

## **Cues for Mate Recognition and the Effect of Prior Experience on Mate Recognition in *Enallagma* Damselflies**

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*In many coenagrionid damselflies, sexually mature females exhibit color polymorphisms, with some females resembling conspecific males. Although it has been suggested that the latter function as male mimics, this does not appear to be the case for those in the genus *Enallagma*. We found that sexually dimorphic coloration of the female abdomen and thorax are important cues for sexual recognition by males. We demonstrate for the first time in the Odonata, that males learn to recognize andromorphs as potential mates. After 2 days in an enclosure, sexually mature males exposed to only andromorphic females initiated more sexual interactions with tethered andromorphs than with heteromorphs, the majority morph in the natural population. Exposure to only heteromorph females tended to decrease males' sexual responses to andromorphs, but not significantly so. Because the frequency of female morphs often varies within a population, learned mate recognition would be advantageous for males that search for mates. Our results lead to a novel, frequency-dependent hypothesis for the occurrence and maintenance of female-limited color polymorphisms.*

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**KEY WORDS:** learning; mate recognition; Coenagrionidae; insect; frequency-dependent selection.

### **INTRODUCTION**

The success of an individual's searching strategy ultimately depends on: (1) the availability and distribution of resources; (2) efficiency in locating resources; and

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(3) the ability of an individual to respond to short-term changes in the environment (Bell, 1991). Cueing to the most frequent resource is one way an organism might forage efficiently when prey vary in frequency over time and space. In several species, particularly in vertebrates, past experience with prey has been shown to affect subsequent foraging behavior either by search image formation (Tinbergen, 1960; Gendron, 1986; Bell, 1991), or by a reduction in search rate when there are multiple types of prey available (e.g. Guilford and Dawkins, 1987). In insects with multiple female color morphs, a male searching for a mate faces problems of discrimination similar to a predator foraging on a polymorphic prey species. Although to recognize flowers or host plants has been demonstrated in foraging hymenoptera and lepidoptera (e.g. Gould, 1985; Papaj and Prokopy, 1989; Weiss, 1997; Cunningham *et al.*, 1998) the effect of prior experience on mate recognition has only rarely been investigated in insects (Roitberg *et al.*, 1993).

In many coenagrionid damselflies, sexually mature females vary in coloration of the thorax and abdomen (Walker, 1953; Dunkle, 1990). Females that are similar in color to conspecific males, have been termed 'andromorphs'; 'heteromorphs' are females that differ considerably from males in coloration (Johnson, 1975). Andromorphs are often considered to be male mimics, a term that seems most appropriate for species such as *Ischnura ramburi* and *I. graellsii*, whose males react similarly to constrained conspecific males and andromorphic females, which closely resemble males in thorax coloration and brightness, abdominal color pattern, and even behavior (Robertson, 1985; Cordero, 1992). A density-dependent hypothesis for the maintenance of color morphs rests on the assumption that andromorphic females mimic males and thereby avoid unwanted male attention at high population density but suffer greater mating failure at low population density (Hinneking, 1987). The hypothesis has enjoyed some support (e.g. Cordero, 1992; Forbes *et al.*, 1995; Cordero *et al.*, 1998), though the validity of the male mimicry hypothesis for andromorphs generally, remains uncertain. A comparative analysis of polymorphic odonates revealed that the sexual response of males to constrained females was correlated with the frequency of a given female morph in the population, suggesting that the encounter rate with females influences a male's propensity to respond sexually to a particular morph (Fincke, 1994a, Van Gossum *et al.*, 1999). Indeed, Forbes (1994) found that male *Enallagma boreale* responded sexually more frequently to andromorphic females in a population where andromorphs were in the majority.

Here, we test the hypothesis that andromorphic *Enallagma* females function as male mimics, by examining the response of mate-searching males to females of two color morphs in field and enclosure experiments. We determine: (1) the relative importance of the dorsal abdomen color as a cue for sexual recognition by males, and (2) if past experience with a particular morph affects a male's subsequent reaction to females of each morph. Our results suggest that the sexually dimorphic coloration of the female abdomen is an effective cue to sexual

identity independent of thorax color, and that a male's response to female color morphs is phenotypically plastic with respect to his prior experience.

## MATERIALS AND METHODS

### Study Species

Males of *Enallaga ebrium* (Forbes, 1994) and *Enallagma civile* (Bick and Bick, 1963; Bick and Hornuff, 1966) do not defend territories but rather actively search for mates around the edges of small ponds where females come to oviposit. A male takes a perched female in tandem by clasping her prothorax with his anal appendages. Copulation then occurs if the female bends her abdomen and makes contact with the male's accessory genitalia located on his second abdominal segment (Robertson and Tennesen, 1984).

In most species of the genus *Enallagma*, males are predominately blue, and are easily distinguishable from females by the bright blue stripes on segments 6–10 of their otherwise black abdomen. The blue thorax of *Enallagma* males is brighter than the blue thorax of andromorphs. Females of both morphs have an abdomen whose dorsal surface is entirely black, whereas the color of the thorax and sides of the abdomen varies among females (Walker, 1953). Overall, the coloration of male and female *E. ebrium* is very similar to that of *E. civile*.

Females in this study were assigned to one of two morph classes. Heteromorphic females were dark green to tan, whereas andromorphic females had a dark to light blue thorax and abdomen. In the *Enallagma ebrium* population studied, morphs were easily classified into two distinct types, whereas coloration in female *Enallagma civile* varied continuously. Often, *E. civile* were intermediate in coloration, predominately green on the dorsal thorax, and dark to light blue on the sides of the thorax and abdomen. Although male *E. civile* do not discriminate between heteromorphs and intermediate females (Moodie, 1995), the latter were not used in any of our mate-discrimination experiments.

### Cues to Sexual Identity in *Enallagma ebrium*

The role of abdomen coloration as a cue to sexual identity was examined in *E. ebrium* at Van Pond on the outskirts of Pellston, Emmet County, Michigan in July 1994. *E. ebrium* was the only *Enallagma* present; it co-occurred with *Lestes retangularis*. The pond was surrounded on three sides by pine woods and has a road on the fourth side. The perimeter (up to 10 m) of the pond was very open, being sparsely vegetated with grasses and raspberry bushes, which made it easy to watch interactions between males and females. To verify that males were searching for females in this area, tandem pairs at the perimeter of the pond were caught, and both the female and male individually marked. The males were released and the lone females were placed on a grass perch. The time at which

the females were first seen in tandem again that day was noted. Over the 11-day study, 65 males and 70 females were marked. More effort was made to find and mark lone females away from the pond as well as females in tandem at the pond, than solo males, which were abundant around the water. Therefore, the total sample of marked individuals does not reflect the typical male-biased sex ratio at the pond.

The reactions of males to live, perched conspecifics were recorded between 1200 and 1600 h (daylight savings time), on six days (19–25 July). An individual was secured to a perch by gluing all six legs with Duco cement to the end of a wooden dowel. The damselfly was positioned such that its abdomen was aligned naturally along the length of the dowel, which was then inserted at an angle into the soil. The 'perched' individual was positioned just below the top of the surrounding grass stems, 50–80 cm from the water's edge, and was used for only one 15-min test period. The following mutually exclusive reactions of males that oriented to a test individual were scored: (1) approach—a male orients to individual and approaches within 5 cm, but then flies off; (2) hover—male hovers over individual and then flies off; (3) grab—male grabs the pronotum or thorax but doesn't form, or attempt to form, tandem; (4) tandem—male forms tandem with a female or, in the case of a test male, the male raises his abdomen to the test individual's pronotum, attempting to form tandem.

Test individuals were either controls (andromorphic or heteromorphic females, and males) or experimentals whose normal abdomen color pattern was experimentally modified. The dorsal blue on the abdomen of males was blackened with a felt-tip marker to resemble the abdomen of a female. Females were modified by painting three blue stripes (Testors light blue enamel paint) on abdominal segments 3, 5, 7 and 8. For some females, only segments 7 and 8 were painted blue so as to resemble the male's conspicuous blue abdominal tip, common in most *Enallagma* and present in both *E. civile* and *E. ebrium*. Random presentation of controls was followed by random presentation of modified individuals. A male-like abdomen decreased the attractiveness of heteromorphs. Thus, we painted one heteromorph with both a male-like abdomen and thorax to determine if this combination failed to elicit any sexual response from males.

Because many of the free-flying males were unmarked, it was possible to score the reaction of the same male multiple times. Nevertheless, none of the marked males whose reaction was scored were ever found orienting twice to a test individual. Males typically cruised through an area and continued around the shore in their search for females.

#### **Effect of Past Experience on Mate Recognition by Male *Enallagma civile***

In mid-June 1994, *Enallagma civile* was studied at Looney Pond 2 (described in Bick and Bick, 1963) located within 1 km of the University of Okla-

homa Biological Station in Marshall County, Oklahoma. The elliptical pasture pond (ca. 135 m perimeter), was bordered on one side by deciduous trees and sparsely vegetated with grass and weed species on the other three sides. Grazing cattle kept the vegetation low and, consequently, all edges of the pond could be clearly seen. The study population of *E. civile* co-occurred with *Enallagma aspersum*, all of whose females were andromorphs; interspecific tandems were not uncommon (Moodie, 1995).

To determine the frequency of *E. civile* morphs, lone females and those in tandem were captured around the pond and a unique number written on the wing with an indelible marker. Females that were marked and released were seen shortly thereafter in tandem with other males, suggesting that males were actively searching for lone females at the pond. Lone males were seen perched and/or searching for females up to 4 m from the edge of the pond. Lone females were rarely observed at the pond and were primarily captured in the adjacent field before 1000 h or after 1700 h. *E. civile* were observed copulating and ovipositing at the pond between 1000 and 1800 h.

From 14 June to 26 June 1994, the reactions of male *E. civile* to live, tethered heteromorphs, andromorphs and males in the field were noted. Individuals were tethered by gluing a monofilament thread to their thorax with Duco cement and tying the line to a small wooden dowel. Individuals were given a short lead (2 cm) which prohibited them from flying. Each tethered individual was presented directly to a focal male, holding the dowel 5 to 7 cm away from a focal male for 1 min, during which time a male's reaction was noted. In this experiment we could not use the more realistic design of allowing males to react naturally to stationary females, as was done with *E. ebrium*. The direct presentation of individuals was used in the enclosure experiment to minimize the time needed to determine the reaction of each male to a test individual. The field trials with *E. civile* were used as a control response for the enclosure experiment where the reaction of individual males was determined. A trial consisted of each female color morph and a male *E. civile*, presented one at a time to 10 different males perched at the pond. The order in which individuals were presented was alternated in each trial. Because many of the males at the pond were not marked, tethered individuals were presented to males perched in different areas around the perimeter of the pond. Focal males that were marked were not distributed by the presentation of a tethered individual and were seen perched in the same area after the trial was completed. Six trials were conducted with 18 different tethered, test individuals. The reaction of the 10 focal males to the test individuals were divided into three mutually exclusive categories: (1) no reaction, (2) approach/hover, (3) grab and (4) tandem formation. A male's response was categorized as an approach/hover if he came within 3 cm of the individual, but did not make contact. Three trials were conducted from 1100 to 1330 h and three from 1430 to 1600 h.

To determine the effect of prior experience on male mate discrimination, male *E. civile* were tested after exposure to either heteromorphic or andromorphic females within a  $3.5 \times 3.5 \times 3.5$  m screened enclosure containing a circular plastic pool (1 m diameter) with pond water and grass. A culture of fruit flies hung from the center of the enclosure provided food for adults. Twenty sexually mature males were caught at the pond, marked, and released inside the enclosure with either 12 andromorphic females or 12 heteromorphic females. Individuals were free to interact and mate in the enclosure for two days prior to the presentation trials. During this time, females were seen copulating and laying eggs in the circular pool. However, both males and females spent much of the time perched on the screened walls. Males were tested on days three through five during which time males and the twelve females remained in the enclosure. Each marked male was presented with a tethered test individual (used in one trial only) and his reaction scored as no reaction, approach/hover, grab or tandem. Males were scored as "discriminating" if they reacted sexually (grab or tandem) to one female morph and but not the other in a single trial. Males that did not react, or that reacted sexually to both morphs within a single trial, were scored as nondiscriminating. From 15 to 20 June, the reaction of males that experienced only andromorphs were tested. Beginning on 17 June, tethered individuals were presented in two trials per day between 1030 and 1530 h for a total of six separate trials during a three-day period. The reaction of 16 individual males to tethered individuals (andromorphic, heteromorphic and male conspecifics) presented one at a time, was tested in 1 ( $n = 2$  males), 2 ( $n = 2$ ), 3 ( $n = 4$ ), 4 ( $n = 4$ ) or 5 ( $n = 4$ ) trials. Two of the 20 males were found dead and 2 were never seen again after they were placed in the enclosure. On June 21, a different set of 20 males and 12 heteromorphic females were collected and introduced into the enclosure. Eighteen of these males were tested during either 1 ( $n = 6$  males), 2 ( $n = 2$ ), 3 ( $n = 4$ ), 4 ( $n = 4$ ) or 5 ( $n = 2$ ) trials from June 23–26. Two males were not seen again after their initial release into the enclosure.

## RESULTS

### Cues Used to Signal Sexual Identity

Andromorphs represented 15% of the 70 *E. ebrium* females marked at Van Pond. Of the 26 females that were separated from their mates and released in an area less than 10 m from the pond's edge, 9 were resighted on the same day. Of these, 7 were found in tandem within  $10.4 \pm 3.8$  s.e. min (1 andromorph and 3 heteromorphs were in tandem within 2 min), indicating that males were actively searching for mates in this area.

The reaction of males to natural and modified females and males is summarized in Table I. Males reacted sexually (i.e. grabbed females or formed

**Table I.** Response of Mate-Searching *E. ebrium* Males to Perched Test Individuals During 15-min Trials Under Field Conditions<sup>a</sup>

Test individual	No. trials	Nonsexual		Sexual		Proportion sexual
		Approach	Hover	Grab	Tandem	
Control female						
Andromorph	5	20	32	16	35	0.50
Heteromorph	6	11	23	21	55	0.69
Modified female						
Andromorph	4	15	39	3	28	0.36
Heteromorph	3	6	27	7	23	0.48
Heteromorph*	1	5	11	4	0	0.20
Control male	4	30	39	1	0	0.01
Modified male	5	21	26	11	12	0.33

<sup>a</sup>Modified females had male-like abdomens and modified males had female-like abdomens. Asterisk (\*) indicates the thorax as well as the abdomen was painted to resemble a male.

tandems) more often to the control heteromorphs than to control andromorphs ( $G = 8.5$ ,  $df = 1$ ,  $P = 0.004$ ). The reaction of males to females whose abdominal tip was colored blue did not differ from their reaction to females whose abdomen had three stripes, so these trials are pooled. The sexual response by males to heteromorphic females whose abdomens were painted to mimic the male's was significantly less than their reaction to control females ( $G = 7.7$ ,  $df = 1$ ,  $P = 0.003$ ). Although andromorphs with modified, male-like abdomens tended to receive fewer sexual responses relative to controls, the trend was not significant ( $G = 3.2$ ,  $df = 1$ ,  $P = 0.07$ ). The heteromorphic female with a striped abdomen and bright blue thorax received even less sexual attention than did heteromorphic females with only male-like abdomens ( $G = 5.1$ ,  $df = 1$ ,  $P = 0.05$ ).

The reaction of males to a conspecific male whose abdomen had been blackened to resemble that of a female was dramatic. Whereas only 1% of the male reactions to male controls were sexual, 33% of male reactions to test males with blackened abdomens were sexual in nature ( $G = 29.2$ ,  $df = 1$ ,  $P = 0.001$ ). In two cases, males achieved tandem with test males and persisted in tandem for up to 1 min before releasing the test individual.

#### Effect on Past Experience on Male Reaction to Color Morphs

Andromorphs represented 17% of the 312 *E. civile* females marked at Looney Pond 2. The distribution of female morphs is summarized in Table II. A male at the edge of the pond (within 2 m) was not more likely to encounter a lone andromorph than a lone heteromorph ( $G = 3.0$ ,  $df = 1$ ,  $P = 0.08$ ). A male was, however, more likely to encounter a lone andromorph at the edge of the pond than in the population as a whole ( $G = 3.8$ ,  $df = 1$ ,  $P = 0.05$ ). Never-

**Table II.** Summary of *E. civile* Female Morph Frequency

	<i>n</i>	Morph frequency	
		Heteromorph	Andromorph
Females in Tandem	217	0.86	0.14
Lone Females	104	0.79	0.21
>2m from pond	81	0.83	0.17
<2m from pond	23	0.65	0.35
Total	321	0.83	0.17

theless, andromorphs were not more likely to be found alone than in tandem ( $G = 2.8$ ,  $df = 1$ ,  $P = 0.10$ ).

Male reactions to tethered individuals presented to them are summarized in Table III. To compare the reaction of males whose experience with females was modified in an enclosure to the reaction of males under field conditions, the number of interactions initiated are pooled across repeated trials. In both the field and enclosure trials, males responded to individuals differently from that expected if sexual interactions were random with respect to sex and color morph (Table III). Under field conditions, males initiated more sexual than nonsexual interactions with heteromorphs than with andromorphs ( $G = 8.2$ ,  $df = 1$ ,  $P = 0.004$ ). This result is similar to that found in an earlier experiment with *E. civile* in which males were allowed to interact with live tethered individuals placed in a stationary position rather than presented directly to perched males (Moodie, 1995).

**Table III.** Male *E. civile* Response to Live Presented Test Individuals

Test individual	Nonsexual		Sexual		Proportion sexual
	No reaction	Approach/hover	Grab	Tandem	
Andromorph	36	9	7	8	0.25
Heteromorph	22	3	7	28	0.58
Male	36	20	4	0	0.07
Enclosure: experience with andromorphs					
Andromorph	32	7	6	9	0.28
Heteromorph	37	13	3	1	0.07
Male	44	8	2	0	0.04
Enclosure: experience with heteromorphs					
Andromorph	28	11	4	5	0.19
Heteromorph	29	6	7	6	0.27
Male	35	9	4	0	0.08

Table IV. Individual Male *E. civile* Discrimination

	Morph discrimination	
	Andromorph > heteromorph	Andromorph < heteromorph
Field	6	26
Experience with andromorphs	8	1
Experience with heteromorphs	5	7

After two days in the enclosure with only andromorphic females, males initiated more sexual interactions with andromorphs than with either heteromorphs ( $G = 8.0$ ,  $df = 1$ ,  $P = 0.005$ ) or males ( $G = 6.7$ ,  $df = 1$ ,  $P = 0.01$ ). Of the 16 individual males, 7 showed no preference or failed to react to females, whereas 89% of those that discriminated exhibited a consistent preference for andromorphs, significantly different from males in the field ( $G = 15.5$ ,  $df = 1$ ,  $P < 0.001$ , Table IV). After two days exposure to only heteromorphic females, males tended to initiate more sexual interactions with heteromorphs but not significantly more ( $G = 2.2$ ,  $df = 1$ ,  $P = 0.14$ ). Of the 12 males that discriminated, 58% consistently preferred heteromorphs, not significantly different from males in the field ( $G = 2.3$ ,  $df = 1$ ,  $P = 0.13$ ). In both experiments, the response of males to tethered males did not differ with male experience to andromorphs or heteromorphs ( $G = 1.0$ ,  $df = 1$ ,  $P = 0.32$ ).

## DISCUSSION

This study contributes two novel results to the investigation of mate recognition in coenagrionid damselflies. First, experiments with *E. ebrium* males suggest that sexually dimorphic coloration independently cues males to the sexual identity of conspecifics. Second, an enclosure experiment with *E. civile* demonstrated that as the result of prior experience, males changed their behavior towards andromorphs in a manner characteristic of learned behavior (see Papaj and Prokopy, 1989). Together, these proximate mechanisms of mate discrimination by males explain why *Enallagma* andromorphs should not be considered as male mimics with respect to coloration, and suggest a novel, frequency-dependent hypothesis for their occurrence. Because our experiments measured male responses to experimentally constrained females, we cannot reject the possibility that *Enallagma* andromorphs mimic males behaviorally.

Several lines of evidence support our conclusion that the color of andromorphic females does not function in male mimicry. First, the natural thorax color of both andromorphs and heteromorphs is at least a partial cue to sexual identity. Both *E. ebrium* and *E. civile* males exhibited greater sexual response

to constrained andromorphic females than to males (see also Fincke, 1994a; Córdoba-Aquilar, 1992). Adding blue striping to a female's abdomen significantly decreased males' sexual reactions to heteromorphs, but not to andromorphs. A heteromorph with both a male-like thorax and abdomen was not taken in tandem by males at all. Additionally, *E. civile* males often respond sexually to *E. aspersum* andromorphs (Moodie, 1995; but see Forbes, 1991).

Finally, the sexually dimorphic, black dorsum of a female's abdomen, common to females of both morphs of *Enallagma* species (Walker, 1953; Paulson, 1974; Garrison, 1978; Fincke, 1994a; Forbes, 1991; Forbes and Teather, 1994), cued males to the sex of conspecifics independent of thorax coloration. *E. ebrium* males with naturally bright blue thoraxes but whose abdomens were experimentally blackened, were often taken in tandem. These results corroborate with the more detailed work of Gorb (1998), who found that a female's black abdomen was one of the most important cues for sexual recognition in *Coenagrion puella*.

Under field conditions, males of both *E. ebrium* and *E. civile* reacted sexually more readily to heteromorphs, the most abundant morph in each population, than to andromorphs, consistent with the hypothesis of learned mate recognition (Fincke, 1994a). Results from the enclosure experiment with *E. civile* provided direct evidence for learning. A male's sexual reaction to heteromorphic females was significantly reduced after two days of exposure to only andromorphic females. Analogous prior experience with heteromorphs, however, did not decrease a male's sexual response to andromorphs, though in both experiments the number of males that actually discriminated was small. Concurrent tests of naïve males with each morph type would have eliminated any possible confounding effects due to differences in age or prior field experience (with *E. aspersum* andromorphs as well) of the males in our two experimental groups.

Comparative data also suggest that a male's reaction to female morphs is not fixed, but varies over his lifetime, or even over a given day. Banks and Thompson (1985) found that daily mating success of male *Coenagrion puella*, another mate-searching species, increased over the first six days of adult life, a finding consistent with learned mate recognition. At Looney Pond, *E. aspersum* males readily took tethered heteromorphic and andromorphic *E. civile* in tandem early in the day when females were rare around the pond, whereas males rarely made such mating mistakes later in the day when females of both species were more common (Moodie, 1995). Additionally, the context in which an *Enallagma* male encounters a female can also affect his behavior towards her (e.g. Fincke, 1985; Forbes and Teather, 1994).

If males learn to recognize females as potential mates, then female color polymorphisms would make it more difficult for males to cue to a specific morph, just as multiple morphs of a prey species make detection by a vertebrate predator more difficult (see Endler, 1991). To the extent that mate-searching males impose a fitness cost to lone females, then males that cue preferen-

tially to the most abundant morph should impose negative frequency-dependent selection on female morphs. If a female's encounters with males increases with density, then an increase in morph types as well as more equitable frequency of morphs should reduce harassment by mate-searching males as density increases. Comparative data appear more consistent with our learned mate recognition hypothesis than with the density-dependent one, which simply predicts andromorph frequency should increase with male density (Hinneking, 1987). Both *I. elegans* and *I. graellsii*, species whose populations can experience relatively high densities, exhibit three color morphs (Hinneking, 1987; Cordero, 1992; Cordero *et al.*, 1998), and among *I. elegans* populations, male preference is correlated with morph frequency (Van Gossum *et al.*, 1999). *Enallagma* species whose females are monomorphic, are also often rare (see Dunkle, 1990); monomorphic females are as likely to be andromorphs as heteromorphs (Moodie, 1995). Finally, in *Nehalennia irene* (Forbes *et al.*, 1994) and *Ischnura graellsii* (Cordero and Egido Pérez, 1998), morph frequency was more equitable in the high density populations relative to low density ones. Interestingly, in two species of *Ischnura*, morph frequencies were more equitable in sympatry than in allopatry (Johnson, 1975), consistent with the hypothesis that males learn to recognize species as well as sex.

Documenting any differential costs to lone female morphs with respect to male encounters has been difficult (Fincke, 1994a,b; Forbes, 1994; but see Forbes, 1991, Cordero *et al.*, 1998). Andromorphic *E. civile* were as likely as heteromorphs to mate (see also Fincke, 1982; Thompson, 1989), an expected result for frequency-dependent selection if morph frequencies were at the stable equilibrium. Additionally, our results suggest that difficulty in quantifying costs might arise because a female's behavior minimizes risks associated with either a minority or majority morph. Given that the fitness cost to a female of not mating at all is much greater than a male's cost of overlooking a mating opportunity, it is not surprising that females can actively seek out, or avoid, males (see also Fincke, 1997). Female *E. ebrium* interrupted in copula had only to remain around the pond before being quickly taken again in tandem. We videotaped an *E. civile* pair attempting to copulate during which the female broke free from the male for several seconds. She subsequently approached the male and was again taken in tandem. Lone andromorphs were not significantly more likely than heteromorphs to frequent the area of high male density around the pond, as they might if the minority morph incurred a lower cost of male harassment. However, the sample size was small and the trend was in that direction (see also Forbes *et al.*, 1995).

Although evidence from four coenagrionid species indicate that differences in female coloration result from one to three Mendelian alleles (Johnson, 1975; Cordero, 1990; Andrés and Cordero, 1999), the proximate mechanism underlying color morphs in *Enallagma* is unknown (see Johnson, 1964). One possibility

is that color is a polyphenic trait. Density-dependent expression of genes controlling color may be triggered by some variable correlated with larval density, such as low food intake. Density-dependent gene expression for body color, as well as migratory behavior, is known for locusts (Pener, 1991). In damselflies, densities above the level at which male harassment inflicts a cost to females would favor a female producing phenotypically plastic egg clutches that expressed multiple morphs, making it more difficult for males to cue to the morph color of any daughter. If phenotypic plasticity of color morphs was the response to frequency-dependent male harassment, then morph frequencies might often be at local equilibria (e.g. Pfennig, 1992), assuming that larval density reliably reflects population density of the emerging adults. Consistently low densities might result in monomorphic species of either color, assuming plasticity carries a cost.

Regardless of the mechanism responsible for female color morphs in a population, cueing to the most abundant morph should make mate-searching more efficient for males, permitting them to track changes in the relative frequency of morphs that occur within or between breeding seasons (e.g. Fincke, 1994a; Cordero *et al.*, 1998). In a butterfly whose andromorphic females were considered male mimics, males also cued preferentially to the most abundant morph (Cook *et al.*, 1994), a result consistent with learned behavior. We predict that color polymorphism should be less advantageous in territorial species, whose females are attracted to oviposition sites defended by males. Interestingly, although wing-color polymorphisms are found in female *Calopteryx splendens*, in this territorial species their primary function is the reduction of interspecific tandems (De Marchi, 1990; see also Johnson, 1975). Whether learned mate recognition (of sex or species) offers a general explanation for the evolution of female-limited color polymorphisms of insects remains to be seen.

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