompson, 1987).  
135 A laying period of two days may therefore actually represent two clutches and is potentially a  
136 good measure of fitness, especially since there is no evidence of morph-specific differences in  
137 lifespan in this or in a closely related polymorphic species (Cordero, 1992; Cordero *et al.*,  
138 1998; Andrés & Cordero Rivera, 2001). Our estimate is also likely to be a good fitness  
139 component given that female damselflies will lay a large proportion of the eggs present in the  
140 ovaries when presented with a favourable environment and left undisturbed (Corbet, 1999),  
141 which is the case here.

142

143 Analysis

144

145 All analyses were carried out in STATISTICA (Statsoft, 2004). We first looked for evidence  
146 of morphological differences between the sexes by carrying out a mixed-model MANOVA  
147 with all 5 morphological measures as dependent variables, and Year (random effect),  
148 Population (random effect), and Sex (fixed effect) as predictor variables (Population and Year

149 were random effects since our dataset represents a subsample of all possible years and  
150 populations, but the results do not change if they are instead treated as fixed effects). All two-  
151 way interactions were included in the model. We also carried out an analysis of  
152 morphological differences between the morphs using the same design, but with a fixed Morph  
153 effect in place of the Sex effect (we could not include both Sex and Morph in the same  
154 analysis since males are monomorphic). There was evidence of highly significant main effects  
155 of both Sex and Morph (see Results), confirming our expectation of the existence of  
156 morphological differences between these groups. In order to make these differences more  
157 readily interpretable in terms of overall size and shape and to avoid any problems associated  
158 with multicollinearity, we therefore performed a principal components analysis on all five  
159 morphological measurements, and selected the first two PCs for further analysis using mixed  
160 models of the same design as above.

161

162 Number of eggs laid was used in the calculation of linear selection gradients on all 5  
163 morphological measures (Lande & Arnold, 1983). Selection analysis was carried out in  
164 several steps. First, morphological measures were standardized by female morph to a mean of  
165 zero and standard deviation of 1 within each morph. Second, relative fecundity was calculated  
166 separately for each morph. Standardized selection gradients were then estimated separately  
167 for each morph using mixed models with fecundity values as the dependent variable, Year  
168 and Population (and their interaction) as random effects to control for inter-population and  
169 inter-year differences in fecundity, and each trait as fixed continuous factors. We then tested  
170 for significant differences in the magnitude and/or direction of selection using a mixed model  
171 with Year and Population (and their interaction) as random factors, each trait as fixed  
172 continuous factors, and morph\*trait interactions for each trait. In this analysis significant trait  
173 effects indicate significant linear selection on that trait which is consistent across morphs, and

174 significant trait\*morph effects indicate that the magnitude and/or direction of selection on that  
175 trait is dependent on female morph. Note that we did not include a main effect of Morph in  
176 this analysis since fecundity values had already been standardized by female morph.  
177 Quadratic selection gradients were also investigated, but were found to be non-significant in  
178 all cases except one (there was some evidence of divergent selection on S4 width in  
179 Androchromes) and are therefore not presented. Similarly, we looked for evidence of  
180 variation in the strength and/or magnitude of selection between years and between  
181 populations (c.f. Gosden & Svensson, 2008) but found none (no significant year\*trait or  
182 population\*trait interactions) so results from this analysis are not presented either.  
183  
184 Conditional independence graphs were constructed after Magwene (2001). This method  
185 represents graphically the relationships between traits that remain after controlling for shared  
186 correlations between traits. This is done by calculating the phenotypic correlation matrix for  
187 the data set, inverting the matrix and then scaling the inverted matrix (Magwene, 2001),  
188 which results in a matrix of partial correlations for the dataset. The matrix of partial  
189 correlations is then tested for significance and strength of edges (Magwene, 2001) and  
190 presented graphically. These conditional independence graphs are a convenient way of  
191 visualizing phenotypic integration between traits (Magwene, 2001; Eroukhmanoff &  
192 Svensson, 2008). Similarity of phenotypic integration (partial correlation) matrices was  
193 analysed using mantel tests, and differences in the magnitude of correlations between groups  
194 were tested using t-tests. Although it would be interesting to see if differences in phenotypic  
195 integration patterns between the sexes and the morphs are also dependent on year and  
196 population, this would unfortunately result in very small sample sizes for some morph-year-  
197 population combinations, leading to unreliable partial correlation estimates. We have instead

198 elected to pool data from all years and populations and focus on general differences between  
199 the sexes and the morphs.

200

## 201 RESULTS

202

203 Results from the MANOVA analyses indicated the existence of highly significant  
204 morphological differences between the sexes ( $F_{5, 4870} = 1424.3, P < 0.0001$ ) and the morphs  
205 ( $F_{10, 4228} = 11.0, P < 0.0001$ ). We therefore used PCA to obtain overall measures of size and  
206 shape for further analysis. PC1 accounted for 63.98% of the total variation and was a measure  
207 of overall size, since the factor loadings for all five traits were positive and large (Table 1).  
208 PC2 accounted for 21.44% of the variation and had relatively high positive loadings on wing  
209 length and abdomen width (S4) and high negative loadings on total length and abdomen  
210 length (Table 1). This means that PC2 can be considered a measure of shape, and that  
211 individuals with positive values of PC2 have relatively shorter, wider abdomens and longer  
212 wings. This pattern of factor loadings for PC2 is qualitatively very similar to that found in a  
213 previous laboratory analysis of morphology (Abbott & Svensson, 2008), and suggests that  
214 results for shape differences are comparable between these studies. All subsequent PCs  
215 accounted for approximately 8% of the variation or less, and were therefore not analysed any  
216 further.

217

218 Analysis of PC1 (body size) showed that differences between populations varied between  
219 years (significant Population\*Year effect, Table 2). Females were larger than males in all  
220 populations (significant effect of Sex, Table 2A, LS means  $\pm$  SEs: females:  $0.623 \pm 0.020$ ,  
221 males:  $-0.656 \pm 0.031$ ), but the degree of sexual size dimorphism varied between populations  
222 (significant effect of Population\*Sex, Table 2A, Figure 1A) and years (significant effect of

223 Sex\*Year, Table 2A, Figure 1B). Size differences between the female morphs trended toward  
224 significance ( $P < 0.08$  Morph effect, Table 2B, Figure 2A), and there was no evidence of  
225 variation in size dimorphism between populations or years (no significant effects of  
226 Population\*Morph or Morph\*Year, Table 2B), in contrast to results for sexual size  
227 dimorphism. Post-hoc tests showed that Infuscans females were significantly larger than  
228 Androchrome and Infuscans-obsoleta females (Fig 2A, all  $P < 0.01$ , LS means  $\pm$  SEs:  
229 Androchromes:  $0.613 \pm 0.027$ , Infuscans:  $0.718 \pm 0.046$ , Infuscans-obsoleta:  $0.578 \pm 0.070$ ).  
230  
231 Differences in PC2 (body shape) between populations were also dependent on year  
232 (significant Population\*Year effect, Table 3). There was sexual dimorphism in body shape  
233 (PC2) in all populations (significant effect of Sex, Table 3A), and the difference between the  
234 sexes was greater in some populations than in others (significant Population\*Sex effect, Table  
235 3A, Figure 1C), but there was no effect of year on sexual dimorphism in shape (no effect of  
236 Year\*Sex, Table 3A). Males had lower values of PC2 than females, in other words longer,  
237 narrower abdomens and shorter wings than females (LS means  $\pm$  SEs: females:  $0.711 \pm 0.021$ ,  
238 males:  $-0.597 \pm 0.033$ ). The female morphs also differed in body shape (significant effect of  
239 Morph, Table 3B). Androchromes had significantly more male-like morphology (i.e. longer,  
240 narrower abdomen and shorter wings) than Infuscans and Infuscans-obsoleta females ( $P <$   
241  $0.0001$ , Figure 2B, LS means  $\pm$  SEs: Androchromes:  $0.577 \pm 0.029$ , Infuscans:  $0.887 \pm 0.049$ ,  
242 Infuscans-obsoleta:  $0.867 \pm 0.075$ ). As with overall size differences, this pattern was constant  
243 across populations (no significant effect of Population\*Morph, Table 3B) and years (no  
244 significant effect of Year\*Morph, Table 3B).  
245  
246 Conditional independence analysis revealed a unique pattern of phenotypic integration in  
247 Infuscans-obsoleta females (Figure 3). Mantel tests demonstrated that all phenotypic

248 integration (partial correlation) matrices were highly related, with correlation coefficients  
249 greater than 0.9 (males vs. Androchromes:  $r = 0.9798$ , males vs. Infuscans:  $r = 0.9640$ , males  
250 vs. Infuscans-obsoleta:  $r = 0.9192$ , Androchromes vs. Infuscans:  $r = 0.9825$ , Androchromes  
251 vs. Infuscans-obsoleta:  $r = 0.9306$ , and Infuscans vs. Infuscans-obsoleta:  $r = 0.9398$ ; all  $P <$   
252  $0.0001$ ). However, from these correlation coefficients we could see that correlations involving  
253 Infuscans-obsoleta were somewhat lower than correlations involving the other two morphs  
254 ( $0.91$ - $0.94$  and  $0.96$ - $0.99$ , respectively), and this difference is in fact significant when tested  
255 using a t-test ( $t = 5.49$ ,  $df = 4$ ,  $P = 0.005$ ). This suggests that phenotypic integration patterns  
256 in Androchromes, Infuscans females, and males are all more closely related to each other than  
257 any of them are to Infuscans-obsoleta females. In contrast, correlations between the sexes are  
258 not lower than correlations within the sexes (i.e. between female morphs;  $t = 0.139$ ,  $df = 4$ ,  $P$   
259  $= 0.896$ ), so there do not seem to be any large overall differences in phenotypic integration  
260 patterns between the sexes. From visual inspection of the phenotypic integration graphs, we  
261 can see that Androchromes and Infuscans females had very similar patterns of phenotypic  
262 integration, differing only in the strength of some of the partial correlations. Likewise, males  
263 had a very similar pattern of phenotypic integration to both Androchromes and Infuscans  
264 females, only differing in the addition of a new weak edge between abdomen length and  
265 thorax width. In contrast, Infuscans-obsoleta females not only lacked two of the edges present  
266 in other females, but also exhibited a unique edge between abdomen width (S4) and total  
267 length. This amounts to a 30% difference in presence/absence of edges (3/10 possible edges)  
268 between Infuscans-obsoleta and the other two morphs. The high partial correlations between  
269 total length and abdomen length seen in all groups are probably because these traits are not  
270 completely independent (abdomen length is a component of total length).  
271

272 There was also evidence that morphological differences had morph-specific fitness  
273 consequences. Selection gradients on total length, abdomen length, abdomen width, and wing  
274 length differed significantly between the morphs (Table 4A). Androchrome females  
275 experienced significant positive selection S4 width, Infuscans females experienced significant  
276 negative selection on total length but positive selection on abdominal length, and Infuscans-  
277 obsoleta females experienced significant positive selection on S4 width but negative selection  
278 on wing length (Table 4B).

279

## 280 DISCUSSION

281

282 Previous research on laboratory-raised individuals from a single population suggested that the  
283 female colour morphs in *Ischnura elegans* differed in morphology (Abbott & Svensson,  
284 2008). In this study we found that morphological differences observed in the field were  
285 generally similar to those previously observed in the laboratory (Abbott & Svensson, 2008).  
286 This study therefore provides clear evidence that the existence of morphological differences  
287 between female colour morphs in *I. elegans* is not simply a laboratory artefact, nor the  
288 property of a single population, but is in fact a consistent feature both over time and across all  
289 12 populations studied here.

290

291 Sexual size dimorphism is common in damselflies and in non-territorial species such as *I.*  
292 *elegans* females are usually larger than males (Corbet, 1999). Both this fact and previous  
293 results (Abbott & Svensson, 2008) led us to expect to find sexual dimorphism in body size  
294 and shape. Indeed, males were smaller than females, with relatively longer, narrower  
295 abdomens and shorter wings (Figure 1). Differences in body shape are likely to be related to  
296 the positions of the sexes during mating and fecundity selection in females, as discussed in

297 Abbott & Svensson (2008). Interestingly, the degree of sexual dimorphism in size and shape  
298 varied between populations and years (Tables 2A and 3A). This could be a result of  
299 differential sensitivity of the sexes to different abiotic or biotic environmental conditions  
300 between populations (Badyaev, 2002). For example, it has previously been found that  
301 photoperiod and temperature jointly affect the degree of SSD in the damselfly *Lestes viridis*  
302 (de Block & Stoks, 2003). Similarly, spatial and temporal fluctuations in the strength of  
303 fecundity selection in females or of sexual selection in males (Gosden & Svensson, 2008)  
304 could also produce varying patterns of SSD. Finally, variation in morph frequencies between  
305 years/populations in combination with overall size differences between the morphs (see  
306 below) could also partly explain spatial and temporal variation in the degree of SSD. Because  
307 Infuscans females are larger overall than the other morphs, populations/years with a high  
308 frequency of Infuscans females could have higher SSD than populations/years with a low  
309 frequency of this morph, assuming male size is more or less constant.

310

311 Though it has previously been found that Androchromes may be larger than the other morphs  
312 in a closely related species (Cordero, 1992), this was not the case in our study populations.  
313 Infuscans females were larger than the other morphs, and Androchrome females had  
314 relatively longer, narrower abdomens and shorter wings than the other morphs (Figure 2).  
315 These consistent morphological differences are particularly striking since they exist despite  
316 clinal variation in body size along the coastal-inland gradient in these populations (Gosden &  
317 Svensson, 2008), and stand in sharp contrast to the observed temporal and spatial variation in  
318 the degree of sexual dimorphism. Female fecundity is often related to body size in insects  
319 (Bonduriansky, 2001), and since previous results (Svensson & Abbott, 2005) indicate that  
320 Infuscans females have higher overall fecundity than the other morphs, it seems reasonable  
321 that this elevated fecundity is partially the result of their larger size. However we did not find



322 any evidence of selection for larger thorax width, which is the best predictor of overall size  
323 (i.e. highest loading on PC1; Table 1), and Infuscans females actually experienced negative  
324 selection on total body length (Table 4). This suggests that other selective pressures than  
325 fecundity selection may be influencing female size, which is rather surprising given  
326 widespread evidence of fecundity selection on size in insects (Bonduriansky, 2001). It is,  
327 however, consistent with previous work in two other damselfly species which have found that  
328 female size was not related to fecundity (Anholt, 1991; Richardson & Baker, 1997).

329

330 The difference in body shape between Androchromes and the other morphs is analogous to  
331 the differences between the sexes, though smaller in magnitude (see Results). One common  
332 explanation of the maintenance of the polymorphism in this and related species is that  
333 Androchrome females are male mimics, and therefore avoid costs of male mating harassment  
334 (e.g. Cordero *et al.*, 1998; Cordero Rivera & Sánchez-Guillén, 2008), and other studies have  
335 found evidence of phenotypic similarity of Androchromes to males in colouration and black  
336 patterning (Joop *et al.*, 2006; Van Gossum *et al.*, 2008). Although the male mimicry  
337 hypothesis only explicitly deals with similarity in colouration between males and  
338 Androchrome females, correlated morphological and colour differences in other polymorphic  
339 species from a range of taxa (see Introduction) suggest that morphological mimicry could also  
340 be a possibility. The more masculine phenotype typical of Androchromes is consistent with  
341 this explanation, although other frequency- and density-dependent factors are known to be at  
342 work in these populations (Svensson *et al.*, 2005; Gosden & Svensson, 2007). Some studies  
343 suggest that Androchromes are always less preferred by males than other morphs (Hammers  
344 & Van Gossum, 2008; Cordero Rivera & Sánchez-Guillén, 2008), while others suggest that  
345 males learn to recognize and prefer common morphs (Van Gossum *et al.*, 2001a; Van Gossum  
346 *et al.*, 2001b; Fincke *et al.*, 2007). Male mimicry and learned mate recognition need not be

347 mutually exclusive, however, for example if Androchromes must reach higher frequencies  
348 than other morphs before males learn to recognize them. Despite evidence of morphological  
349 male mimicry in Androchromes, we did not find any clear evidence of selection for  
350 masculinized morphology in Androchromes or, alternatively, against masculinized  
351 morphology in the other morphs. It is possible that Androchromes are already at or near their  
352 morphological optimum and only experience weak stabilizing selection on morphology. It is  
353 also possible that our fecundity estimates did not capture aspects of fitness that are subject to  
354 selection for masculinization, for example if more masculinized morphology in  
355 Androchromes affects survival. However, weak stabilizing selection is unlikely since we  
356 found no evidence of stabilizing selection for any trait in Androchromes (data not shown),  
357 and there is no evidence of differences in lifespan between morphs in a related polymorphic  
358 species (Andrés & Cordero Rivera, 2001), which speaks against effects of survival selection.  
359 This suggests that morphological similarity between males and Androchromes could be the  
360 result of pleiotropic effects at the morph locus rather than selection for masculinized  
361 morphology. Alternatively, Androchromes could suffer a trade-off between maximising their  
362 fecundity and minimising male mating harassment through male mimicry (Gosden and  
363 Svensson, submitted) resulting in no net selection for masculinized morphology.

364  
365 Conditional independence analysis (Magwene, 2001) also revealed differing patterns of  
366 phenotypic integration between the morphs. Interestingly, rather than seeing a large difference  
367 in the pattern of phenotypic integration between the sexes, which is what one might expect  
368 based on the existence of sexual dimorphism in size and shape in *I. elegans* (see above), the  
369 largest difference in phenotypic integration was between Infuscans-obsoleta females and the  
370 other morphs (Figure 3). This is consistent with laboratory results on morphology (Abbott &  
371 Svensson, 2008) and development time (Abbott & Svensson, 2005), which also found that

372 Infuscans-obsolata females were the most divergent morph. Why this large difference in the  
373 pattern of phenotypic integration between Infuscans and Infuscans-obsolata females does not  
374 seem to be reflected in a large difference in PC2 (body shape) is unknown, but could simply  
375 be because PC2 is capturing other aspects of shape variation than the phenotypic integration  
376 analysis (Jackson, 1991). This is possible since PC2 is likely to be more heavily influenced by  
377 differences in shape between the sexes than by differences in shape between the morphs. One  
378 of the unique features of the pattern of phenotypic integration in Infuscans-obsolata was the  
379 presence of an edge between abdominal width (S4) and total length. Furthermore, the  
380 strongest positive selection gradient in the selection analysis was on S4 width in Infuscans-  
381 obsolata females ( $\beta > 0.3$ , Table 4). It is tempting to speculate that these two results are  
382 related, and that strong selection on abdominal width in Infuscans-obsolata females has  
383 resulted in increased phenotypic integration of this trait compared to the other morphs.  
384 Similarly, the strongest negative selection gradient in the selection analysis was on wing  
385 length in Infuscans-obsolata females ( $\beta < -0.3$ , Table 4), and Infuscans-obsolata is the only  
386 group lacking significant integration between abdomen length and wing length. Perhaps  
387 strong negative selection on wing length in this morph has resulted in a decoupling of wing  
388 length and abdomen length. However *why* Infuscans-obsolata females experience such strong  
389 selection on these particular traits is currently unknown. More research on differing patterns  
390 of phenotypic and genetic integration of traits between the morphs is obviously needed if a  
391 detailed understanding of their evolution is to be achieved.

392

393 If fecundity selection for increased size or for morphological male mimicry in Androchromes  
394 cannot explain the morph-specific patterns of selection on morphology seen here, another  
395 possibility could be that each morph is selected to be better adapted to slightly different  
396 ecological conditions. Morph frequencies in this species differ both between geographical

397 regions in Europe (Gosden, 2008) and between newly-established and older populations  
398 within southern Sweden (Svensson & Abbott, 2005), suggesting a role for ecological  
399 specialization and local adaptation in determining morph frequencies. Note that ecological  
400 differences between the morphs and the existence of negative frequency-dependence are not  
401 mutually exclusive. Ecological differences between the morphs could determine the range of  
402 morph frequencies that are stable in different populations or regions, while frequency-  
403 dependence could regulate morph frequency dynamics within that range (Andrés *et al.*, 2000;  
404 Abbott *et al.*, 2008). For example, ecological determination of stable ranges of morph  
405 frequencies have been found in the candy-strip spider *Enoplagantha ovata* (Oxford, 2005).  
406 The existence of ecological differences between the morphs and their interaction with other  
407 factors is a potentially productive area for future research.

408

409 We have previously argued that the female morphs in *I. elegans* may be pursuing alternative  
410 phenotypically integrated strategies (Abbott & Svensson, 2008). The existence of correlated  
411 differences in morphological (this study), behavioural (Van Gossum *et al.*, 2001a; Gosden &  
412 Svensson, 2007), and life history traits (Abbott & Svensson, 2005; Svensson & Abbott, 2005)  
413 between morphs of *I. elegans* in our study populations support this idea, as does recent  
414 research showing differential effects of male mating harassment on the morphs (Gosden and  
415 Svensson, submitted). Although more research is needed before full knowledge of the nature  
416 of these strategies is achieved, this system has the potential to become a model system for the  
417 evolution of alternative female sexual polymorphisms (Svensson *et al.*, in press).

418

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595

Table 1: Factor loadings for the first and second principal components calculated from five morphological traits. PC1 is a measure of overall size and accounted for 63.98% of the total variation in morphology between individuals. PC2 is a measure of body shape, where individuals with positive values of PC2 have longer wings and wider but shorter abdomens, and accounted for 21.44% of the total variation in morphology between individuals.

Measurement	Loading PC1	Loading PC2
Total length	0.8234	-0.4916
Abdomen length	0.7930	-0.5397
Thorax width	0.8449	0.0925
S4 width	0.7086	0.6181
Wing length	0.8224	0.3850

Table 2: Results of statistical analysis of body size (PC1) using mixed models. Population and Year are random effects, as are all interactions with Population and Year. Sex and Morph are fixed effects, and were included in separate analyses (see Methods). N = 4937 (all individuals) for Sex (A), and N = 2196 (females only) for Morph (B).

Effect	Df	MS	F	<i>P</i> -value
A)				
Population	11	46.18	20.14	<0.0001
Sex	1	570.8	423.9	<0.0001
Year	3	36.99	19.40	0.0001
Population*Sex	11	1.200	2.832	0.0011
Population*Year	33	2.108	4.975	<0.0001
Sex*Year	3	2.004	4.730	0.0027
Error	4874	0.424		
B)				
Population	11	20.49	24.21	<0.0001
Morph	2	1.221	3.116	0.0768
Year	3	11.92	17.04	<0.0001
Population*Morph	22	0.448	0.990	0.4733
Population*Year	33	1.393	3.077	<0.0001
Morph*Year	6	0.359	0.792	0.5761
Error	2118	0.453		

Table 3: Results of statistical analysis of body shape (PC2) using mixed models. Population and Year are random effects, as are all interactions with Population and Year. Sex and Morph are fixed effects, and were included in separate analyses (see Methods). N = 4937 (all individuals) for Sex (A), and N = 2196 (females only) for Morph (B).

Effect	Df	MS	F	<i>P</i> -value
A)				
Population	11	14.95	8.946	<0.0001
Sex	1	596.6	860.7	<0.0001
Year	3	13.29	15.57	<0.0001
Population*Sex	11	1.131	2.310	0.0081
Population*Year	33	1.407	2.873	<0.0001
Sex*Year	3	0.432	0.882	0.4498
Error	4874	0.490		
B)				
Population	11	4.971	6.676	<0.0001
Morph	2	11.89	16.09	0.0005
Year	3	13.21	16.71	<0.0001
Population*Morph	22	0.572	1.106	0.3318
Population*Year	33	0.986	1.906	0.0015
Morph*Year	6	0.824	1.594	0.1449
Error	2118	0.517		

Table 4: Summary of results of selection gradient analysis for five morphological traits (significant values are highlighted in bold). A) Results of analysis to identify traits with morph-specific variation in the magnitude and/or direction of selection. There was evidence of variation in overall fecundity levels between years and populations, and of overall positive selection on S4 width and wing length. However, all traits except thorax width also showed evidence of morph-specific effects on the magnitude and/or direction of selection. B) Morph-specific selection gradients for all five morphological traits (SEs reported in brackets) calculated from separate analyses for each morph (see Methods). Androchrome females experienced significant positive selection on S4 width, Infuscans females experienced significant negative selection on total length but positive selection on abdominal length, and Infuscans-obsolata females experienced significant positive selection on S4 width but negative selection on wing length.

A)

Effect	Df	MS	F	<i>P</i> -value
Population	11	1.864	1.692	0.1116
<b>Year</b>	3	2.943	3.323	<b>0.0251</b>
<b>Year*Population</b>	32	1.249	2.380	<b>&lt;0.0001</b>
Total length	1	0.051	0.096	0.7563
Abdomen length	1	0.352	0.671	0.4130



Thorax width	1	0.004	0.007	0.9328
<b>S4 width</b>	1	8.885	16.94	<b>&lt;0.0001</b>
<b>Wing length</b>	1	2.915	5.556	<b>0.0185</b>
<b>Total length*Morph</b>	2	1.623	3.093	<b>0.0457</b>
<b>Abdomen length*Morph</b>	2	1.943	3.703	<b>0.0249</b>
Thorax width*Morph	2	0.050	0.094	0.9100
<b>S4 width*Morph</b>	2	3.490	6.653	<b>0.0013</b>
<b>Wing length*Morph</b>	2	1.999	3.810	<b>0.0224</b>
Error	1535	0.525		

B)

Trait	Androchrome	Infuscans	Infuscans-obsoleta
Total length	0.0838 (0.0476)	<b>-0.1576 (0.0761)</b>	0.0478 (0.3467)
Abdomen length	-0.0521 (0.0514)	<b>0.1680 (0.0710)</b>	0.1659 (0.3319)
Thorax width	-0.0003 (0.0371)	0.0109 (0.0500)	-0.0646 (0.1427)
S4 width	<b>0.0918 (0.0306)</b>	-0.0023 (0.0411)	<b>0.3620 (0.1404)</b>

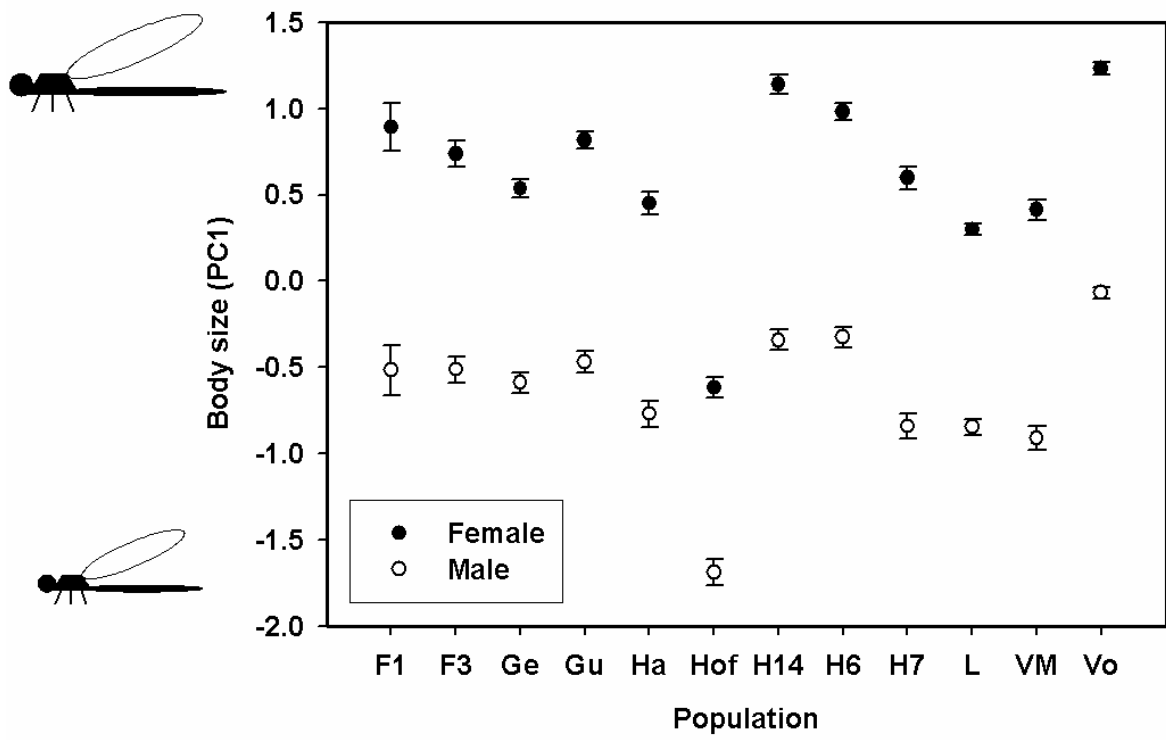
Wing length	0.0088 (0.0295)	0.0007 (0.0472)	<b>-0.3739 (0.1805)</b>
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Figure 1: Sexual dimorphism in body size (PC1) according to A) population, and B) year, and sexual dimorphism in C) body shape (PC2) according to population. Population abbreviations are as follows: F1 = Flyinge 30A1, F3 = Flyinge 30A3, Ge = Genarp, Gu = Gunnesbo, Ha = Habo, Hof = Hofterupssjön, H14 = Höje å 14, H6 = Höje å 6, H7 = Höje å 7, L = Lomma, VM = Vallby mosse, and Vo = Vombs vattenerk. Females are always significantly larger than males, but the degree of sexual size dimorphism varied between populations and years. Similarly, males have relatively longer, narrower abdomens and shorter wings than females (lower values of PC2) but the magnitude of differences in body shape between the sexes varied between populations. Error bars denote SEs. Note that cartoon damselflies are for illustrative purposes only and do not reflect the magnitude of actual differences between the sexes.

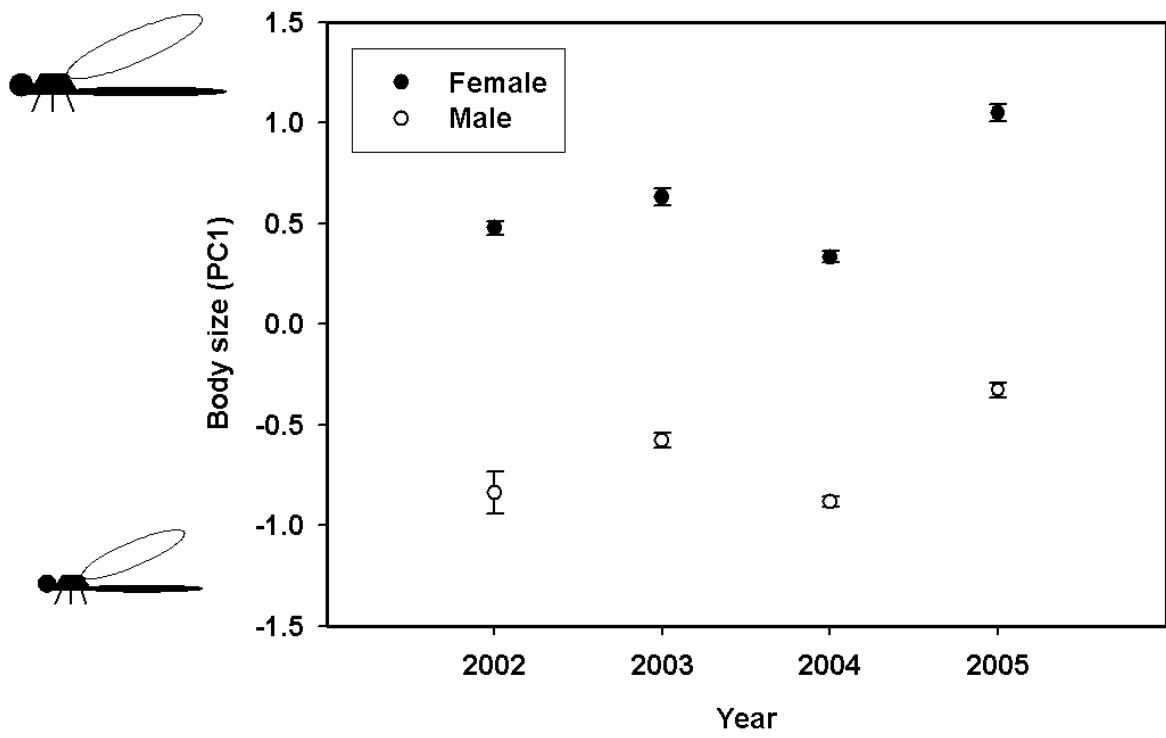
Figure 2: Differences in between the morphs in A) Body size (PC1). Infuscans females are the largest overall. B) Body shape (PC2). Androchromes are most male-like in shape, while Infuscans and Infuscans-obsoleta females are less male-like and very similar in shape. Error bars denote SEs. Note that cartoon damselflies are for illustrative purposes only and do not reflect the magnitude of actual differences between the morphs.

Figure 3: Phenotypic integration graphs for A) Males (N = 2741 individuals), B) Androchrome females (N = 1457 individuals), C) Infuscans females (N = 564 individuals), and D) Infuscans-obsoleta females (N = 176 individuals). Partial correlations which are significant at the 0.05 level are shown, and values are reported adjacent to lines between traits. Strong edges are indicated by heavy lines, weak edges by light lines. The high partial correlations between total length and abdomen length present in all groups are because these

traits are not completely independent. Note the unique pattern of phenotypic integration in *Infuscans-obsolata* females.

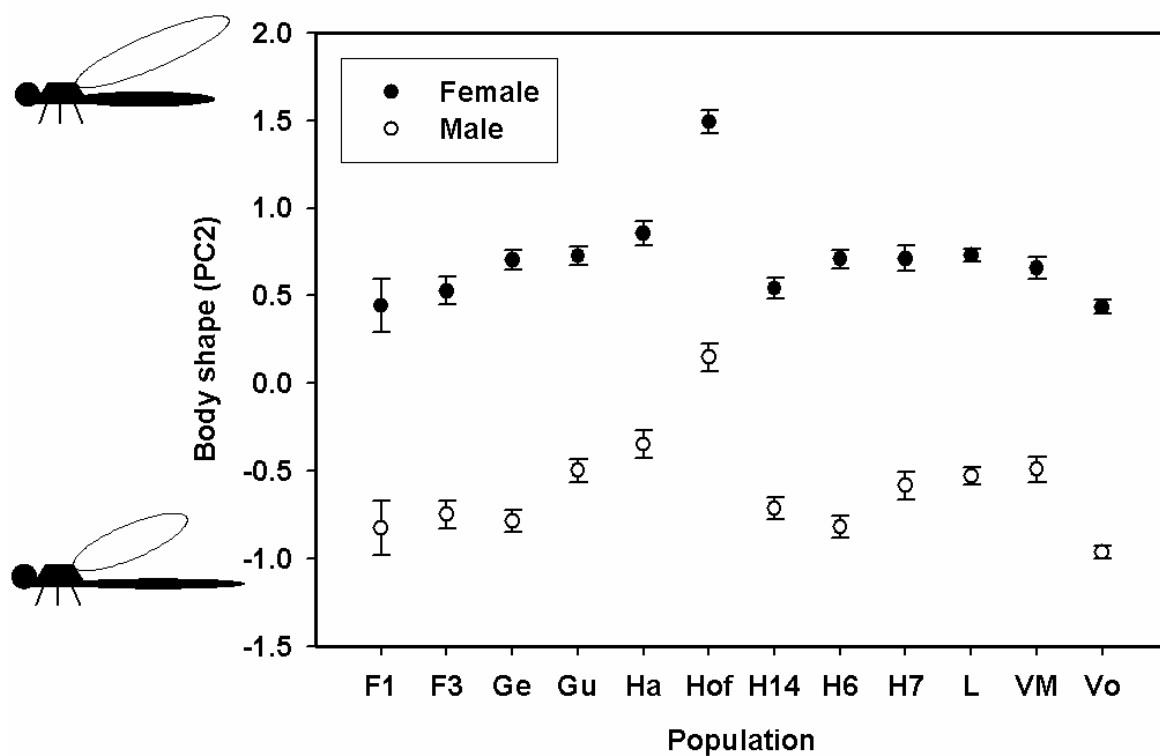


596 Figure 1A



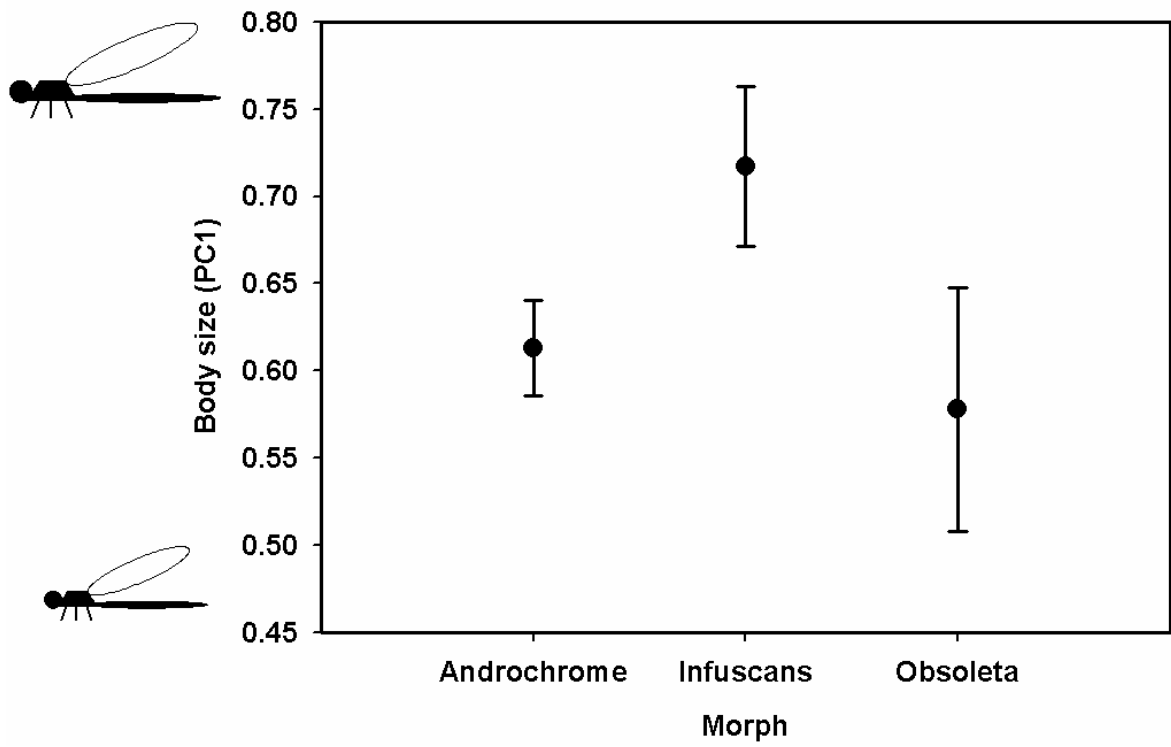
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598 Figure 1B



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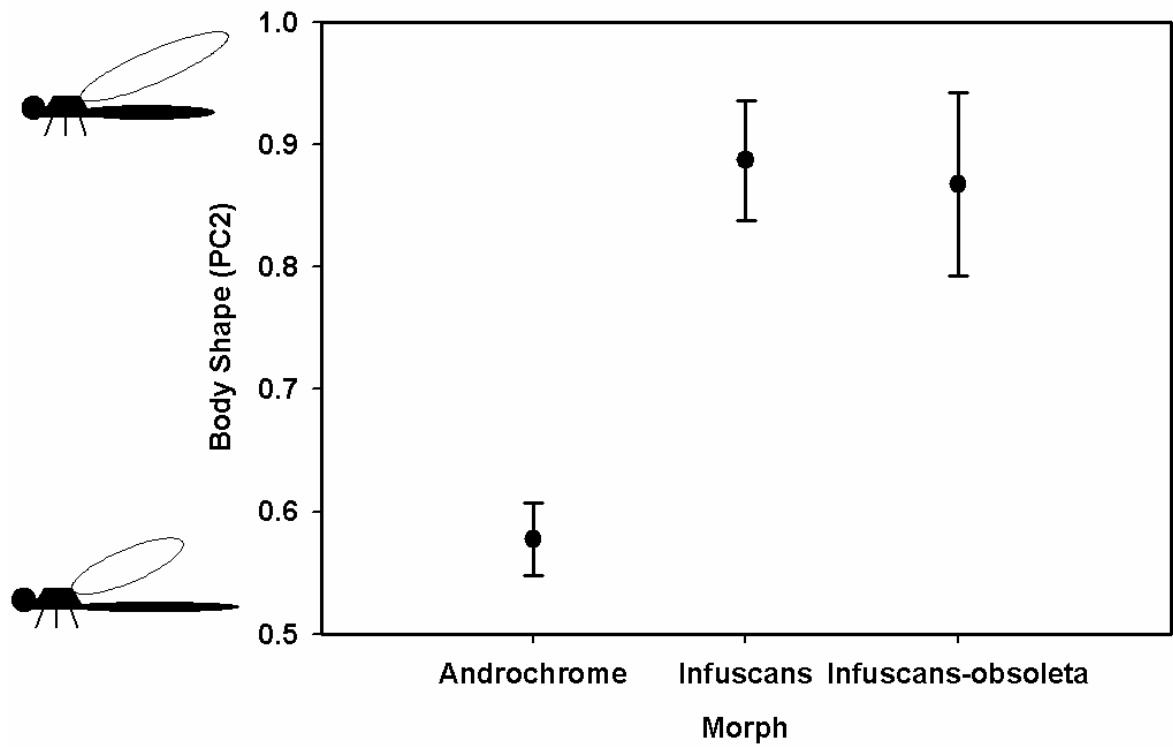
600 Figure 1C



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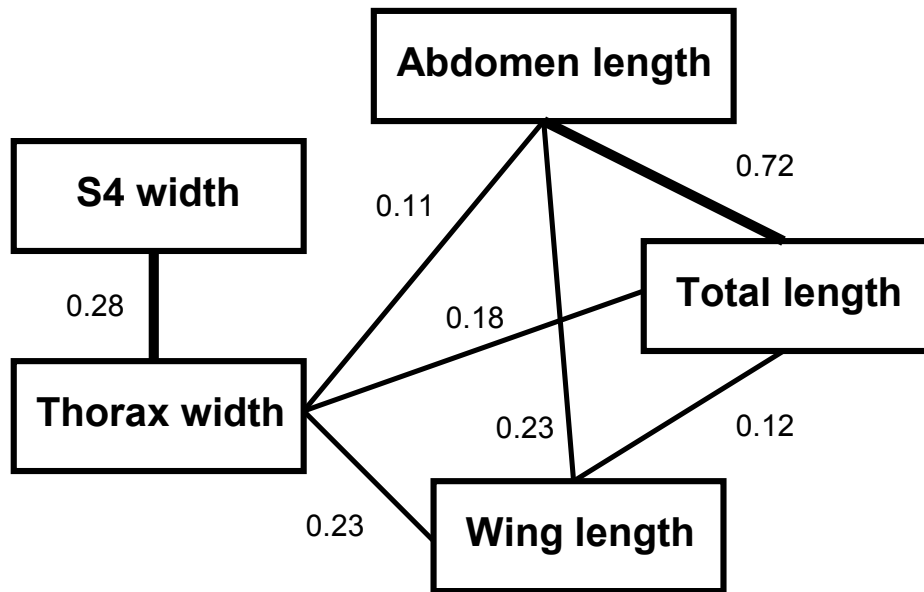
602 Figure 2A





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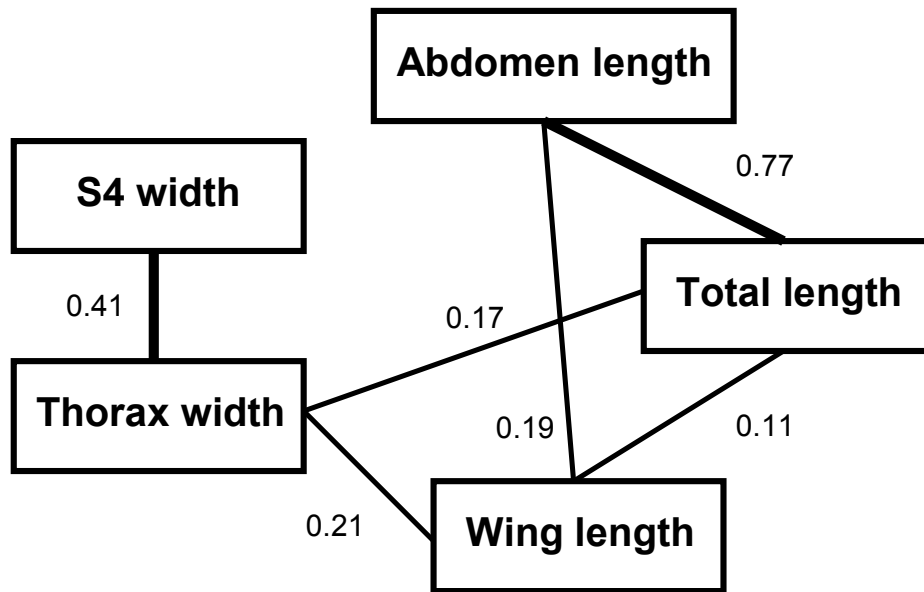
604 Figure 2B



## Males

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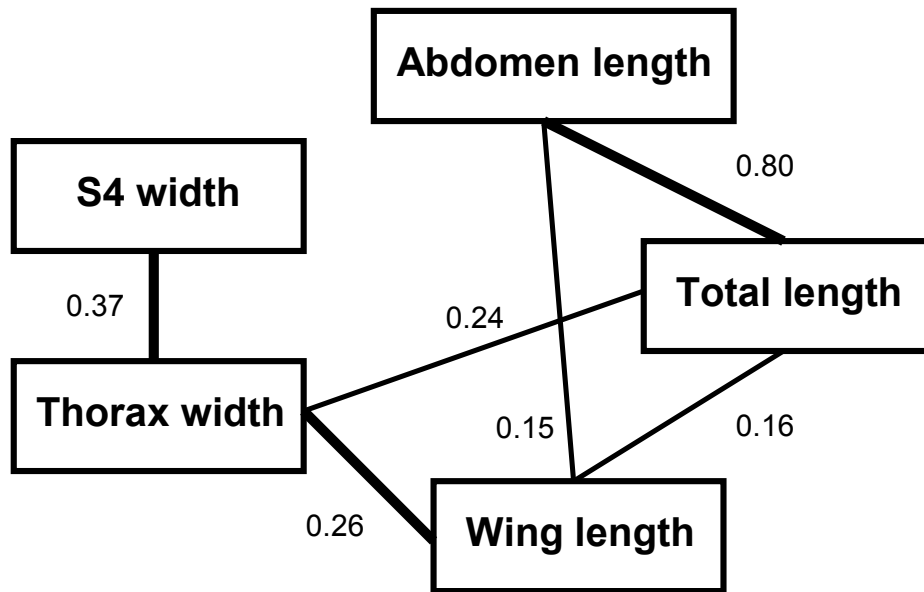
606 Figure 3A



## Androchrome

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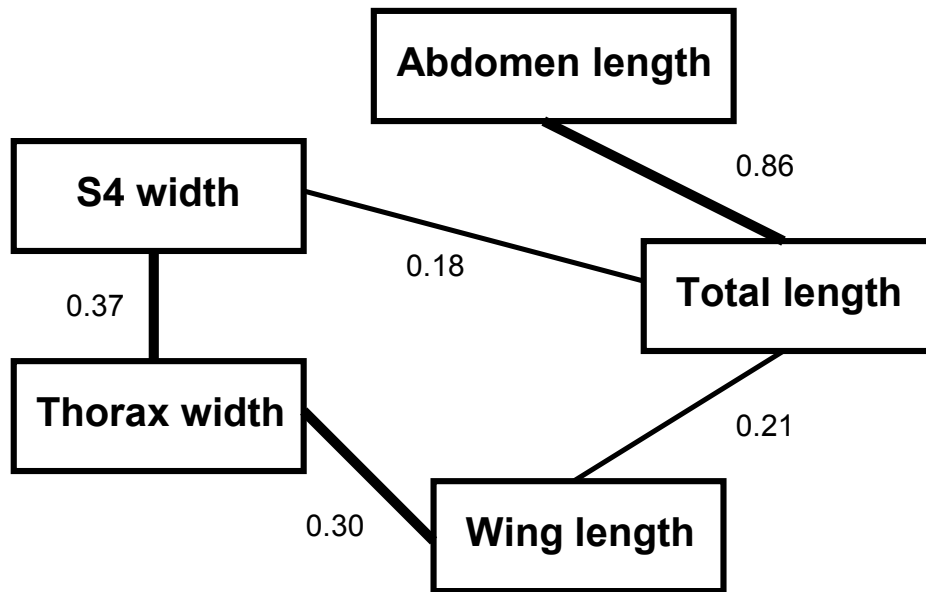
608 Figure 3B



## Infuscans

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610 Figure 3C



## Infuscans-obsoleta

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612 Figure 3D

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