



Male-like females of a damselfly are not preferred by males even if they are the majority morph

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Animals searching for prey and males searching for mates share similar problems of detection if their targets are diverse in colour or physical appearance. There is good evidence for predators switching their preferences for prey in a frequency-dependent way; predators focus on the most common form, and the decreased predation on rarer forms allows multiple forms to survive. Frequency-dependent mate selection has also been proposed to explain the maintenance of several female colour morphs in damselflies. However, the fact that one of the female morphs is coloured like a male (androchrome) and behaves similarly to males suggests the phenomenon of male mimicry in this system as an alternative explanation for the polymorphism. We compared androchrome frequencies in populations and mating pairs in *Ischnura elegans*, over a range of androchrome frequencies (8–90%). In 22 of 23 samples androchromes mated less often than expected (significantly in 13 samples). We found no evidence for males switching their preferences in a frequency-dependent way. A test of male preference for female morphs in a population with 85% androchromes indicated that males behaved indiscriminately and did not prefer the commonest (male-like) morph. Our results support androchrome male mimicry rather than learned mate recognition by males (a purely frequency-dependent model) as the main mechanism behind the maintenance of this sex-limited colour polymorphism.

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Frequency-dependent selection is a powerful force maintaining stable polymorphisms in nature (Heino et al. 1998). For instance, diversity in prey is thought to contribute to the coexistence of different prey types because predators concentrate on the most common type (Bond & Kamil 2002), switching their preferences in relation to prey frequency. Less common forms of prey persist in this system because of their decreased predation. As another example, studies of Batesian mimicry show that predators avoid harmless mimics (*Lampropeltis* spp.) of venomous coral snakes (*Micrurus* and *Micruroides* spp.) only in areas that are inhabited by these dangerous snakes, in a clear case of frequency-dependent mimicry (Pfennig et al. 2001).

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Some damselflies are polymorphic in body coloration, with the polymorphism usually restricted to the female sex. One of the female morphs is coloured like the male (androchrome) and one or more are not (gynochromes; Cordero & Andrés 1996). Based on their male-like appearance, androchrome females have been considered to be male mimics and the maintenance of this polymorphism has been explained as the result of a sexual conflict of interests over mating frequency, with androchrome females avoiding unwanted male attention by mimicking males (Robertson 1985; Hinnekint 1987; Cordero 1992; Cordero et al. 1998; Andrés et al. 2002). This polymorphism is very common among the Odonata (Fincke et al. 2005). Fincke (1997) proposed that, similarly to the coexistence of multiple prey forms mentioned above, the existence of several colour morphs among females would lead to frequency-dependent mate selection by males and to a stable polymorphism; Fincke (2004) explicitly rejected the idea of male mimicry in this system.

Several studies have supported Miller & Fincke's (1999) learned mate recognition (LMR) hypothesis. Van Gossum et al. (2001a) tested male preference for androchrome or gynochrome females in a binary choice experiment. Males were given the opportunity to 'choose' between two females inside a small cage. Those that tried mating with one of the female morphs were then maintained for 2 days in an outdoor insectary with the nonpreferred morph. A second test showed that almost all males now preferred the morph initially rejected. A third test after 2 additional days in an insectary with the morph not chosen in the second test showed that again males changed their preference. This was interpreted as males forming a search image for the commonest morph in the population (Van Gossum et al. 2001a). More surprisingly, when males were given the opportunity to choose between another male and one female morph, some of them tried to mate with males instead of females, and this was also reversible in the same way (Van Gossum et al. 2005).

The male mimicry and the LMR hypotheses produce clearly divergent predictions when androchrome females are the majority morph in the population. If males learn the appearance of females, then if most females resemble males, males should prefer this morph to the rarer gynochrome females (frequency-dependent selection; Fincke 2004). In contrast, if females mimic males, then males should behave indiscriminately when most females are androchromes, because otherwise they would lose most mating opportunities (Robertson 1985), and androchrome females should not be preferred to gynochrome females (Sherratt 2001). Unfortunately, androchrome females are rarely the commonest morph (Fincke et al. 2005), and this has delayed addressing this question.

We tested this critical prediction by studying male preference in a population of the damselfly *Ischnura elegans*, where 85% of females are androchrome, and by estimating androchrome mating frequency in populations with low and high proportions of androchrome females. *Ischnura elegans* has three female morphs, one androchrome and two brown gynochromes: *infuscans* and *rufescens-obsolata*. The genetic basis of this polymorphism is controlled by three alleles in an autosomic locus (Sánchez-Guillén et al. 2005).

METHODS

Population and Mating Frequencies

In northwest Spain androchrome frequency varies markedly between populations of *I. elegans* (Sánchez-Guillén et al. 2005). We selected the Louro lagoon as the main study site for the present study because it had 85% androchrome females in samples taken in 2000–2001. The rarest morph, *rufescens-obsolata*, was so rare (1%) that this population was effectively dimorphic. We sampled three localities with contrasting androchrome frequencies: Foz, Cedeira and Doniños (see Sánchez-Guillén et al. 2005, for Universal Transverse Mercator coordinates of these sites). We estimated the mating

frequency of female morphs by recording all mating pairs observed in transects during the daily period of reproductive activity (1000–1500 hours). Population frequency was estimated from mature females found alone (i.e. *violacea* and *rufescens* females were not taken into account because both are immature colour phases). Damselflies were marked or retained in cages to avoid counting the same specimen twice. We marked damselflies by writing a number on their wings with an indelible black marker. Observed and expected frequencies (from the population proportion) of female morphs in copula were compared with a chi-square test.

Test of Male Preferences

A live-models' presentation experiment was done with the Louro population in June 2001. The experiment consisted of the presentation of live individuals tethered to a wooden stick by a fine wire (see Cordero 1989 and Cordero et al. 1998 for details). The model had great freedom of movement and was highly attractive to males. Three mature individuals of each phenotype (blue males, blue androchromes and olive-green *infuscans* gynochromes) were presented to males until 10 responses were recorded. To obtain this number of responses required between 7 and 41 min. The *rufescens-obsolata* morph could not be included in the tests because it represented less than 1% of females. Three males did not respond to the model and were not considered in the analyses. Three trials (involving nine models) were made on 2 consecutive days. The order of model presentation was random for each trial. When possible, we marked males that responded to the model to avoid testing them twice. Responses were categorized as approach (the male approached to a few centimetres from the model, without physical contact), contact (the male approached the model and touched it), attempted tandem (the male approached and perched on the model, curving the abdomen in an attempt to achieve tandem) and tandem (the male grasped the model with his anal appendages). The last two categories show that the tested males were sexually interested. Results were analysed with chi-square tests.

RESULTS

Population and Mating Frequencies

Table 1 presents the results of our sampling in four populations in northwest Spain, and a review of literature data for seven additional sites (most of them previously unpublished). Androchrome frequencies were highly variable from 8 to 90%. There were significant differences between population and copulation frequencies in 13 of 23 samples. In all but one sample, androchrome females mated less frequently than expected, even when they represented up to 90% of the population (Fig. 1a). The only exception is based on only six mating pairs (Louro, Spain, Table 1), and such a small sample is unlikely to be reliable (Cordero Rivera & Andrés 2001). As expected, *infuscans* females mated more often than their population frequency

Table 1. A comparison of morph frequency in populations of *I. elegans* throughout Europe

Locality	Country	Source	Date	N	Proportion in population			Frequency in mating pairs			χ^2_2	P
					A	I	O	A	I	O		
Anglesey	U.K.	Lord 1961	1959–1960	462	0.385	0.193	0.422	11	16	22	7.93	0.019
Dunham Park	U.K.	Parr & Palmer 1971	1965, 1966, 1970	1118	0.309	0.295	0.396	25	45	64	9.45	0.009
Dunham Park	U.K.	Banham 1990	Jun–Aug 1985	108	0.250	0.343	0.407	15	23	38	2.80	0.247
Dunham Park	U.K.	Banham 1990	Jul–Aug 1986	249	0.305	0.257	0.438	11	26	28	9.11	0.010
Woodchester	U.K.	Banham 1990	Jun–Jul 1978	424	0.722	0.184	0.094	36	36	9	38.74	<0.001
Woodchester	U.K.	Banham 1990	Jun–Jul 1980	240	0.654	0.254	0.092	23	12	3	0.77	0.679
Woodchester	U.K.	Banham 1990	Jun–Jul 1981	306	0.670	0.209	0.121	42	17	7	0.97	0.615
Woodchester	U.K.	Banham 1990	Jun–Jul 1982	304	0.707	0.171	0.122	55	21	20	9.64	0.008
Woodchester	U.K.	Banham 1990	Jun–Jul 1983	423	0.626	0.336	0.038	28	27	0	7.24	0.027
Woodchester	U.K.	Banham 1990	Jun–Jul 1984	399	0.634	0.178	0.188	51	26	13	7.78	0.020
Woodchester	U.K.	Banham 1990	Jun–Jul 1985	314	0.589	0.331	0.080	27	21	10	7.95	0.019
Woodchester	U.K.	Banham 1990	Jul 1985	402	0.664	0.236	0.100	29	28	11	17.29	<0.001
Woodchester	U.K.	Banham 1990	Jun–Jul 1987	172	0.663	0.145	0.192	34	17	5	12.98	0.002
Pocklington canal	U.K.	Banham 1990	Jul–Aug 1987	181	0.486	0.221	0.293	124	64	93	2.62	0.270
La Tur du Valat	France	Banham 1990	Sep 1985	133	0.586	0.248	0.165	44	140	84	198.24	<0.001
Refuge de Gibier	France	Banham 1990	May 1986	75	0.307	0.600	0.093	6	17	2	0.68	0.713
Refuge de Gibier	France	Banham 1990	Sep 1986	21	0.095	0.810	0.095	1	5	0	0.90	0.639
Castelporziano	Italy	Cordero et al. 1998	Jun–Aug 1994	690	0.483	0.262	0.255	235	220	92	60.17	<0.001
Louro	Spain	This study	Jul 2004	102	0.882	0.108	0.010	153	34	1	13.24	0.001
Louro	Spain	This study	Jul 2005	52	0.904	0.096	0.000	16	3	0	2.04	0.361
Cedeira	Spain	This study	Jul 2004	26	0.077	0.885	0.038	0	11	0	1.43	0.488
Foz	Spain	This study	Jul 2004	47	0.362	0.617	0.021	6	13	1	1.02	0.600
Doniños	Spain	This study	Aug 2004	16	0.125	0.875	0.000	0	8	0	2.51	0.285

Sample size (N) indicates the number of mature females examined in each locality and year. The number of females found in mating pairs is compared with the expected proportion based on the population frequency. A: androchrome; I: *infuscans*; O: *rufescens*–*obsoleta*.

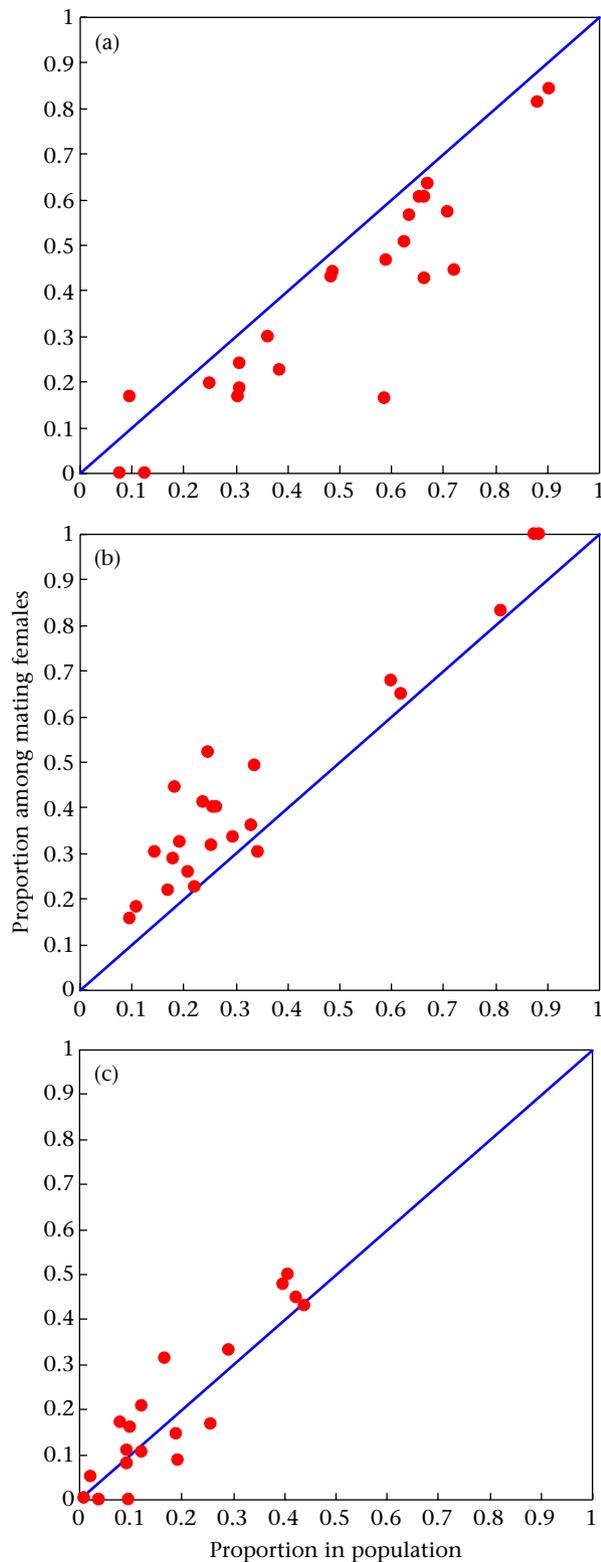


Figure 1. Population and mating frequencies of polymorphic females of *Ischnura elegans*. (a) Androchromes, (b) *infuscans* and (c) *rufescens-obsolata*. The diagonal indicates the expected relation if females mate in direct proportion to their population frequency. Had males switched preference, points should be below the diagonal for female frequencies below 50% and above the diagonal thereafter (i.e. a sigmoidal curve). Note that *rufescens-obsolata* females were never the majority morph.

(Fig. 1b), in agreement with previous tests of male preferences for live models in this species (Cordero Rivera & Andrés 2001). Finally, *rufescens-obsolata* females, the only morph that was never the dominant phenotype (Table 1, Fig. 1c) seemed to mate as expected for their population frequency.

Male Preferences

Males clearly discriminated between males and females ($\chi^2_3 = 19.3$, $P < 0.001$), but the percentage of males that were sexually interested in androchrome (73%) and gynochrome (80%, *infuscans*) females was the same ($\chi^2_3 = 0.41$, $P = 0.939$; Fig. 2). This indicates that, when androchromes were the majority morph, males did not discriminate between female morphs.

DISCUSSION

We found evidence for a difference between female morphs of *I. elegans*: androchrome females tended to mate less than expected, and gynochrome females more than expected. This finding is so robust that results from many populations and years consistently indicate that the probability of mating is greater for *infuscans* and *obsolata* females than for androchromes (Fig. 1). The extensive data set compiled by Banham (1990) is based not only on his personal observations but also on data recorded by students during field courses. Lord (1961) also found that androchrome females mated less often than expected. Therefore the main result is also robust to a possible observer bias. Androchromes, which tend to perch higher in vegetation (Van Gossum et al. 2001b), might be more conspicuous during sampling and if androchromes were overrepresented in the population surveys, then this might explain why they appear under-represented in mating pairs. This explanation seems unlikely, however, because our study includes several populations, and although androchromes might be more conspicuous in habitats with complex vegetation, this would not be the case in grassy habitats for instance, where places to hide are scarce. Second, in contrast to this idea, Van Gossum et al. (2004) showed that androchromes and gynochromes are equally detectable by human observers. Therefore, Fig. 1 clearly shows that androchrome females mate less often than expected from their population frequency.

Even at high androchrome frequency, the deviation between observed and expected mating frequencies of androchromes did not decrease, a result that might be predicted if males do not distinguish between female morphs in androchrome-dominated populations. The fact that androchromes still mated less often than expected suggests that these females actively avoid mating.

Our results are at variance with a purely frequency-dependent mechanism of mate recognition, as hypothesized by the LMR model (Fincke 2004). Androchrome females have been found to mate less often than expected in other *Ischnura* species (Robertson 1985; Cordero Rivera & Egido Pérez 1998; Sirot et al. 2003). The lower mating

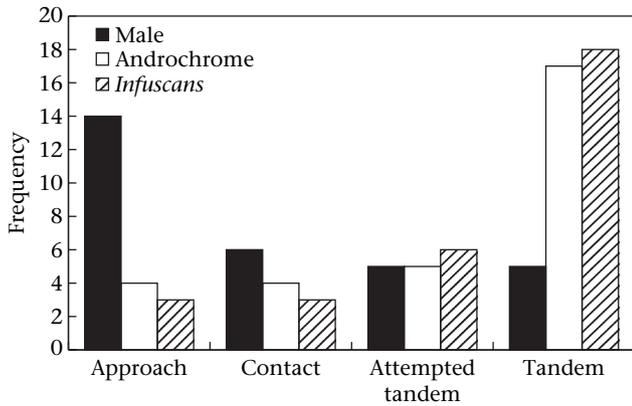


Figure 2. Results of a model presentation to test male preference for female morphs in a population with 85% androchromes. Numbers of males that approached, touched the female or showed a sexual response (attempted tandem and tandem) are shown.

frequency of androchromes is further supported by the finding that they store less sperm (Cordero et al. 1998). The same result had been found by Banham (1990), although Cordero et al. (1998) were unaware of this when their study was done. We can therefore conclude that the evidence for lower mating frequency in androchrome *I. elegans* is strong.

It is especially relevant that we have studied one site with approximately 90% androchromes, but, nevertheless, even under this extreme frequency, males did not prefer this morph. The results of the model presentation (Fig. 2) suggest that male mimicry is an important mechanism for androchrome maintenance, and are not compatible with LMR predictions. Even the rare *rufescens-obsolata* morph (with a frequency of only 1%) had no problems mating. Males were so indiscriminate that one mating pair between a male *I. elegans* and a female *Pyrrhosoma nymphula* was found at Carnota, a locality also with 90% androchromes (Sánchez-Guillén et al. 2005). Nevertheless, male mimicry alone cannot explain the existence of several gynochrome phenotypes, a fact that has long been recognized (e.g. Cordero et al. 1998, page 196).

Our results and also those of Sánchez-Guillén et al. (2005) show that androchrome frequency is very variable between populations of *I. elegans*, even in the same region. These populations might be at different equilibria or simply out of equilibrium. Our results (Table 1) indicate that morph frequencies remain fairly stable from year to year. Therefore, we are inclined to think that these populations are in equilibrium, but to test this we need a long-term study, which is currently under way.

A review of male responses to female morphs in odonates suggested that males usually prefer the gynochrome morph (Cordero Rivera & Andrés 2001), but the scarcity of tests on populations where androchromes were the most common morph prevented a firm conclusion. The observation of male–female interactions in another polychromatic *Ischnura* showed that androchromes were less likely than gynochromes to receive mating attempts in encounters with males, although they did not mate less frequently; contrary to the LMR hypothesis,

the rarer morph was more likely to receive mating attempts (Sirot et al. 2003). Furthermore, in *Ceriagrion tenellum*, another member of the same family, and *I. elegans*, males prefer to mate with gynochrome females when live, tethered females are presented, but are indiscriminate when the models are presented dead (Cordero et al. 1998; Andrés et al. 2002). These results indicate that female (refusal) behaviour is important, and androchromes are not only coloured like males, they also behave like males (see also Utzeri 1988).

A recent survey of Scandinavian populations of *I. elegans* suggests that morph fecundities are negatively affected by frequency- and density-dependent male mating harassment; the frequency-dependent processes were enough to maintain the female polymorphism in a genetic model (Svensson et al. 2005). Morphs differed in fecundity (*infuscans* was most fecund) and morph frequencies in the populations changed rapidly, with a general decrease in androchrome frequency from 2000 to 2003 (Svensson & Abbott 2005). In the same period (2000–2005) our Louro population had a significant increase in androchrome frequency (from 86 to 90%; unpublished data), but in other populations morph frequencies are stable (see for instance the Woodchester and Dunham Park populations in Table 1). In this context, female fecundity seems to be one of the key variables, because Banham (1990) found that androchrome and *rufescens-obsolata* females have lower fecundity than *infuscans*. Svensson et al. (2005) estimated morph mating probabilities in the field and used them as an estimate of the degree of male mating harassment towards the three morphs, implicitly assuming that male harassment is frequency dependent. They found that the proportion of copulating androchromes (the most common morph) was significantly affected by both male density and the frequencies of the three female morphs, which is consistent with the expectation from density- and frequency-dependent male mating harassment. Nevertheless, our results indicate that androchromes can avoid mating, probably by behaving like males (Cordero et al. 1998). Svensson et al. (2005) found that across all populations and years androchrome females were found less often in copula than *infuscans* females but not than *infuscans-obsolata*; unfortunately detailed population and mating frequencies were not given.

Our results are also at variance with studies where male ‘preference’ for female morphs was tested in binary choice experiments (Van Gossum et al. 2001a, 2005). Males of *I. elegans* confined with one female morph during 2 days tended to prefer this morph when two females were presented simultaneously in a small cage. We think that the explanation for this discrepancy is due to two important facts: first, in nature males almost never have the opportunity to choose between two females (in fact, in our long experience in field work with ischnurans, we have never observed a male finding two females simultaneously); second, females retained in small cages are unable to reject male approaches, and therefore males might be guided only by female coloration, excluding behaviour. Consequently, binary choice experiments in small cages are unnatural and their results probably not informative in this context (Cordero Rivera & Andrés 2001). Under field

conditions, males are highly mobile and continually search for females. Androchrome and gynochrome females behave in a different way, androchromes being more aggressive towards males, and gynochromes more cryptic (Van Gossum et al. 2001b). We conclude that male mimicry is widespread in ischnurans, and this fact cannot be ignored in discussions about the maintenance of this polymorphism. Mimicry, frequency dependence and density dependence among both adults and larvae (Abbott & Svensson 2005; I. González de Castro & A. Cordero Rivera, unpublished data) are the ingredients of an adaptive mechanism to maintain this polymorphism. Future work should test whether these results are a peculiarity of ischnurans or are general in polymorphic damselflies.

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