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Density-Dependent Male Mating Harassment, Female Resistance, and Male Mimicry

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abstract: Genetic variation in female resistance and tolerance to male mating harassment can affect the outcome of sexually antagonistic mating interactions. We investigated female mating rates and male mating harassment in natural populations of a damselfly (*Ischnura elegans*). This damselfly species has a heritable sex-limited polymorphism in females, where one of the morphs is a male mimic (androchrome females). The three female morphs differ in mating rates, and these differences are stable across populations and years. However, the degree of premating resistance toward male mating attempts varied across generations and populations. Male mating harassment of the female morphs changed in a density-dependent fashion, suggesting that male mate preferences are plastic and vary with the different morph densities. We quantified morph differences in male mating harassment and female fecundity, using path analysis and structural equation modeling. We found variation between the morphs in the fitness consequences of mating, with the fecundity of one of the nonmimetic morphs declining with increasing male mating harassment. However, androchrome females had lower overall fecundity, presumably reflecting a cost of male mimicry. Density-dependent male mating harassment on the morphs and fecundity costs of male mimicry are thus likely to contribute to the maintenance of this female polymorphism.

Keywords: tolerance, sexual conflict, path analysis, mating behavior, polymorphism, fecundity.

Introduction

Phenotypically visual polymorphisms, such as color polymorphisms, are excellent model systems in ecological population genetics to study the links between genetic variation, evolutionary processes, and speciation (Gray and McKinnon 2007). Recently there has been an increased interest in female sexual polymorphisms (Sinervo et al. 2000; Härdling and Bergsten 2006; Reinhardt et al. 2007; Svensson et al. 2009), along with increased attention to the ecological causes of variation in female fitness (Chapman et al. 2003; Gavrilets and Hayashi 2005; Svensson et al. 2005; Lew et al. 2006; Mappes et al. 2008). Some female polymorphisms might reflect different reproductive tactics and responses among females to cope with male mating harassment (Härdling and Bergsten 2006; Gosden and Svensson 2007). In other cases, female polymorphisms might result from density-dependent female-female interactions and changes in the social environment (Sinervo et al. 2000; Svensson et al. 2001*a*; Vercken et al. 2007). These studies on female polymorphisms demonstrate how fitness differences among morphs can arise from either intra- or intersexual interactions.

Empirical work using laboratory studies of *Drosophila melanogaster* has found that different genotypes can be adapted to different density environments, with a trade-off between fitness at high and low densities (Mueller and Ayala 1981; Mueller 1988; Borash et al. 1998). However, empirical data from natural populations are more limited (Svensson and Sinervo 2000; Mappes et al. 2008). Field studies on side-blotched lizards (*Uta stansburiana*) have shown that different color morphs show differential changes in their fitnesses with increasing density (Sinervo et al. 2000). The ecological and physiological mechanisms mediating such density-dependent interactions between morphs are still largely unknown. Potential mechanisms include interference competition between juveniles (Svensson and Sinervo 2000) and immune suppression caused by social stress at high densities (Svensson et al. 2001*b*). A role for sexual conflict in driving density-dependent selection has also been suggested (Gavrilets 2000; Martin and Hosken 2003).

In the context of sexual conflict, the formation of a stable female polymorphism might prevent males from overcoming female resistance in traditional coevolutionary arms races (Holland and Rice 1998; Arnqvist and Rowe 2002). Instead, males could become trapped between the different female genetic clusters, unable to effectively adapt

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to any particular female morph (Gavrilets and Waxman 2002); alternatively, males form plastic mate preference behaviors, or search images, to adapt to the different morphs in a more flexible way (Fincke 2004; Gavrilets and Hayashi 2005). Female polymorphisms have potentially evolved as a direct response to male mating harassment in some species (Härdling and Bergsten 2006; Reinhardt et al. 2007). The development of such morphs is particularly likely when male harassment negatively affects female fitness (Magurran and Seghers 1994; Le Galliard et al. 2005; Gosden and Svensson 2007) and when there is genetic variation in female susceptibility to male mating harassment (Linder and Rice 2005; Lew et al. 2006; Gosden and Svensson 2007). Heritable traits involved in these social interactions between phenotypes can be considered "interacting phenotypes" (Moore et al. 1997) and are part of an evolving and dynamic social environment. When such interacting phenotypes are involved in antagonistic interactions, this may lead to the emergence of multiple response traits rather than cycles between the same traits (Moore and Pizzari 2005), which in turn can result in differential sensitivity among morphs to a varying social environment (Sinervo and Lively 1996; Svensson et al. 2001*a*; Gosden and Svensson 2007; Pryke et al. 2007; Vercken et al. 2007; Mappes et al. 2008). Investigating the fitness responses of different heritable morphs to changing social conditions is thus crucial to understanding sexual conflict in particular and social evolution in general.

Here we present data from an experimental field study on male mating harassment on females in a small damselfly species (*Ischnura elegans*) with a heritable female-limited color polymorphism. This species has been extensively studied in the past with respect to male-female mating interactions (Gosden and Svensson 2007), female fecundity (Svensson and Abbott 2005), and frequency-dependent evolutionary dynamics of heritable female color morphs (Svensson et al. 2005). It is usually thought that the multiple female morphs in *I. elegans* and other damselfly species are maintained by negative frequency-dependent selection (Sherratt 2001; Svensson et al. 2005) through learned mate recognition and plastic male mate preferences, leading to increased harassment on common morphs (Van Gossum et al. 2001; Fincke 2004). An alternative but not mutually exclusive hypothesis is that the male-colored female morph (henceforth called the "androchrome" female morph) mimics males to cope with the negative consequences of male mating harassment (Robertson 1985; Cordero et al. 1998). Experimental studies on male mating behavior suggest a plastic component in male mate choice (Van Gossum et al. 2001), whereas some field studies suggest that there could also be a strong innate male bias against a particular female morph regardless of its frequency in the population (Cordero Rivera and Sanchez-Guillen 2007; Gosden and Svensson 2007; Svensson et al. 2009).

Using an experimental technique that involves marking field-caught males with a transferable dust, we recently estimated levels of harassment and mating rates for three female morphs under natural field conditions (Gosden and Svensson 2007). Here we extend this earlier work by presenting more-detailed data about differences among the three morphs in their mating behaviors. This includes data on morph differences in the rejection rate of male mating attempts ("female resistance") and the morph-specific fitness consequences of multiple mating and male copulation attempts ("female tolerance"), which jointly leads to morph-specific fecundity costs of male mating harassment. We investigated the links between male mating harassment, multiple matings, female fecundity, and other female morphological traits, using path analysis and structural equation modeling. Results in this study suggest that the fitness of the morphs changes between environments with different degrees of density-dependent male mating harassment.

Material and Methods

Study Species

The damselfly *Ischnura elegans* is found throughout Europe, with the northern end of its distributional range occurring in southern Sweden (Askew 1988). In southern Sweden, *I. elegans* emerge as adults from the larval stage in late May and onward. Adult males are monomorphic in coloration, but the females occur in three discrete color morphs: androchromes (A), infuscans (I), and infuscans-obsoleta (IO). Androchrome females are malelike in coloration (blue) and melanin patterning and have therefore traditionally been considered "male mimics" (Robertson 1985; Svensson et al. 2009). Infuscans females have malelike melanin patterning but are brownish to greenish in coloration. Infuscans-obsoleta females are reddish-brownish in coloration, with weak melanin patterning. Female morph development in *I. elegans* is controlled by a single locus with three alleles in a dominancy hierarchy, where A > I > IO (Sanchez-Guillen et al. 2005), and six genotypes give rise to the three visible phenotypes.

The populations in this study are subject to rapid spatial and temporal fluctuations in female morph frequencies (Svensson and Abbott 2005). The androchrome frequencies in this study varied between 49% (Vombs population, 2005) and 91% (Höje Å 6 population, 2007), with a mean androchrome frequency of 68% across all populations and years. These rapid morph-frequency fluctuations are caused in part by negative frequency-dependent selection arising from male mating harassment and antagonistic male-female interactions (Svensson et al. 2005; Gosden and Svensson 2007). During their reproductive season, males search out and attempt to grab the females by their prothorax (Corbet 1999), using a clasper organ on the end of the males' abdomen (cerci). The female can then respond by bringing her abdomen up to the male's secondary sexual organs, forming a mating wheel so mating can take place (Corbet 1999), or can refuse to mate and hence reject the male. Females mate with multiple males (Cooper et al. 1996; Gosden and Svensson 2007), and males are nonterritorial, engaging in scramble competition for access to females (Corbet 1999).

Fieldwork and Experiments

We collected and marked males from three different populations outside Lund in southern Sweden (Lomma: $n = 1{,}518$; Höje Å 6: $n = 729$; Vombs Vattenverk: $n = 673$) during the summers of 2005 ($n = 690$), 2006 ($n = 1{,}215$), and 2007 ($n = 1{,}015$). Males were caught and marked with one of five available and easily distinguishable colors of fluorescent dust (Gosden and Svensson 2007). We marked equal numbers of males in all five color classes within each population throughout the experiments in all summers. Males were dusted in two separate places on their body: on the clasping organ located at the end of the abdomen (cerci) and on the genitalia. Dusted males were released in the same location where they were caught. Males were found with the presence of dust several weeks after these dusting sessions, indicating that once the dust was applied, it was present on the male for the rest of its life. The populations were visited for male dusting sessions several times over each summer. We returned to each population at regular intervals over the field seasons and caught as many males and females as possible during intense and time-monitored catching sessions. The proportions of recaptured dusted males to nondusted males did not differ between years or populations (two-factor ANOVAs, population: $F = 0.599$, $\mathrm{df} = 2, 4$, $P = .592$; year: $F = 0.012$, $\mathrm{df} = 2, 4$, $P = .987$), indicating that the probability of a female encountering a dusted male was approximately equal for all years and populations. There were also no differences between populations and years in the proportions of males of each color class that were recaptured (population × color: $F = 0.719$, $\mathrm{df} = 8, 20$, $P = .673$; year × color: $F = 0.834$, $\mathrm{df} = 8, 20$, $P = .584$). This strongly suggests that the different colors do not influence male survival differently; hence, the proportions of each color type do not vary significantly across space and time.

In this article, male and female densities are expressed as the number of individuals caught per person per minute. This density estimate is thus corrected for the total catching time (catching effort) and the number of people doing the catching. Field-caught males and females were brought to an indoor laboratory, where we checked for the presence of fluorescent dust under a dissecting microscope. The presence of fluorescent dust on the prothorax of a female indicated a male clasping attempt, and presence on the female's genitalia showed that mating had occurred with a dusted male. When females were found with traces of several different colors of fluorescent dust (1–5), this indicated that they had been clasped by and/or had mated with several different males in the field prior to capture. In a controlled experiment, we verified that dust on the genitalia of a female likely resulted from mating rather than precopulatory genital contact with a male (see the appendix in the online edition of the *American Naturalist*).

We measured five morphological traits on the captured females: forewing length, total body length, abdomen length, thorax width, and width of the fourth abdominal segment (S4). Four of these five traits show significant heritabilities (h^2, forewing length: 0.463; total body length: 0.346; abdomen length: 0.242; thorax width: 0.173) when animals have been raised in a common-garden environment (Abbott 2006). The genetic correlations between these five morphological traits are positive in all cases (range 0.025–1.035) and are significant in eight of the 10 cases (Abbott 2006). Females were subsequently set up and left to lay eggs for 2 days in oviposition jars before being released. On day 3, the eggs were counted (Svensson and Abbott 2005). Our fecundity estimate is only a component of total female lifetime fecundity, but this fitness component is likely to be correlated with lifetime fecundity and may reflect 10%–50% of lifetime fecundity in damselflies, according to previously published studies (Fincke 1986; Banks and Thompson 1987; Corbet 1999). It is worth noting that several of the studies from which these estimates of variation in clutch size are taken (Fincke 1986; Banks and Thompson 1987) were conducted in the field; therefore, each measured clutch was laid over a relatively short period, compared with the 2 days in which our females were allowed to lay eggs in the laboratory. Given that many damselfly females will lay most or all of the eggs present in their ovaries in good and undisturbed conditions (Corbet 1999), it is highly likely that our per-clutch fecundity estimate is even more strongly connected to lifetime fecundity than was the case in these previous studies. Moreover, the short life span of these female damselflies in the field (maximum 1–2 weeks) should make even a cross-sectional and instantaneous measure of fecundity like this a good measure of overall female fecundity.

Basic Definitions and General Statistical Analyses

In this article we define "female resistance" as the covariance (slope of the regression line) between the number of matings (Y-axis) and the number of claspings (X-axis). "Number of matings" is the minimum number of males that had mated with a female, judged by the presence of fluorescent dust on her genitalia. The difference in the number of matings between the female morphs is also a measure of "relative mating rate" of the different morphs in the local populations, as these matings had been accumulated over a similar time period for the different morphs. The proportion of females caught with colored dust did not differ among populations, years, or morphs (population: $F = 0.388$, $\mathrm{df} = 2, 20$, $P = .684$; year: $F = 2.109$, $\mathrm{df} = 2, 20$, $P = .148$; morph: $F = 1.965$, $\mathrm{df} = 2, 20$, $P = .166$). This indicates that the proportion of females encountering a dusted male was more or less equal across all populations. Finally, morph differences in the number of male clasping attempts, judged by the presence of fluorescent dust on the female thorax, provides a measure of "male mating harassment" on female morphs.

All statistical tests were performed (and their assumptions checked) using STATISTICA (StatSoft 2003). To examine differences in mating rates within and among populations between years, we investigated how the numbers of matings were influenced by female morph, population, year, and all two-way interactions, using a general linear model (GLM). We were particularly interested in the morph × population and morph × year interactions, as these reveal whether the number of matings for each morph changed between populations and years (significant interactions) or, conversely, whether the mating rates of the morphs were relatively stable across years and populations (nonsignificant interactions).

To investigate spatial and temporal variation in morph-specific female "resistance" to male mating attempts, we used a GLM with number of matings as the dependent variable and population, year, morph, male clasping attempts, and all interaction terms as predictor variables. We did not include an intercept in this regression model, as it is not biologically possible for a female to mate without first being clasped by the male. This analysis will thus reveal whether female resistance to matings differs spatially and temporally and between morphs, in contrast to the analysis above, which tests only whether the realized number of matings shows evidence of spatiotemporal variation. The slopes of the morph-specific regression lines of the number of realized matings (dependent variables) versus claspings (predictor variables) reflect the degree of morph-specific resistance to male mating harassment (lower slope = stronger resistance). A 1 : 1 slope would reflect a hypothetical situation in which every male clasping attempt toward a female ends in a mating, that is, complete lack of female resistance (Gosden and Svensson 2007).

We were interested in evaluating the level of male harassment on the female morphs at different population densities. We were primarily interested in the relative success of androchromes, which have been suggested to be male mimics, and in how they compare to the other two morphs in the amount of male harassment encountered. In this analysis we therefore divided the three morphs into two groups: androchrome and nonandrochrome (infuscans and infuscans-obsoleta) females. We then investigated the total relative effect of morph density on the experienced degree of male mating harassment on the androchrome and nonandrochrome morphs. Using population-specific data for male clasping attempts in each year, we examined the effects of group density on male mating harassment. As in the previous analyses, we used a GLM with male claspings as the dependent variable and population, year, group, and group density as independent variables and the two-way interaction between group and group density. As our data set represents a subsample of all possible years and populations, they were included as random effects; however, all significant results remain if they were instead treated as fixed effects. Nonsignificant variables were removed in the order determined by the highest P values and the lowest sum of squares (SS).

In the more in-depth comparisons of morph differences on the fecundity costs of male mating harassment, we analyzed the effects of year, population, morph, matings, male clasping attempts, and the interactions between morph × matings and morph × clasping attempts in a GLM. Year and population were included as random effects. The model remained unchanged if year and population were instead treated as fixed. The slopes of the morph-specific regression lines within the GLM reflect the tolerance level for multiple matings within each of the morphs; that is, a negative slope signifies low tolerance levels to higher mating rates. Significant interactions indicate that the morphs differ in their tolerance to male mating harassment and/or mating in regard to fecundity. We used data for only two of the morphs, androchromes and infuscans, because of the low sample size ($n = 46$) and few matings (number of matings: zero, $n = 5$; one, $n = 38$; two, $n = 3$) of the rarest morph (infuscans-obsoleta).

Path Analysis and Structural Equation Modeling

We used path analysis and structural equation modeling to further investigate female fecundity variation in the two most common morphs, androchrome and infuscans. We were not able to include the infuscans-obsoleta morph in this analysis, since it is too rare to obtain meaningful sample sizes (Svensson and Abbott 2005). We investigated the links between male mating harassment, realized matings, fecundity, and the five morphological traits described above. To control for fecundity variation arising from differences between populations and years, we used the fecundity residuals (corrected for year and population) as independent variables. The morphological traits were linked together in the path models by two-way arrows (correlations). The overall fit of the models was evaluated using goodness-of-fit tests in which the observed covariance matrix was compared with the expected covariance matrix predicted if a particular model were true (Mitchell 2001). If the model explains the covariance among variables in a way that is not distinguishable from the observed relationship, the goodness-of-fit test results are nonsignificant and the model can be provisionally accepted (Mitchell 2001). Models were reduced and derived from the basic model by constraining paths with high P values and low parameter estimates to 0. We assumed that a female must be clasped before mating and must mate to lay eggs; therefore, these paths were kept regardless of P values and low parameter estimates. Both manifest variables and latent variables were free to vary in these analyses. Before analysis all variables were standardized to mean 0 and unit variance (Mitchell 2001; Svensson et al. 2001*a*, 2002).

Because we found strong links between fecundity and body traits in androchrome females (see "Results"), we assessed the fitness effects in androchromes of the morphological traits on fecundity by estimating the standardized linear selection gradients (Lande and Arnold 1983) on all five traits. Selection gradients were estimated from the covariance between relative fecundity and standardized morphological traits, using a GLM (Lande and Arnold 1983). Population and year were included as random effects, but the results remained unchanged when these variables were instead treated as fixed effects.

Results

Stable Morph Differences in Mating Rates across Years and Populations

Across all populations, morph differences in the average number of matings were remarkably stable (fig. 1) and in accordance with previous findings (Gosden and Svensson 2007). Infuscans females always had the highest number of matings ($F = 14.911$, df = 2, 1,312, $P < .001$, $N =$ 1,327; fig. 1) and always had a significantly higher mating rate than the androchrome females (Tukey honestly significant difference [HSD] test, $P < .001$). The small sample size in infuscans-obsoleta females was probably the major reason why this morph did not differ significantly from the two other morphs ($N = 48$; Tukey HSD, A vs. IO: $P = .92$; I vs. IO: $P = .10$). The differences between androchrome and infuscans females remain significant even if the rarest morph (IO females) is excluded from the analysis. The relative rank ordering of the different morph mating rates did not differ between populations (morph × population: $F = 0.372$, df = 4, 1,312, $P =$ .83; fig. 1*a*) or years (morph × year: $F = 1.166$, df = 4, 1,312, $P = .32$; fig. 1*b*). This stable morph difference in mating rates suggests that infuscans females have an overall higher mating rate across all populations and years. This is consistent with another recent study that indicated that androchrome females have an intrinsically lower overall mating rate than infuscans females (Cordero Rivera and Sanchez-Guillen 2007).

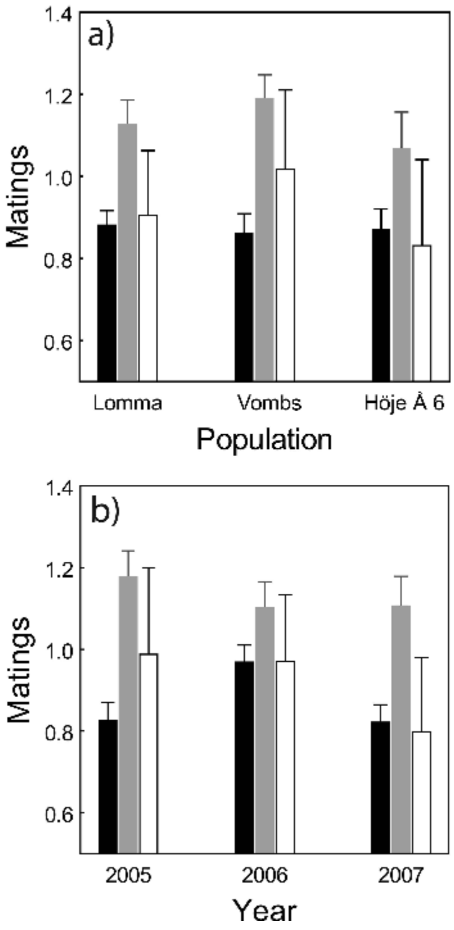

Figure 1: Differences in mating rates (+SE) between the three female color morphs (*black*, androchrome, $n = 895$; *gray*, infuscans, $n = 384$; *white*, infuscans-obsoleta, $n = 48$). These three morphs differ significantly in terms of number of obtained matings (see "Results"). These morph differences are stable across both populations (*a*) and years (*b*). See "Results" for test statistics. Infuscans females have the highest mating rate across all populations and years.

Female Resistance and Susceptibility to Male Harassment

The three different morphs varied in their resistance to male mating attempts (fig. 2; table 1). This morph-specific

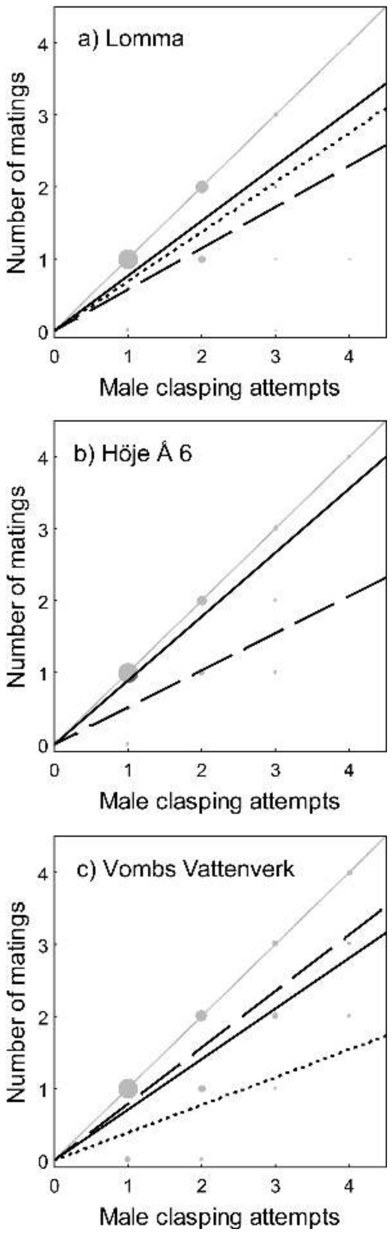

Figure 2: Variation among female morphs in resistance to male mating attempts across three populations in southern Sweden. The plots show the relationships between the number of matings (Y-axis) and the number of male clasping attempts for each morph (X-axis) in the three populations of Lomma (*a*), Höje Å 6 (*b*), and Vombs (*c*). The thin gray line marks a (hypothetical) 1 : 1 slope, where every clasping attempt by a male results in a mating. The slopes of the regression lines below the 1 : 1 line reveal morph-specific levels of female resistance toward mating attempts from males. *Solid black line*, androchrome; *dashed line*, infuscans; *dotted line*, infuscans-obsoleta (excluded from Höje Å 6 because of low sample size and lack of variation between matings and claspings). Sizes of the data points are proportional to the sample size at each position (Lomma: range 1–334, mean = 48.8; Höje Å 6: range 1–180, mean = 30.1; Vombs: range 2–239, mean = 31.5).

resistance differed between populations, as reflected by a significant three-way interaction (morph × population × male clasping attempts; fig. 2; table 1). Hence, unlike mating rate, which was remarkably stable and showed evidence of a more or less fixed intrinsic morph difference across populations and years (fig. 1), morph-specific resistance differed between populations (fig. 2; table 1). This suggests that resistance toward unwanted male mating attempts is a more dynamic trait that is not simply associated with a fixed value in a particular morph (fig. 2; table 1). In addition, we also found evidence of temporal differences (between years) in morph-specific resistance (morph × year × male clasping attempts; table 1). Again, this demonstrates that premating resistance is a more dynamic and flexible trait than the number of realized matings (fig. 1). The four-way interaction was also significant (morph × population × year × male clasping attempts; table 1), which shows that female reluctance to mate changes between years and populations and that no morph is fixed for any particular level of resistance.

The regression slopes of all three morphs (except for IO females in Lomma; table A1 in the online edition of the *American Naturalist*) were significantly lower than unity (1 : 1) in all populations (fig. 2). Thus, all three female morphs showed some degree of resistance toward male mating attempts, although the magnitude of this resistance differed, revealed as morph-specific regression slopes that differed among populations (table A1; fig. 2). Low sample size and lack of variation in matings and claspings in the infuscans-obsoleta females meant that this morph could not be included in Höje Å 6 analyses (table A1; fig. 2*b*). The resistance difference between these two common morphs (androchrome and infuscans) in Lomma and Vombs remained significant even when the rarest morph (infuscans-obsoleta) was excluded from the analysis.

The effects of morph-group density on male mating harassment differed between androchrome and nonandrochrome females (fig. 3). Male mating harassment toward androchrome females showed no significant relationship with androchrome density ($\beta = 0.694$, $r^2 = 0.149$, $P = .305$; fig. 3), whereas the number of male claspings increased with increasing density of the nonandrochrome females ($\beta = 5.465$, $r^2 = 0.558$, $P < .001$; fig. 3). Thus, susceptibility to male mating harassment was density dependent in nonandrochrome females but more independent of androchrome female density. As a consequence, the relationships between the number of male claspings and density differed significantly between androchrome and nonandrochrome females (morph density × morph: $F = 11.71$, $\mathrm{df} = 1, 21$, $P = .003$; fig. 3). The interaction remained significant when only the two most common morphs (androchrome and infuscans) were in-

Table 1: Differences between three female morphs in their resistance to male mating attempts across populations and years

	SS	df	MS	*F*	*P*
Year	.214	2	.107	1.143	.319
Population	.431	2	.215	2.305	.1
Morph	3.304	2	1.652	17.682	<.001[†]
Male claspings	194.99	1	194.99	2,087.2	<.001[†]
Year × population	1.402	4	.35	3.751	.005***
Year × morph	1.397	4	.349	3.738	.005***
Population × morph	.582	4	.146	1.558	.183
Year × male claspings	.234	2	.117	1.255	.286
Population × male claspings	.545	2	.273	2.917	.054*
Morph × male claspings	2.254	2	1.127	12.062	<.001[†]
Year × population × morph	1.928	6	.321	3.44	.002***
Year × population × male claspings	3.368	4	.842	9.014	<.001[†]
Year × morph × male claspings	2.047	4	.512	5.478	<.001[†]
Population × morph × male claspings	1.214	4	.304	3.249	.012**
Year × population × morphs × male claspings	3.002	6	.5	5.355	<.001[†]
Error	119.21	1,276	.093		

Note: The intercept was not included in the regression model, as it is not biologically possible for a female to mate without first being clasped by the male. Four independent variables and all two-, three-, and four-way interactions are shown (i.e., a complete model). Type III sums of squares were used. Full model: $F = 122.591$, df = 51, 1,276, $r^2 = 0.823$, $P < .001$.

* $P < .10$.

** $P < .05$.

*** $P < .01$.

[†] $P < .001$.

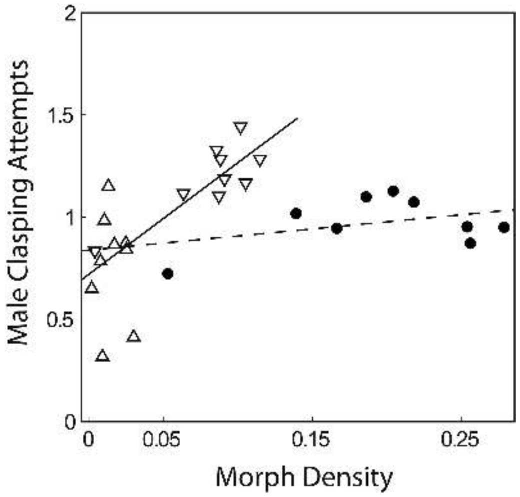

Figure 3: Differences between morphs (*circles*, androchromes; *triangles pointing down*, infuscans; *triangles pointing up*, infuscans-obsoleta) in the impact of morph density on male mating harassment (clasping attempts). Nonandrochrome females experience an increased number of male claspings with increasing density, whereas androchromes show a lower sensitivity to male claspings as their density increases. The two regression slopes differ significantly from each other (see "Results"). Note the lower overall densities of infuscans and infuscans-obsoleta females compared with androchrome females.

cluded in this analysis (morph density × morph: $F = 6.992$, df = 1, 21, $P = .021$). Note that the densities of both the infuscans and the infuscans-obsoleta females never reached that of androchrome females in any of our populations and that androchrome females were always the most common morph (fig. 3). The effect of population was not significant and was therefore not included in the final analysis.

Path Analysis and Structural Equation Modeling

The structure of our basic path model is shown in figure A1 in the online edition of the *American Naturalist*. The models we present here were "nested" within this basic model, meaning that some weak and nonsignificant paths were reduced to 0, as long as the fit of the model was increased (see "Material and Methods"). The correlation paths between all morphological traits for both morphs were kept, although they are not shown in the figures for the sake of clarity (fig. 4). All but one of these correlations were significant (for infuscans, S4 abdomen was marginally above significance, $P = .058$).

The path models for the two most common morphs differed with respect to how morphological traits affected fecundity (fig. 4). Although the full path models for both female morphs showed a good fit (androchromes: $\chi^2 = 6.172$, df = 10, $P = .801$; infuscans: $\chi^2 = 5.102$, df =

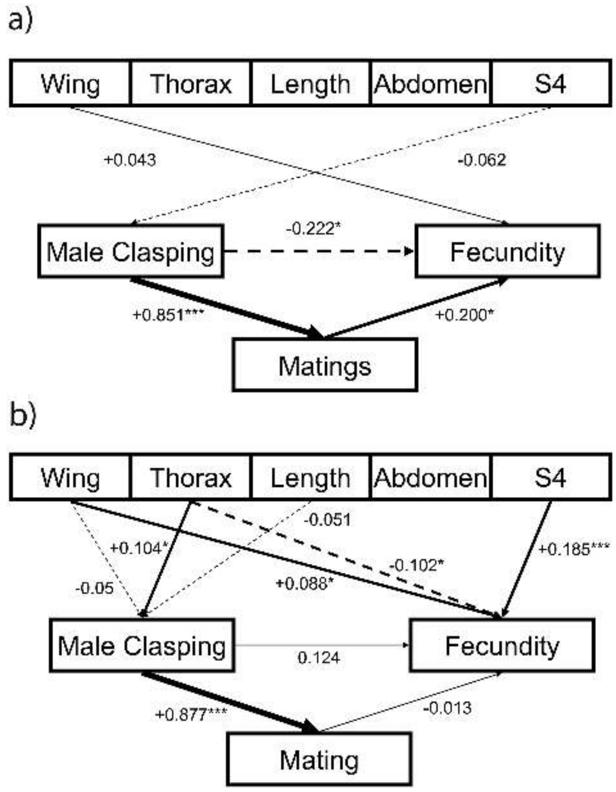

Figure 4: Path diagrams for the two most common morphs, obtained from the basic model (fig. A1). We arrived at this model from the basic model by constraining the weak and nonsignificant paths to 0 (see "Material and Methods"). The two morphs differ in terms of how their fecundity is affected by morphology, number of matings, and the degree of male mating harassment. *a*, Infuscans females ($n = 352$) are negatively affected by male clasping in terms of their fecundity but have a positive relationship between number of matings and fecundity. *b*, Androchrome females ($n = 714$) show strong and significant relationships with morphological traits and male clasping/fecundity. Solid lines depict positive paths and dashed lines negative paths. The magnitude of each path coefficient is reflected by the thickness of the paths. Correlated (two-way paths) between morphological traits were omitted for clarity. Three asterisks, $P < .001$; one asterisk, $P < .05$.

10, $P = .884$), the reduced models improved the fit, and the goodness-of-fit test results were high and nonsignificant (androchromes: $\chi^2 = 8.452$, $\mathrm{df} = 14$, $P = .864$; infuscans: $\chi^2 = 7.179$, $\mathrm{df} = 19$, $P = .993$). The morphological traits had no strong effects on female fecundity in the infuscans morph, but in this morph there were instead strong direct effects of male harassment and number of matings (fig. 4*a*). In infuscans females, there was a strong and significant negative link between male clasping attempts and fecundity (fig. 4*a*). However, there was also an indirect positive effect of male clasping attempts on female fecundity through the positive links between clasping and matings and between matings and fecundity. Thus, infuscans females were both directly and negatively affected by male mating harassment, although they also gained a small indirect fecundity advantage through the effects of male claspings on their mating rate. The direct negative effect of claspings on fecundity ($P_{\mathrm{clasp,\,fec}} = -.222$; fig. 4*a*) does, however, outweigh the indirect positive effects on fecundity through increased number of matings ($P_{\mathrm{clasp,\,mate}} \times P_{\mathrm{mate,\,fec}} = .17$; fig. 4*a*).

The relationships in androchrome females were different; there, fecundity was linked more strongly with morphological traits and less strongly with male harassment and mating (fig. 4*b*). A particularly interesting path in androchromes is the positive link between the fourth abdominal segment (S4) and fecundity. This segment is considerably narrower in males than in females (mean ± SD, males: 0.7 ± 0.08 mm; females: 0.95 ± 0.1 mm; $F = 5{,}836.071$, $\mathrm{df} = 1, 3{,}145$, $P < .001$). It is also 0.5 SD thinner in androchrome females than in the two other female morphs (mean ± SD, A: 0.94 ± 0.1 mm; I: 0.99 ± 0.1 mm; IO: 1 ± 0.1 mm; $F = 38.718$, $\mathrm{df} = 2, 1{,}287$, $P < .001$; Tukey post hoc tests, A vs. I: $P < .001$; A vs. IO: $P < .001$).

The selection gradients on the morphological traits in androchrome females were consistent with the path analysis. Both wing length and the fourth abdominal segment showed significant positive selection gradients ($\beta = 0.112$, $P = .012$ and $\beta = 0.196$, $P < .001$, respectively), and there was also a tendency for negative selection on thorax width ($\beta = -0.084$, $P = .071$). Of particular interest was the significant positive selection for a greater abdomen thickness in androchrome females. The magnitude of this selection gradient implies that an increase of 1 SD in abdomen thickness in androchrome females will increase their relative fecundity by approximately 20%. The morph difference of 0.5 SD between androchromes and infuscans (see above) is thus predicted to lower relative fecundity in androchrome females by approximately 9%–10%, which is slightly below the difference in mean fecundity between androchromes and infuscans females that we reported previously (15%–20%; Svensson and Abbot 2005).

Fecundity Consequences of Male Mating Harassment

There was a difference between androchrome and infuscans females in the effects of male clasping attempts on fecundity (morph × claspings: $F = 6.343$, $\mathrm{df} = 1, 1{,}058$, $P = .012$). Overall female fecundity was higher in the infuscans females than in the androchrome females (morph: $F = 6.35$, $\mathrm{df} = 1, 1{,}058$, $P = .012$), consistent with previous findings (Svensson and Abbott 2005). However, although androchrome females had lower mean fecundity than infuscans females, they were less sensitive to male mating harassment (claspings; fig. 5). In infuscans females

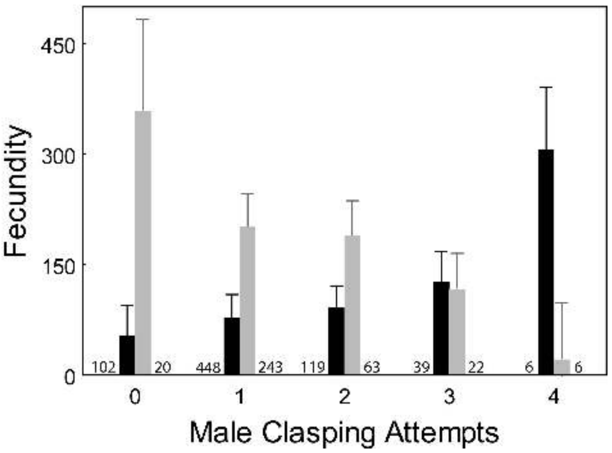

Figure 5: Effect of male harassment on female fecundity in the two most common morphs (sample sizes are given next to the bars). Androchrome females (*black*) are less sensitive than infuscans females (*gray*) in terms of how fecundity is affected by male clasping attempts (see "Results").

we found a significant and negative effect of increased male mating harassment ($\beta = -76.045$, $P = .007$; fig. 5). As a consequence, at high levels of male mating harassment, the fecundity advantage of infuscans females over androchrome females was lost (fig. 5). Thus, the rank ordering in terms of fecundity switched between infuscans and androchrome females with increased intensity of male mating harassment (fig. 5). We found no significant difference between androchromes and infuscans females in the effects of multiple matings on fecundity (morph × matings: $F = 2.526$, $\mathrm{df} = 1, 1058$, $P = .112$).

Discussion

The three female morphs in *Ischnura elegans* have stable mating rates across years and populations, and there is no evidence that the rank ordering in mating rates of the different morphs changes spatially or temporally (fig. 1). Androchrome females mate at a significantly lower rate than infuscans females (fig. 1), which could be either a result of male mimicry, making it more difficult for males to visually detect androchrome females (Robertson 1985), or a result of active male mate choice for the more fecund infuscans females (Svensson and Abbott 2005; Svensson et al. 2009). These two potential explanations might act in concert, and they of course do not need to be mutually exclusive. The combined effect would be to reinforce the observed differences in mating rates between the different female morphs across years and populations (fig. 1).

We conclude from these results that fluctuating mating rates and morph differences in overall mating rates are unlikely to drive frequency-dependent selection in this system and to explain the maintenance of this polymorphism. In contrast, precopulatory male mating harassment is likely to play a more important role, as indicated by the spatial and temporal fluctuations in female responses to male mating attempts (see below). The results in this study also support a role for sexual conflict in density-dependent selection, since the different morphs are differentially affected by male mating harassment at different densities (figs. 3, 5).

In contrast to the stability of relative mating rates in the female morphs, morph-specific female resistance to male harassment fluctuated considerably (fig. 2; table 1). Androchrome females showed less resistance to male mating attempts overall, and they were more likely to accept male matings, consistent with our previous study (Gosden and Svensson 2007). However, here we have demonstrated that resistance to male clasping attempts not only differed between morphs but also showed large spatial and temporal variation (table 1; fig. 2). The androchrome and infuscans morphs differed in their resistance to mating attempts in two populations (Höje Å 6 and Lomma; table A1; fig. 2*a*, 2*b*) but were more similar in the third population (Vombs; table A1; fig. 2*c*). It is interesting to note that the population in which infuscans females showed the lowest level of overall resistance (Vombs; fig. 2*c*) was also the population with the highest density of infuscans females. Although further data are clearly needed, it could indicate that when infuscans females are common in a population, they are more prone to accept male mating attempts because of the potential costs associated with resisting them. Lower resistance toward male mating attempts could potentially be beneficial in terms of convenience polyandry (Thornhill and Alcock 1983), since females in copula will be removed from further male harassment. Across all populations, androchromes show relatively little change in their resistance to males (table A1), suggesting that androchrome females are, overall, more likely to accept male mating attempts, perhaps because of lower overall mating opportunities in this morph (Gosden and Svensson 2007).

The spatial and temporal variability of female resistance toward male mating harassment suggests that the number of observed matings in the field will underestimate the true level of male mating harassment in this system. Two recent studies (Cordero Rivera and Sanchez-Guillen 2007; Hammers and Van Gossum 2008) questioned whether frequency-dependent male mating harassment was likely to maintain this female polymorphism. Their main line of reasoning was based on findings that show infuscans females are found in copula more often than androchrome females (regardless of frequency), which is inconsistent with the hypothesis that frequency-dependent selection maintains this polymorphism. Their arguments were based on the assumption that as a morph becomes more common, it also suffers increased mating harassment, which would simply be expected to translate into a higher proportion of common morphs mating (Cordero Rivera and Sanchez-Guillen 2007; Hammers and Van Gossum 2008). The results in our study cast some doubts on this interpretation. It is important to underscore that the differences in absolute mating rates among morphs do not reflect all the effects of male mating harassment, as morphs also show considerable spatiotemporal variation in their resistance to male mating attempts (fig. 2; tables 1, A1). Our results suggest that a given level of male mating harassment (number of clasping attempts) will have different consequences in terms of the number of matings for the different morphs. This makes the straightforward prediction of higher mating rates in the most common morph somewhat questionable and suggests that premating struggles and failed male mating attempts might be equally important, if not more important, causes of sexual conflict in this system.

Moreover, the fact that infuscans females have the highest mating rates (fig. 1) and the highest fecundity of all three morphs (Svensson and Abbott 2005) but still suffer from increased male mating harassment with increasing density (figs. 3, 4*a*, 5) suggests that there is no simple and single linear relationship between morph-specific mating rate and morph-specific fecundity (Gosden and Svensson 2007). Our results suggest that the different morphs are likely to be behaviorally, morphologically, and physiologically adapted to different levels of male mating harassment (figs. 4, 5), which makes it difficult to compare their overall mating rates and use mating rate as a proxy for the effect of male mating harassment among morphs. This is important because the fecundity consequences of mating rates and male clasping attempts differ between at least two of the morphs (figs. 4, 5). The results in this article suggest that male mimicry and density-dependent mating harassment might interact in maintaining this female polymorphism.

We wish to reiterate that although our estimates of premating harassment through male clasping attempts are likely to be correlated with total male mating harassment in the field, it is still a conservative estimate of the overall level of harassment faced by the morphs (figs. 1–5). The reason for this is twofold. First, our measure of the number of claspings is a minimum estimate since we had only five distinguishable fluorescent dust colors available. Second, other forms of male mating harassment, such as precopulatory chases, may also affect female condition and female fecundity (Arnqvist and Rowe 2005) but would not leave any trace of colored dust on females. Therefore, the overall level of male mating harassment in the field is likely to be substantially higher than only the harassment that leads to realized matings in the end (Cordero Rivera and Sanchez-Guillen 2007; Hammers and Van Gossum 2008).

Female density has previously been shown to have different fitness effects on female morphs in lizards (Sinervo et al. 2000; Svensson et al. 2001*b*; Vercken et al. 2007). In this study, females encounter different male responses as a result of increasing density, with androchromes being relatively unaffected by their own density, whereas nonandrochrome females face higher male mating harassment with increasing density (fig. 3). At low female densities, all morphs face similar levels of harassment (fig. 3). This might indicate that at low female densities, either the advantage of being a male mimic is lost as males expand their search image or males show no preference for any particular morph, resulting in more random male mate preferences. Random male mate preferences would presumably be adaptive for males at low densities because of the higher risks of remaining unmated (Kokko and Rankin 2006), particularly in a short-lived species such as *I. elegans*. As densities of females increase, thereby reducing male search costs, males can possibly afford to become more selective, targeting the more fecund infuscans morph (fig. 3) as an adaptive male strategy (cf. Bonduriansky 2001). Thus, male mate choice of female morphs is unlikely to be fixed in the form of a biased preference toward a particular morph (Svensson et al. 2009) but instead seems to be dynamic and affected by the density of the morphs (fig. 3). Such plastic male mate preferences have also been documented in experimental studies on *I. elegans* and other damselfly species (Van Gossum et al. 2001; Fincke et al. 2007).

The path analyses suggest different relationships with fecundity between the two most common morphs (fig. 4). Androchrome fecundity was more strongly influenced by the morphological traits, whereas infuscans females had a weaker relationship between morphology and mating but a stronger relationship between male harassment and mating rate (fig. 4). Androchrome females are generally thought to be male mimics (Robertson 1985). As a result of this male mimicry, the lower levels of male mating harassment found in this study could be the result of makes not perceiving them as females as often as the other morphs (Cordero et al. 1998; Svensson et al. 2009). It is interesting that abdomen thickness in the androchrome females was positively correlated with androchrome fecundity (fig. 4*b*) and that fecundity selection favored thicker abdomens ($\beta = 0.196$; see “Results”). Males have thinner abdomens than females, and among the female morphs androchrome females have the thinnest abdomens (see “Results”). This more malelike abdomen shape in androchrome females may be adaptive in terms of increasing overall androchrome morphological similarity to males (Abbott and Svensson 2008). However, the results in this study suggest that selection on fecundity works in the opposite direction, since androchrome females with thicker abdomens had higher fecundity (fig. 4*b*). This indicates the potential for a trade-off in androchrome females between the mimicry advantage of thinner, more malelike abdomens, which will allow them to pass as more convincing males, and the fecundity advantage of thicker abdomens, which presumably allows for the storage of more eggs or energy reserves for oviposition. Alternatively, the thinner abdomen in androchrome females is not adaptive per se but is rather a maladaptive correlated response to selection for becoming a male mimic, for example, in terms of body coloration.

For a mimic to be successful, it must not become too common in relation to the model (Ruxton et al. 2004). The relative advantage of male mimicry among androchrome females might therefore be context dependent on the relative densities of the other two female morphs. In contrast to the situation in androchrome females, fecundity in infuscans females was strongly influenced by male mating harassment, and an increased level of harassment lowers fecundity (figs. 4*a*, 5).

Different mating strategies within one sex (females in this case) can potentially lead to the maintenance of multiple heritable morphs in a spatially and temporally variable environment (fig. 5). If the intensity of male mating harassment varies spatially and temporally, androchrome females might be favored under high male mating harassment, whereas infuscans females might instead be favored when male mating harassment is lower (fig. 5). Thus, a necessary condition for morph maintenance through selection in a heterogeneous selective environment is fulfilled in this system: the relative rank ordering of the fitness of the female morphs becomes reversed with changing environmental conditions (Levene 1953; Lively 1986; Svensson et al. 2001*a*).

In *I. elegans*, females could avoid males either by relying on deceptive visual coloration traits such as male mimicry (i.e., androchrome females) or by relying on behavioral resistance and rejecting male mating attempts (i.e., infuscans females; Gosden and Svensson 2007). The densities of the different morphs are known to influence sexual selection on male body size (Gosden and Svensson 2008), indicating the potential for dynamic feedback loops in this system between interacting phenotypes of the sexes (Moore et al. 1997; Moore and Pizzari 2005). To this we can add the effects of frequency-dependent (Svensson et al. 2005) and density-dependent (this study) antagonistic mating interactions that seem to affect the performance and fitnesses of these female morphs (figs. 3, 5). In sexual conflict, one sex can be expected to carry a higher conflict load (Chapman 2006; Rice et al. 2006) due to lowered fitness caused by the other sex. In the polymorphic species *I. elegans*, this sexual conflict load arising from male mating harassment seems to have been divided and shared among the three female morphs. Thus, each morph suffers from some of the conflict costs, depending on current environmental conditions. Recent theory (Gavrilets 2000; Kokko and Rankin 2006) and empirical evidence (Arnqvist 1992; Blanckenhorn et al. 2000; Martin and Hosken 2003) have examined the role of density-dependent selection in sexual conflict. Our study on this female polymorphism in *I. elegans* also suggests that sexual conflict through male mating harassment might lead to density-dependent selection. This density-dependent selection can potentially maintain a female polymorphism, in this system where one of the females is a male mimic.

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Literature Cited

Abbott, J. 2006. Ontogeny and population biology of a sex-limited colour polymorphism. PhD diss. Department of Ecology, Lund University.

Abbott, J. K., and E. I. Svensson. 2008. Ontogeny of sexual dimorphism and phenotypic integration in heritable morphs. Evolutionary Ecology 22:103–121.

Arnqvist, G. 1992. Spatial variation in selective regimes: sexual selection in the water strider *Gerris odontogaster*. Evolution 46:914–929.

Arnqvist, G., and L. Rowe. 2002. Antagonistic coevolution between the sexes in a group of insects. Nature 415:787–789.

———. 2005. Sexual conflict. Princeton University Press, Princeton, NJ.

Askew, R. R. 1988. The dragonflies of Europe. Harley, Colchester.

Banks, M. J., and D. J. Thompson. 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. Journal of Animal Ecology 56:815–832.

Blanckenhorn, W. U., C. Muhlhauser, C. Morf, T. Reusch, and M. Reuter. 2000. Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. Ethology 106:577–593.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biological Reviews of the Cambridge Philosophical Society 76:305–339.

Borash, D. J., A. G. Gibbs, A. Joshi, and L. D. Mueller. 1998. A genetic polymorphism maintained by natural selection in a temporally varying environment. American Naturalist 151:148–156.

Chapman, T. 2006. Evolutionary conflicts of interest between males and females. Current Biology 16:R744–R754.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41–47.

Cooper, G., P. L. Miller, and P. W. H. Holland. 1996. Molecular genetic analysis of sperm competition in the damselfly *Ischnura elegans* (Vander Linden). Proceedings of the Royal Society B: Biological Sciences 263:1343–1349.

Corbet, P. S. 1999. Dragonflies: behaviour and ecology of Odonata. Harley, Colchester.

Cordero, A., S. S. Carbone, and C. Utzeri. 1998. Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). Animal Behaviour 55:185–197.

Cordero Rivera, A., and R. A. Sanchez-Guillen. 2007. Male-like females of a damselfly are not preferred by males even if they are the majority morph. Animal Behaviour 74:247–252.

Fincke, O. M. 1986. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata, Coenagrionidae). Evolution 40:791–803.

———. 2004. Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. Animal Behaviour 67:833–845.

Fincke, O. M., A. Fargevieille, and T. D. Schultz. 2007. Lack of innate preference for morph and species identity in mate-searching *Enallagma* damselflies. Behavioral Ecology and Sociobiology 61: 1121–1131.

Gavrilets, S. 2000. Rapid evolution of reproductive barriers driven by sexual conflict. Nature 403:886–889.

Gavrilets, S., and T. I. Hayashi. 2005. Speciation and sexual conflict. Evolutionary Ecology 19:167–198.

Gavrilets, S., and D. Waxman. 2002. Sympatric speciation by sexual conflict. Proceedings of the National Academy of Sciences of the USA 99:10533–10538.

Gosden, T. P., and E. I. Svensson. 2007. Female sexual polymorphism and fecundity consequences of male mating harassment in the wild. PLoS One 2:e580.

———. 2008. Spatial and temporal dynamics in a sexual selection mosaic. Evolution 62:845–856.

Gray, S. M., and J. S. McKinnon. 2007. Linking color polymorphism maintenance and speciation. Trends in Ecology & Evolution 22: 71–79.

Hammers, M., and H. Van Gossum. 2008. Variation in female morph frequencies and mating frequencies: random, frequency-dependent harassment or male mimicry? Animal Behaviour 76:1403–1410.

Härdling, R., and J. Bergsten. 2006. Nonrandom mating preserves intrasexual polymorphism and stops population differentiation in sexual conflict. American Naturalist 167:401–409.

Holland, B., and W. R. Rice. 1998. Chase-away sexual selection: antagonistic seduction versus resistance. Evolution 52:1–7.

Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? density-dependent effects in mating systems. Philosophical Transactions of the Royal Society B: Biological Sciences 361:319–334.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Le Galliard, J.-F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the USA 102: 18231–18236.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. American Naturalist 87:331–333.

Lew, T. A., E. H. Morrow, and W. R. Rice. 2006. Standing genetic variance for female resistance to harm from males and its relationship to intralocus sexual conflict. Evolution 60:97–105.

Linder, J. E., and W. R. Rice. 2005. Natural selection and genetic variation for female resistance to harm from males. Journal of Evolutionary Biology 18:568–575.

Lively, C. M. 1986. Canalization versus developmental conversion in a spatially variable environment. American Naturalist 128:561–572.

Magurran, A. E., and B. H. Seghers. 1994. A cost of sexual harassment in the guppy, *Poecilia reticulate*. Proceedings of the Royal Society B: Biological Sciences 258:89–92.

Mappes, T., M. Koivula, E. Koskela, T. A. Oksanen, T. Savolainen, and B. Sinervo. 2008. Frequency and density-dependent selection on life-history strategies: a field experiment. PLoS One 3:e1687.

Martin, O. Y., and D. J. Hosken. 2003. The evolution of reproductive isolation through sexual conflict. Nature 423:979–982.

Mitchell, R. J. 2001. Path analysis: pollination. Pages 217–234 *in* S. M. Scheiner and J. Gurevitch, eds. Design and analysis of ecological experiments. Oxford University Press, New York.

Moore, A. J., and T. Pizzari. 2005. Quantitative genetic models of sexual conflict based on interacting phenotypes. American Naturalist 165:S88–S97.

Moore, A. J., E. D. Brodie, and J. B. Wolf. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. Evolution 51:1352–1362.

Mueller, L. D. 1988. Evolution of competitive ability in *Drosophila* due to density-dependent natural selection. Proceedings of the National Academy of Sciences of the USA 85:4383–4386.

Mueller, L. D., and F. J. Ayala. 1981. Trade-off between *r*-selection and *K*-selection in *Drosophila* populations. Proceedings of the National Academy of Sciences of the USA 78:1303–1305.

Pryke, S. R., L. B. Astheimer, W. A. Buttemer, and S. C. Griffith. 2007. Frequency-dependent physiological trade-offs between competing colour morphs. Biology Letters 3:494–497.

Reinhardt, K., E. Harney, R. Naylor, S. Gorb, and M. T. Siva-Jothy. 2007. Female-limited polymorphism in the copulatory organ of a traumatically inseminating insect. American Naturalist 170:931–935.

Rice, W. R., A. D. Stewart, E. H. Morrow, J. E. Linder, N. Orteiza, and P. G. Byrne. 2006. Assessing sexual conflict in the *Drosophila melanogaster* laboratory model system. Philosophical Transactions of the Royal Society B: Biological Sciences 361:287–299.

Robertson, H. M. 1985. Female dimorphism and mating-behavior in a damselfly, *Ischnura ramburi*: females mimicking males. Animal Behaviour 33:805–809.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press, Oxford.

Sanchez-Guillen, R. A., H. Van Gossum, and A. Cordero Rivera. 2005. Hybridization and the inheritance of female colour polymorphism in two ischnurid damselflies (Odonata: Coenagrionidae). Biological Journal of the Linnean Society 85:471–481.

Sherratt, T. N. 2001. The evolution of female-limited polymorphisms in damselflies: a signal detection model. Ecology Letters 4:22–29.

Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240–243.

Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

StatSoft. 2003. STATISTICA (data analysis software system). Version 6. StatSoft, Inc., Tulsa, OK.

Svensson, E., and B. Sinervo. 2000. Experimental excursions on adaptive landscapes: density-dependent selection on egg size. Evolution 54:1396–1403.

Svensson, E., B. Sinervo, and T. Comendant. 2001*a*. Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. Evolution 55:2053–2069.

———. 2001*b*. Density-dependent competition and selection on immune function in genetic lizard morphs. Proceedings of the National Academy of Sciences of the USA 98:12561–12565.

———. 2002. Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. Journal of Evolutionary Biology 15:1034–1047.

Svensson, E. I., and J. Abbott. 2005. Evolutionary dynamics and population biology of a polymorphic insect. Journal of Evolutionary Biology 18:1503–1514.

Svensson, E. I., J. Abbott, and R. Härdling. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. American Naturalist 165:567–576.

Svensson, E. I., J. K. Abbott, T. P. Gosden, and A. Coreau. 2009. Female polymorphisms, sexual conflict and limits to speciation processes in animals. Evolutionary Ecology 23:93–108.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, MA.

Van Gossum, H., R. Stoks, and L. De Bruyn. 2001. Reversible frequency-dependent switches in male mate choice. Proceedings of the Royal Society B: Biological Sciences 268:83–85.

Vercken, E., M. Massot, B. Sinervo, and J. Clobert. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology 20:221–232.

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A blue male *Ischnura elegans* mating with his female doppelgänger. Photograph by Erik Svensson.