

# Mistakes in sexual recognition among sympatric Zygoptera vary with time of day and color morphism (Odonata: Coenagrionidae)

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## ABSTRACT

In odonates, female specific color polymorphisms appear to be an evolutionary response to sexual harassment, but we know little about the decision rules males use when searching for variable females. For two sympatric species of *Enallagma*, we measured male responses to live female variants under field conditions, early and later in the day. In the morning, when the operational sex ratio was the most male-biased and female density the lowest, males of the polymorphic *E. civile* did not discriminate among conspecific female morphs, and reacted sexually to the andromorphic females of *E. aspersum*, a monomorphic species. Then, male *E. aspersum* did not favor conspecific females over *E. civile* morphs. Both morph types were more confusing for males than were conspecific male signals. However, after 13:00 h, males of both species made few mistakes, and *E. civile* males reacted sexually relatively less often to conspecific andromorphs, the minority morph in this population. The changes in a male's sexual response suggested that they cued to female-specific traits when females were scarce, increasing their detection of potential mates at the expense of making mistakes with heterospecific females. When females of both species were more abundant, a male's behavior was consistent with cueing to morph-specific features. Analyses of comparative data suggested that for several genera, males of polymorphic species were more likely to mistake heterospecific females as mates than males of monomorphic congeners. Our results best support the learned mate recognition hypothesis for the evolution and maintenance of female-specific polymorphisms.

## INTRODUCTION

An organism searching for resources in its environment is constrained by: (1) its perceptual skills, (2) the availability and distribution of resources and the costs incurred while obtaining them, and (3) its level of physiological need relative to a

particular resource (Bell 1991). Variance in male lifetime mating success of zygoptera whose males search for mates is determined primarily by the amount of time spent searching at the breeding site (Fincke 1982, 1986; Banks & Thompson 1985; Stoks 2000) rather than a male's ability to fight for and defend oviposition sites. Hence, as competition among mate-searching males increases, they should come under strong selection to correctly identify potential mates while not pursuing 'distractors', or unsuitable individuals, such as conspecific males or females of other species. Scrutiny of potential mates and distractors should lead to unwanted attention toward both. When sexual harassment interrupts the pursuits of single females (e.g. foraging, resting, or egg-laying) to the extent of decreasing fitness (e.g. Sirot & Brockman 2001), females are expected to have evolved mechanisms to reduce unwanted male attention.

Female specific color polymorphisms, which characterize several families of Zygoptera and Anisoptera, appear to be an evolutionary response to sexual harassment by mate-searching males (Fincke 2004). Heteromorphs are female variants that are distinctly different from males in coloration, in contrast with male-like andromorphs (Johnson 1964). Most explanatory hypotheses assume that relative to heteromorphs, andromorphs are inherently more difficult to recognize as 'female' by either heterospecific males (Johnson 1975) or conspecific males (Robertson 1985; Hinnikint 1987; Sherratt 2001). This assumption that underlies male mimicry hypotheses is supported by detection tests on *Ischnura* and *Ceriagrion*, whose andromorphs most closely resemble males in coloration as well as behavior, and whose males exhibited low sexual response toward both andromorphic females and conspecific males (Robertson 1985; Cordero 1989; Cordero & Andrés 2001). However, in similar tests, male *Enallagma* (Fincke 1994; Miller & Fincke 1999) and *Coenagrion* (Gorb 1998) reacted sexually to either female morph more often than they did to conspecific males. Moreover, males of both *Enallagma* (Miller & Fincke 1999) and *Ischnura* (Van Gossum et al. 2001) have been induced to switch from a natural temporary bias for the majority heteromorph to a preference for the minority andromorph, after experiencing only the latter for two days. Finally, in some natural populations, andromorphs are the majority, or even the sole, female type (Fincke 2004; Fincke et al. 2005), defying the logic of Hilton's (1987) argument that heteromorphs should be viewed as 'typical females'.

In contrast with the above explanatory hypotheses, the learned mate recognition (LMR) hypothesis (Miller & Fincke 1999), first intimated by Fincke (1994) and explained in detail by Fincke (2004), does not assume any innate, or pre-existing sensory bias (Ryan et al. 1990) for morph-specific signal characters. The LMR hypothesis predicts that with rising per capita mating attempts, multiple conspecific female types are selectively favored because such variation in female signals makes it more difficult for a male to detect (i.e., correctly identify as a potential mate) any one type, thereby reducing per capita sexual harassment. A male's detection problem increases with increasing overlap in sensory space of conspecific female signals and any distractor signal (Fincke 2004). If males learn to recognize individuals as potential mates, it follows that they should make mistakes, not only with other males, but with heterospecific females of both morph types, especially when species are sympatric with congeners of similar size and color patterns (e.g. Corbet 1999: 491).

A male's sexual response to a female morph is predicted to vary as a function of his experience with it. The LMR hypothesis proposes that equilibrium morph frequencies are maintained by negative frequency-dependent selection, mediated via learning males that, within the limits of a male's memory, use the decision rule, 'cue to the morph most often detected'.

Although the data to date offer general support for the LMR hypothesis (Fincke 2004), we know little about the conditions under which a male's decision rule optimizes his search efficiency. Species experiencing low harassment are predicted to have only a single female type, and then the decision rule would presumably be to cue to general conspecific female characters. In polymorphic species, the operational sex ratio (OSR) and population density of both con- and heterospecifics are predicted to independently affect a male's ability to learn details of female characteristics as well as the benefits of doing so. Hence, over ecological time when the cost of a mistake is negligible relative to the benefit of a mating with a conspecific, males of polymorphic species may benefit from cueing to general, female-specific characteristics rather than morph-specific ones (Fincke 2004).

Here, we compare the temporary signal bias of males in the polymorphic *Enallagma civile* (Hagen) with that of sympatric male *E. aspersum* (Hagen), whose females are all andromorphic. Specifically, we ask whether, over the course of a day, natural changes in density or OSR alters a male's response to female signals, and by inference, the decision rule he uses. Analyses of comparative data indicate that heterospecific females may often be effective signal distractors for males, especially those that search for polymorphic females.

## MATERIALS AND METHODS

*Enallagma civile* is a common species found throughout the United States and Canada (Dunkle 1990). *E. aspersum* ranges throughout the eastern half of the US and is at the western edge of its range in Oklahoma (Bick & Bick 1957). Males of both species do not defend oviposition sites but rather, actively search for females near oviposition areas at the edge of ponds (Bick & Bick 1963; Bick & Hornuff 1966).

As is typical of the genus, *E. civile* and *E. aspersum* males are predominately blue, distinct from females by bright blue stripes on S6-10, of otherwise blue and black abdomens (Plate IVa). The dorsum of the abdomen of an *Enallagma* female is predominately black. Among the polymorphic females of *E. civile*, thorax coloration and the color of the sides of the abdomen varies. For sexually mature females marked in the field, the following three types are known to be stable over a 14-day span (O.M. Fincke and A. Fargevieille unpubl.). Andromorphs have a dark to light blue thorax and abdomen, but the blue coloration is less bright than that of the male (Walker 1953; Plate IVb). Heteromorphs are either green or tannish (hereafter 'green morph', Plate IVc), or intermediate in color pattern. The latter, which may not represent a distinct genetic morph, are predominately green or tan on the dorsal thorax, but dark to light blue on the sides of the abdomen, and sometimes on the sides of the thorax (Plate IVd). Thus, they differ from the intermediate female of

*E. boreale* Selys, which have blue thoraxes with blue and green on the abdomen (Forbes 1991). In *E. aspersum*, heteromorphs are unknown (Walker 1953). All of those females are blue, but are somewhat brighter than andromorphic *E. civile* (Plate IVe).

#### Female morph frequency and population density

The work was conducted from 12 June through 13 July 1993, at Looney Pond 2, an elliptical pasture pond (ca 135 m perimeter), located within 1 km of the University of Oklahoma Biological Station in Marshall County, Oklahoma (33°52'57"N, 96°48'02"W). The pond was surrounded by sparse vegetation, kept low by grazing cattle. Both *E. civile* and *E. aspersum* were observed copulating and ovipositing at the pond between 10:00 h and 18:00 h local time. Solar noon was at 14:31 h. Throughout the day, lone females and those in tandem near the pond and in the surrounding field were captured, marked by writing a unique number on the wing with an indelible marker, and released.

The density of males and females was measured using 15, 1-m<sup>2</sup> sites marked with wooden stakes and flagging tape, located in areas of the pond where pairs of both species were observed ovipositing. The number of lone males, lone females, and tandems of both *E. civile* and *E. aspersum* were recorded during instantaneous scan samples. All sites were censused from 13-18 June ( $n = 7$  times), 23-29 June ( $n = 6$ ), and 6-13 July ( $n = 4$ ), resulting in 17 scans per site. Global density was estimated by averaging density across the 15 sites for censuses taken early in the day (i.e. 11:00 - 14:00 h) and later (> 14:00 - 18:00 h), which corresponded to the time periods when male response towards female color morphs was tested. Daily temperature averaged 32°C; no census occurred on rainy or overcast days. The operational sex ratio (sexually mature males : females) was calculated for all samples for which at least one female was seen. Throughout, means are given  $\pm$  s.d.,  $t$ - and Fisher exact tests are two-tailed;  $p$  values refer to the latter test unless stated otherwise.

#### Response by *E. civile* and *E. aspersum* males toward female color morphs

On 10 days between 17 June and 7 July, the reaction of male *E. civile* and *E. aspersum* to tethered individuals was noted during 6 trials conducted earlier (10:30 - 13:00 h) and six trials done later in the day (> 13:00 - 16:30 h). A live individual was tethered by gluing a monofilament thread to the thorax and tying the line to a small wooden dowel placed 0.5 m above the water in oviposition sites. Tethered individuals were given a short lead (2 cm), which prohibited them from flying. The three types of females and male *E. civile* controls were placed at the site one at a time; an individual was used only once during a single 15-min trial. A complete trial with all four individuals required 1-2 h. Marking or capturing males that interacted would have disrupted the trial. In all 9 cases involving a marked male, after reacting, the male moved to other areas without interacting a second time, as was the case for similar, previous tests with marked *Enallagma* species (Fincke 1994; Miller &

Fincke 1999). Hence we here assume independence of males reacting in these trials. Male responses to the tethered individual were divided into four categories. An 'approach' was scored when a male oriented within 5 cm. of the individual but then flew off. A 'grab' was indicated when a male grabbed the pronotum or thorax but did not attempt to form tandem. In a 'tandem' response, the male clasped the prothorax with his anal appendages. A 'takeover attempt' occurred when a male tried to takeover a female already in tandem with another male. In four of the 12 presentations, female and male *E. aspersum* were also presented. For the statistical analysis of male reactions to tethered individuals, take-over attempts were excluded as a class of responses because a tandem pair offers a more obvious signal that a conspecific female is present than does a lone individual. However, excluding this class of responses did not change any conclusion drawn from these results. The total number of interactions initiated by males was used in combination with the density of lone males to indirectly assess changes in male search rate. Searching intensity of males was estimated as the total proportion of such interactions that were sexual (i.e. grab, tandem, take-over attempt).

#### Analyses of comparative data on male mistakes

To determine the extent to which heterospecific females contribute to male detection mistakes more generally, we searched for reports of heterospecific tandems among the Zygoptera of North America (excluding Mexico) and Europe. We tested whether the presence of female variants increases the probability that males mistake heterospecific females as potential mates. Data were analyzed by genera to minimize phylogenetic effects (see Felsenstein 1985). We compared the proportion of female color polymorphic species known to make at least one such mistake with that of their monomorphic congeners, whose females are all a single type (for details and list, see Fincke et al. 2005). We also compared the mean number of unique mistake types known per species.

## RESULTS

#### Female *Enallagma civile* morph frequency

Only five lone females were seen during censuses of the plots on the pond; three of these were seen before 13:00 h. The other 49 lone females were seen in the surrounding field, most before 10:00 h or after 17:00 h. Tandem females that were marked and released near the pond were often observed shortly thereafter in tandem with other males, suggesting that males were actively searching for lone females around the pond. The frequency of *E. civile* female morphs and their status when caught, is summarized in Table 1. Andromorphs were not less likely than intermediate or heteromorphic females to be found in tandem ( $G = 2.01$ ,  $df = 1$ ,  $p = 0.16$ ). Nor were intermediate females more likely to be found in tandem than andromorphic or heteromorphic females ( $G = 1.95$ ,  $df = 1$ ,  $p = 0.16$ ).

Table 1. Status and frequency of female *Enallagma civile* during the month-long study period.

	<i>n</i>	M o r p h f r e q u e n c y		
		Andromorph	Intermediate morph	Green morph
Tandem females	72	0.24	0.51	0.25
Lone females	54	0.35	0.39	0.26
Total	126	0.29	0.45	0.26

### Male density and sex ratio

The density of male *E. civile* at the pond, summarized in Table 2, peaked at approximately 14:00 h (Fig. 1). The average male density tended to be lower in the morning relative to samples taken after 13:00 h ( $t = 2.02$ ,  $df = 15$ ,  $p = 0.06$ ). Female density was significantly correlated with an increase of male density at the pond (Fig. 2,  $r = 0.72$ ,  $df = 15$ ,  $p = 0.05$ ). However, as more females arrived at the pond later in the day, sex ratio of *E. civile* decreased (Fig. 1), with twice as many males to females in earlier versus later samples ( $t = 3.61$ ,  $df = 12$ ,  $p = 0.004$ ). The number of lone males at the pond did not increase during the day ( $t = 0.84$ ,  $df = 15$ ,  $p = 0.41$ ) but later in the day significantly more males were in tandem with females ( $t = 3.94$ ;  $df = 10$ ,  $p < 0.01$ ).

The average density of male *E. aspersum* ( $0.62 \pm 0.60$ ,  $n = 17$ ), which also peaked near 14:00 h (Fig. 3), was less than half that of male *E. civile* ( $1.64 \pm 0.64$ ,  $n = 17$ ;  $t = 4.16$ ,  $df = 30$ ,  $p < 0.001$ ). Earlier in the day mean density of *E. aspersum* males tended to be lower ( $0.38 \pm 0.40$ ,  $n = 8$ ) than later ( $0.89 \pm 0.71$ ,  $n = 9$ ), but the trend was not significant ( $t = 1.78$ ,  $df = 11$ ,  $p = 0.10$ ). Because female *E. aspersum* were rare and present in only two of the morning samples, sex-ratio differences between later and earlier samples were not tested.

### Search rate and intensity

The number of total interactions initiated by male *E. civile* toward female *E. civile* morphs did not differ with time of day (earlier,  $n = 104$ ; later,  $n = 108$ ;  $G = 0.08$ ,  $df = 1$ ,  $p = 0.78$ ). Given that the density of lone males did not change, this suggests that male search rate did not decrease, despite a decrease in search intensity during the day. Of the interactions initiated by male *E. civile* toward female *E. civile* morphs earlier in the day, 75% were sexual. In contrast, only 57% of the interactions in trials done later in the day were sexual ( $G = 7.31$ ,  $df = 1$ ,  $p = 0.01$ ).

### Response of male *E. civile* to conspecific female morphs

The responses of male *E. civile* to live, tethered test individuals are summarized in Table 3. Males did not interact sexually with conspecific test males. Overall, male responses to intermediate females did not differ from their responses to green females (Table 3,  $p = 0.44$ ). The sexual reaction to pooled heteromorphs was not

significantly different from that expected from their global frequency ( $\chi^2 = 1.69$ ,  $df = 1$ ,  $0.5 > p > 0.1$ ). Male *E. civile* initiated more sexual interactions (i.e. grab, tandem) with single heteromorphic females than with andromorphic ones ( $p < 0.0001$ ).

Early in the day ( $\leq 13:00$  h) there was no difference in a male's reaction to the three female types ( $p = 0.27$ ), whereas later in the day ( $> 13:00$  h), a male's sexual reaction differed among morphs ( $p < 0.001$ ). Males initiated significantly more sexual interactions with andromorphs ( $p < 0.01$ ) and intermediate females ( $p < 0.02$ ) early in the day compared with later in the day. In contrast, the proportion of sexual interactions initiated with green did not change significantly between the two periods (Table 3;  $p = 0.25$ ).

#### Response of *E. aspersum* males toward *E. civile* female morphs

The sexual reaction of *E. aspersum* toward female *E. civile* did not differ among the three colour types (Table 3,  $p = 0.64$ ). Male *E. aspersum* initiated more interactions with female *E. civile* earlier in the day (i.e. 20/56) compared with later in the day (2/12,  $G = 28.47$ ,  $df = 1$ ,  $p < 0.001$ ). During the detection tests, a total of 22 interspecific sexual interactions between male *E. aspersum* and tethered female *E. civile* were observed, of which 17 were tandem formations. Male *E. aspersum* were never seen to interact sexually with tethered male *E. civile*, either in the preference tests or in the field.

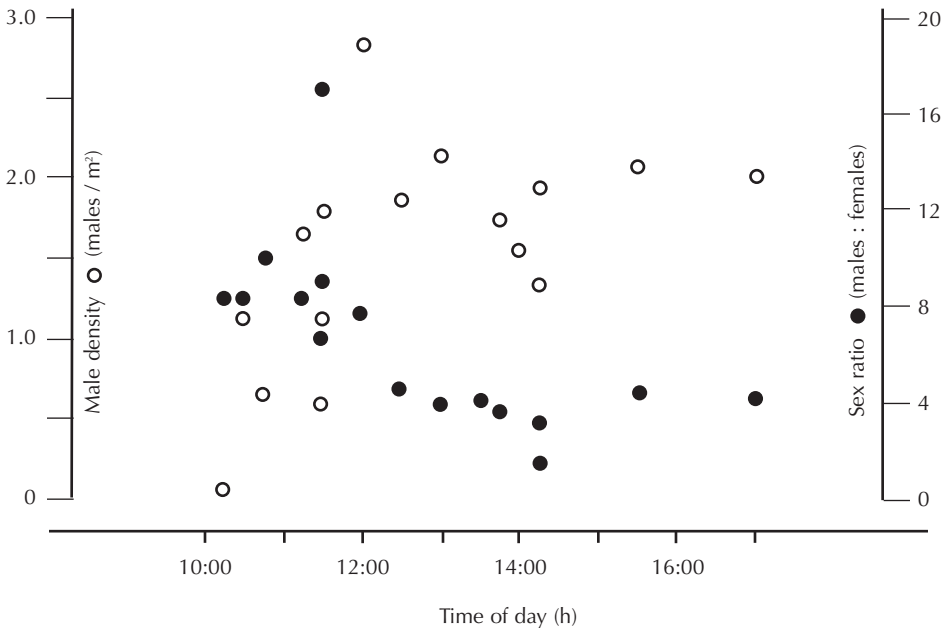


Figure 1: Density of male *Enallagma civile* (open circles) and sex ratio (closed circles) at the pond during the day.

Responses of *Enallagma* males toward *E. aspersum* individuals

The response of *E. civile* and *E. aspersum* males toward *E. aspersum* males and females was recorded for four trials (two earlier, and two later in the day, Table 4). The sexual response of *E. civile* males toward conspecific females of both morphs was greater than it was toward *E. aspersum* females ( $p = 0.05$ ). Male *E. civile* initiated significantly more sexual interactions with *E. civile* heteromorphs than with female *E. aspersum* ( $p = 0.03$ ). However, their sexual response toward conspecific andromorphs (15/27) was not significantly different from their response to andromorphs of *E. aspersum* ( $p = 0.1$ ). But male *E. aspersum* were even less likely to discriminate between female conspecifics and female *E. civile* ( $p = 1.0$ ). All of their sexual interactions with female *E. civile* were initiated earlier in the day, as were the two tandems with conspecific *E. aspersum* females.

## Naturally occurring interactions with heterospecific females

During the censuses, three interspecific tandem pairs were observed between *E. civile* and *E. aspersum* under natural conditions. This represented 3.6% of the *E. civile* and 25.0% of the *E. aspersum* pairs seen during censuses. In two cases the identification was unambiguous because *E. aspersum* males were captured in tandem, one with an andromorphic and another with a heteromorphic female *E. civile*. In addition, harassment of an *E. civile* tandem by a male *E. aspersum* was observed at an oviposition site. One uncooperative *E. aspersum* female in tandem with a male *E. civile*, dragged her abdomen in the water while flying over the pond. The resulting erratic flight eventually resulted in the female's release. None of the three interspecific pairs were seen to copulate or oviposit.

Among North American and European Zygoptera, we found 101 unique species combinations with males observed to have mistaken heterospecific females for potential mates (Table 5). The most types of mistakes (52%) were between different species in the same genus, but 29% involved different genera in the same family, 17% involved different zygopteran families, and 2% involved a mistake by a zygopteran male with an anisopteran female. Within each family, males of female polymorphic species tended to exhibit a greater number of unique mistakes per species than males of monomorphic species (General Linear Model: Calopterygidae,  $F_{1,10} = 5.4$ ,  $p = 0.04$ ; Lestidae  $F_{1,23} = 35.6$ ,  $p = 0.0001$ ; Coenagrionidae  $F_{1,105} = 6.9$ ,  $p = 0.01$ ; Platycnemididae,  $F_{1,2} = \text{infinity}$ ,  $p = 0.0001$ ). Within genera, the trend remained significant for *Calopteryx*, *Lestes*, *Enallagma*, and *Platycnemis* (Table 6).

Table 2. Mean density of *Enallagma civile* males at the pond on the 13 census days.

	<i>n</i>	Male density / m <sup>2</sup>			Sex ratio / m <sup>2</sup>
		Total males	Lone males	Pairs	
< 13:00 h	9	1.31 ± 0.83	1.26 ± 0.57	0.16 ± 0.14	0.12 ± 0.04
≥ 13:00 h	8	2.02 ± 0.63	1.5 ± 0.59	0.52 ± 0.19	0.28 ± 0.14

Table 3. Response of *Enallagma civile* and *E. aspersum* males to live female *E. civile* color variants in eight 15-min trials, half done early, and half done later in the day. Green and intermediate females are two types of heteromorphs.

Test individual	Nonsexual approach	Sexual approach			Proportion sexual
		Grab	Tandem	Take-over attempt	
<i>E. civile</i> ♂ initiating					
Interactions initiated ≤ 13:00 h					
Andromorph ♀	10	2	17	0	0.66
Intermediate ♀	7	3	28	3	0.83
Green morph ♀	9	1	22	2	0.74
<i>E. civile</i> ♂	6	0	0	0	0.00
Interactions initiated > 13:00 h					
Andromorph ♀	26	8	5	0	0.33
Intermediate ♀	14	3	12	2	0.55
Green morph ♀	6	9	21	2	0.84
<i>E. civile</i> ♂	7	0	0	0	0.00
<i>E. aspersum</i> ♂ initiating					
Interactions initiated ≤ 13:00 h					
Andromorph ♀	18	0	1	6	0.28
Intermediate ♀	7	1	0	3	0.36
Green morph ♀	11	2	0	7	0.45
<i>E. civile</i> ♂	9	0	0	0	0.00
Interactions initiated > 13:00 h					
Andromorph ♀	3	0	0	0	0.00
Intermediate ♀	3	1	0	1	0.40
Green morph ♀	4	0	0	0	0.00
<i>E. civile</i> ♂	4	0	0	0	0.00

The seven coenagrionids that accounted for over half of the mistakes in that family were all polymorphic (i.e. *Ischnura elegans*, 15%; *E. cyathigerum*, 10%; *Pyrrhosoma nymphula*, 9%; *E. carunculatum*, 7%; *E. civile* and *I. pumilio*, 6% each). Within Lestidae, *L. sponsa*, the only polymorphic species, accounted for 32% of the mistake categories recorded for that family.

## DISCUSSION

This is the first study to show that under natural conditions, a male's sexual response towards female morphs of both con- and heterospecifics varies over the course of a day, apparently in response to changes in the density of females in the search area. Male *Enallagma civile* did not discriminate against the minority andromorphs early in the day (Table 3) when female density was low and, consequently, OSR

was relatively high. Assuming global morph frequency is stable over the course of a day for *E. civile*, as it is known to be for large samples of marked *E. hageni* and *E. boreale* (O. Fincke unpubl.), our data suggest males increased their detection of andromorphs earlier in the day. This could be due to: (1) a slower searching rate earlier in the day, (2) a greater searching intensity earlier in the day, and/or (3) refinement in a male's search image for the majority female type later in the day. In all cases, the frequency with which males encounter females may be the basis for a change in male behavior.

We found no difference in the total number of interactions between earlier and later detection trials. Because there was no change in the density of lone males, although overall male density was higher later in the day, search rate must not have changed, or at best, decreased later in the day. A slower search rate early in the day also seems unlikely given the generally higher OSR earlier in the day, which should increase any premium for a quick male reaction to a female in the area. Searching intensity, or the likelihood that a male interacts sexually with an encountered female, was greater early in the day towards andromorphs and intermediate females. For both *Enallagma* species, an increase in search intensity resulted in more mistakes with congeneric females compared to later in the day when conspecific females were more abundant (Tables 3, 4). Then, males more readily recognized heteromorphic (intermediate and green) females as potential mates than andromorphic ones, which were the minority. Assuming that males reacting in the morning and the afternoon do not represent two distinctly different sets of individuals, the duration of a male's temporary sensory bias for a morph type, apparently the limit of his memory, was less than a day.

Table 4. Response of male *Enallagma civile* and male *E. aspersum* to live test individuals in four 15-min trials that included *E. aspersum*.

Test individual	Nonsexual approach	Sexual approach		Proportion sexual
		Grab	Tandem	
<i>E. civile</i> ♂ initiating				
<i>E. aspersum</i> ♀	9	0	3	0.25
<i>E. civile</i> , andromorphic ♀	12	3	12	0.56
<i>E. civile</i> , green morph ♀	7	3	12	0.68
<i>E. aspersum</i> ♂	4	0	0	0.00
<i>E. aspersum</i> ♂ initiating				
<i>E. aspersum</i> ♀	5	0	2	0.29
<i>E. civile</i> , andromorphic ♀	10	0	5	0.33
<i>E. civile</i> , green morph ♀	6	0	3	0.33
<i>E. aspersum</i> ♂	8	0	0	0.00

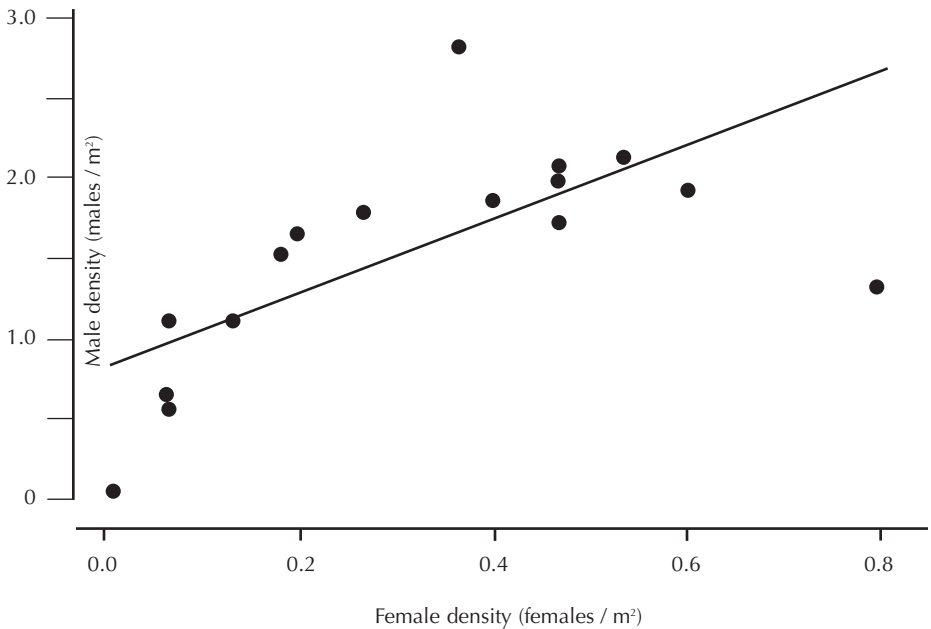


Figure 2: Densities of male and female *Enallagma civile* at the pond ( $r = 0.72$ ,  $df = 15$ ,  $p = 0.05$ ).

Our results are most consistent with a change in the decision rule, from cueing to a female-specific dark abdominal dorsum early in the day, to a sensory bias towards morph-specific thorax color later in the day. Utzeri & Belfiore (1990) concluded that mistakes in sexual recognition may often be an adaptive reaction, occurring when the cost of a mistake is less than the cost of a missed mating opportunity. Our data support this interpretation. Although an alternative possibility is that the motivational state of searching males changes over the day, this is unlikely for several reasons. Many *Enallagma* males fail to get a single mating in their entire lives (e.g. Fincke 1982). Hence it seems unlikely that a male's motivation to mate would decrease if he hasn't found a mate by early afternoon, even if the intensity of his search decreased due to the reaction of an increasing number of females that become unreceptive as they complete egg-laying. Moreover, whereas an unmotivated male is expected to initiate few interactions per se, it is unclear why a decrease in motivation should result in proportionally fewer mistakes with heterospecific females, unless there was a concomitant change in sensory processing. Finally, in other species, similar shifts in male search tactics over the course of a day are known to occur in response to changing female density. For example, *E. hageni* males are more likely to use a searching tactic earlier in the day and a waiting tactic later in the day as the number of lone, receptive females decreased (Fincke 1985, 1986a). In the afternoon, *E. civile* males exhibited a sensory bias for green (but not for

intermediate females) above that expected from their global frequency. This could result if males had an innate sensory bias towards this heteromorph as implied by Sherratt (2001). However, learning experiments with naïve males failed to support that conclusion (O. Fincke & A. Fargevielle unpubl.). The result would be expected if green females assorted to microhabitats differentially compared to intermediate or blue females. But no significant morph-specific microhabitat sorting was found (Miller & Fincke 1999). Alternatively, thorax color may be a more reliable signal of a potential mate than the more variable color of the sides of the female abdomen. Both intermediate and green females have similarly colored thoraxes and would thus appear similar if approached from above or from behind (see Gorb 1998). This interpretation is supported by the fact that when green and intermediate females are pooled, males did not approach them more often than expected by their global frequency.

A second finding of this study is that for both *E. civile* and *E. aspersum*, hetero-specific females, even andromorphic ones, are more confusing to a mate-searching male than are conspecific males (Tables 3, 4). The female-specific dark dorsal abdominal coloration that is characteristic of the genus is known to signal sexual identity to males in *E. ebrium* (Hagen) (Miller & Fincke 1999). That same function likely explains why the *Enallagma* males in the current study were not seen to

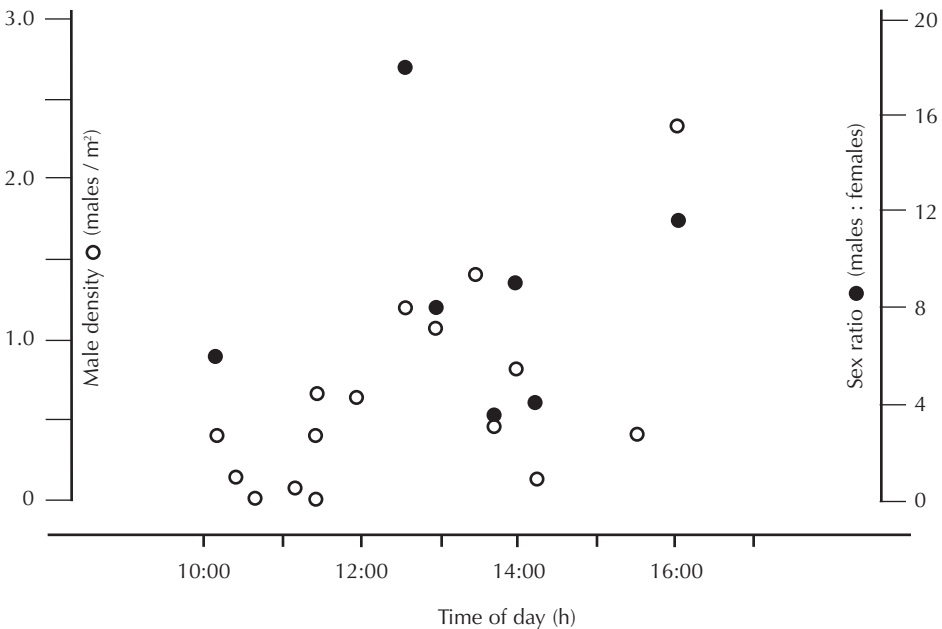


Figure 3: Density of male *Enallagma aspersum* (open circles) and sex ratio (closed circles) at the pond during the day.

naturally pair with other males, mistakes that have been documented in *Ceriagrion*, *Ischnura* and *Nehalennia* (reviewed by Utzeri & Belfiore 1990), whose andromorphs are more similar to males. Not only did male *E. aspersum* not discriminate among any of the female *E. civile* morphs, early in the day they reacted sexually toward congeneric females as frequently as they did toward conspecific ones. This result contrasts with those of Forbes (1991), who found that *E. boreale* heteromorphs attracted more attention from congeneric males than did andromorphs. Forbes & Teather (1994) found variation in the male response of *E. ebrium* that was unrelated to time of day and remains unexplained. However, in both studies, the methods differed from our own; their females were pinned next to a male or pinned next to another morph type whereas ours were presented singly.

Our results are also at odds with Hinnekint's (1987) prediction that at low density, andromorphs suffer from greater mating failure relative to heteromorphs because males are more likely to overlook them. Rather, we found that in the morning, when the density of both males and females were lowest, males of the locally rare, monomorphic *E. aspersum* reacted sexually to females of both congeners more than they did to males. The density of *E. aspersum* was significantly lower than that of the polymorphic *E. civile*. *E. aspersum* appears to have been abnormally rare at our site because it was at the edge of its range. This species was not observed at the study site during the subsequent breeding season (June - July 1995). Indeed, its consistently low density at our study site may explain why, in contrast to the trend indicated by the comparative data, males of *E. aspersum* made so many mistakes with both morphs of *E. civile*.

The reduced harassment that a female might gain from her similarity with the sexual signals of congeners carries the potential cost of greater harassment from heterospecific males. However, the magnitude of that cost depends on the density and OSR of the distractor species. In our study, *E. civile* females likely gained a greater benefit from their similarity with *E. aspersum* than vice versa because the density of male *E. aspersum* and its OSR was low relative to *E. civile*. Consistent with the LMR hypothesis, tandems with heterospecific females were not uncommon (Table 5). With the exception of *Calopteryx*, males making mistakes were those that must search for mates (reviewed by Fincke 2004). In *Calopteryx splendens*, andromorphic females occur in only a few populations (De Marchi 1990). Within several genera, males of female polymorphic species were known to make more kinds of mistakes with heterospecific females than their monomorphic congeners, as expected if an increase in the number of female variants increases the difficulty of learning potential mates (Fincke 2004). In *Lestes sponsa*, andromorphic females are rare within a population but occur in many populations (Jödicke 1997). This species was found in tandem with *L. viridis* on 18 occasions (Stoks 1995). Males that learn species identity, as *E. aspersum* apparently did in our study, should benefit when they are often syntopic with species whose females are of similar size and color.

For *E. civile*, no morph mated more often than another, consistent with findings from studies of lifetime mating success (e.g. Fincke 1982; Thompson 1989; Stoks 2000), suggesting that harassment need not lead to copulations in order to exert a cost on females. In this study, copulation by interspecific pairs or subsequent

Table 5. Mistakes made by males with heterospecific females under natural conditions reported for North American and European Zygoptera. In cases of multiple types of action, only the most sexually intense is listed. The wheel formation, required for copula, requires a tandem female to raise her abdomen to engage a male's penis. Action abbreviations — T: tandem; W: wheel; AT: attempt tandem; AW: attempt wheel; OV: oviposition. (t): interaction was with a teneral female.

### Intrageneric

♂	♀	Action	Source
<b>Calopterygidae</b>			
<i>Calopteryx aequabilis</i> Say	<i>Calopteryx maculata</i> (Beauvois)	W	Waage (1975)
<i>splendens</i> (Harris)	<i>virgo</i> (Linnaeus)	T	R. Hoess unpubl
<i>virgo</i>	<i>splendens</i>	W	Lindeboom (1996)
<b>Coenagrionidae</b>			
<i>Argia emma</i> Kennedy	<i>Argia vivida</i> Hagen in Selys	AT	Paulson (1974)
<i>plana</i> Calvert	<i>moesta</i> (Hagen)	OV	Bick & Bick (1981)
<i>tibialis</i> (Rambur)	<i>moesta</i>	T	Bick & Bick (1981)
<i>Coenagrion mercuriale</i> (Charpentier)	<i>Coenagrion ornatum</i> (Selys)	T	G. Reeder unpubl.; K. Sternberg unpubl.
<i>puella</i> (Linnaeus)	<i>hastulatum</i> (Charpentier)	T	G. Reeder unpubl.
<i>puella</i>	<i>pulchellum</i> (Vander Linden)	W	Steiger (1988); G. Reeder unpubl.
<i>pulchellum</i>	<i>puella</i>	T	R. Hoess unpubl.
<i>Enallagma aspersum</i> (Hagen)	<i>Enallagma geminatum</i> Kellicott	T	Bick & Bick (1981)
<i>aspersum</i>	<i>civile</i> Hagen	T	herein
<i>boreale</i> (Selys)	<i>carunculatum</i> Morse	T	Paulson (1974)
<i>boreale</i>	<i>cyathigerum</i> (Charpentier)	T	Paulson (1974)
<i>carunculatum</i>	<i>basidens</i> Calvert	T	D. Huntington; Plate IVf
<i>carunculatum</i>	<i>boreale</i>	T	Paulson 1974
<i>civile</i>	<i>aspersum</i>	T	herein
<i>civile</i>	<i>carunculatum</i>	T	Garman (1917); Bick & Bick (1981)
<i>cyathigerum</i>	<i>boreale</i>	T	Paulson (1974)
<i>cyathigerum</i>	<i>praevarum</i> (Hagen)	AT	Paulson (1974)
<i>ebrium</i> (Hagen)	<i>boreale</i>	T	Forbes (1991)
<i>ebrium</i>	<i>hageni</i> (Walsh)	AT	O. Fincke unpubl.
<i>pollutum</i> (Hagen)	<i>dubium</i> Root	T	Tennessen (1975); Bick & Bick (1981)
<i>pollutum</i>	<i>signatum</i> (Hagen)	T	Tennessen (1975)
<i>praevarum</i>	<i>cyathigerum</i>	T	Paulson (1974)
<i>signatum</i>	<i>pollutum</i>	T	Tennessen (1975)
<i>Ischnura damula</i> Calvert	<i>Ischnura demorsa</i> (Hagen)	T	Johnson (1975)
<i>demorsa</i>	<i>damula</i>	T	Johnson (1975)
<i>elegans</i> (Vander Linden)	<i>graellsii</i> (Rambur)	W	Cordero (1989); Jödicke (1996)

**Intrageneric** (continued)

♂	♀	Action	Source
Coenagrionidae (continued)			
<i>Ischnura graellsii</i>	<i>Ischnura elegans</i>	W	Jödicke (1996)
<i>pumilio</i> (Charpentier)	<i>elegans</i>	AT	K. Sternberg unpubl.
<i>pumilio</i>	<i>graellsii</i>	W	Cordero (1989)
<i>Nehalennia gracilis</i> Morse	<i>Nehalennia irene</i> (Selys)	AT	Hilton (1983)
<i>irene</i>	<i>gracilis</i>	AT	Hilton (1983)
Lestidae			
<i>Lestes barbarus</i> (Fabricius)	<i>Lestes sponsa</i> (Hansemann)	T	K. Sternberg unpubl.
<i>barbarus</i>	<i>viridis</i> (Vander Linden)	T	Loibl (1958); Utzeri & Belfiore (1990);
<i>disjunctus</i> Selys	<i>vigilax</i> Hagen in Selys	T	Kellicott (1895)
<i>dryas</i> Kirby	<i>sponsa</i>	T	Wesenberg-Lund (1913); K. Sternberg unpubl.
<i>inaequalis</i> Walsh	<i>disjunctus australis</i> Walker	T	Bick & Bick (1981)
<i>rectangularis</i> Say	<i>congener</i> Hagen	T	Bick & Bick (1981)
<i>rectangularis</i>	<i>unguiculatus</i> Hagen	T	Bick & Hornuff (1965)
<i>sponsa</i>	<i>barbarus</i>	T	Stoks (1994); K. Sternberg unpubl.
<i>sponsa</i>	<i>dryas</i>	AW	K. Sternberg unpubl.
<i>sponsa</i>	<i>virens vestalis</i> Rambur	AW	K. Sternberg unpubl.
<i>sponsa</i>	<i>viridis</i>	AW	Timm (1906); G. Reder unpubl.
<i>unguiculatus</i>	<i>dryas</i>	T	Bick et al. (1977)
<i>virens vestalis</i>	<i>barbarus</i>	T	Utzeri et al. (1987)
<i>virens vestalis</i>	<i>viridis</i>	T	Utzeri et al. (1987); Jödicke et al. (1989)
<i>viridis</i>	<i>barbarus</i>	T	Utzeri et al. (1987); K. Sternberg unpubl.
<i>viridis</i>	<i>sponsa</i>	T	K. Sternberg unpubl.
<i>viridis</i>	<i>virens vestalis</i>	T	Jödicke et al. (1989)
<i>Sympetma fusca</i> (Vander Linden)	<i>Sympetma paedisca</i> (Brauer)	T	Bilek (1963)
Platycnemididae			
<i>Platycnemis pennipes</i> (Pallas)	<i>Platycnemis acutipennis</i> Selys	OV	M. Lohr; Plate IVg

**Intergeneric**

## Calopterygidae

<i>Hetaerina americana</i> (Fabricius)	<i>Calopteryx maculata</i>	W	Weichsel (1984)
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## Coenagrionidae

<i>Argia emma</i>	<i>Enallagma carunculatum</i>	AT	Paulson (1974)
<i>sedula</i> (Hagen)	<i>basidens</i>	T	Bick & Bick (1981)
<i>Coenagrion puella</i>	<i>cyathigerum</i>	W	Parr (1976)
<i>Enallagma basidens</i>	<i>Argia apicalis</i> (Say)	T	Bick & Bick (1981)
<i>carunculatum</i>	<i>emma</i>	AT	Paulson (1974)

## Intergeneric (continued)

♂	♀	Action	Source
Coenagrionidae (continued)			
<i>Enallagma carunculatum</i>	<i>Ischnura cervula</i>	AT	Paulson (1974)
<i>carunculatum</i>	<i>perparva</i> McLachlan in Selys	T	Paulson (1974)
<i>civile</i>	<i>Argia moesta</i>	W	Kellicott (1895)
<i>civile</i>	<i>vivida</i>	T	Garrison (1979)
<i>cyathigerum</i>	<i>Coenagrion puella</i>	AT	Peters (1988)
<i>cyathigerum</i>	<i>Ischnura denticollis</i>	AT	Paulson (1974)
<i>cyathigerum</i>	<i>Telebasis salva</i> (Hagen)	AT	Paulson (1974)
<i>hageni</i>	<i>Ischnura cervula</i>	T	Bick & Bick (1981)
<i>Erythromma lindenii</i> (Selys)	<i>Enallagma cyathigerum</i>	AT	K. Sternberg unpubl.
<i>Ischnura elegans</i>	<i>Coenagrion puella</i>	W	H. Hunger unpubl.
<i>elegans</i>	<i>pulchellum</i>	T	Bilek (1963)
<i>elegans</i>	<i>Enallagma cyathigerum</i>	W	Parr (1976)
<i>elegans</i>	<i>Erythromma lindenii</i>	T	B. Kunz; Plate IVh
<i>elegans</i>	<i>najas</i> (Hansemann)	T	Paine (1996)
<i>elegans</i>	<i>Pyrrhosoma nymphula</i> (Sulzer)	W	A. Cordero unpubl.
<i>perparva</i>	<i>Enallagma anna</i>	T	Bick & Bick (1981)
<i>pumilio</i>	<i>Coenagrion puella</i>	W	R. Hoess unpubl.
<i>pumilio</i>	<i>Enallagma cyathigerum</i>	W (t)	Bedjanič (1994)
<i>Pyrrhosoma nymphula</i>	<i>Coenagrion lunulatum</i>	T	Claessens (1989)
<i>nymphula</i>	<i>mercuriale</i>	T	Clausen (1990)
<i>nymphula</i>	<i>puella</i>	AT	R. Hoess unpubl.
<i>nymphula</i>	<i>Ischnura elegans</i>	T	H. von Hagen unpubl.
Lestidae			
<i>Lestes viridis</i>	<i>Sympecma fusca</i>	AT	K. Sternberg unpubl.

## Different family

## Calopterygidae

<i>Calopteryx splendens</i>	<i>Platycnemis pennipes</i>	T	Moore (1953)
<i>Hetaerina americana</i>	<i>Argia plana</i>	T	Bick & Bick (1981)

## Coenagrionidae

<i>Argia tibialis</i> Rambur	<i>Lestes dryas</i>	AW	Williamson (1920)
<i>Coenagrion ornatum</i>	<i>Platycnemis pennipes</i>	T	B. Kunz; Plate IVi
<i>Enallagma cyathigerum</i>	<i>dryas</i>	T	Scheffler (1970)
<i>Ischnura elegans</i>	<i>sponsa</i>	T	Stoks (1995)
<i>elegans</i>	<i>viridis</i>	T	E. & W. Postler unpubl.
<i>elegans</i>	<i>Sympecma fusca</i>	T	E. & W. Postler unpubl.
<i>erratica</i> Calvert	<i>Lestes disjunctus</i>	T	Paulson & Cannings (1980)
<i>Pyrrhosoma nymphula</i>	<i>barbarus</i>	AT	K. Sternberg unpubl.
<i>nymphula</i>	<i>Sympecma fusca</i>	T	T. Kirchen unpubl.

## Lestidae

<i>Lestes disjunctus australis</i>	<i>Enallagma cyathigerum</i>	T	Bick & Bick (1981)
<i>sponsa</i>	<i>Ceriagrion tenellum</i> (de Villers)	T	Claessens (1989)
<i>sponsa</i>	<i>Enallagma cyathigerum</i>	T	Kunath (1991);

**Different family** (continued)

♂	♀	Action	Source
Lestidae (continued)			
<i>Lestes sponsa</i>	<i>Enallagma cyathigerum</i>	T	E. & W. Postler unpubl.
<i>sponsa</i>	<i>Erythromma najas</i>	T	Tümpel (1922)
<i>viridis</i>	<i>viridulum</i> (Charpentier)	T	Jurzitza (1966)
Platycnemididae			
<i>Platycnemis pennipes</i>	<i>Coenagrion puella</i>	AT	K. Sternberg unpubl.

**With Anisoptera**

## Coenagrionidae

<i>Enallagma cyathigerum</i>	<i>Anax imperator</i> Leach	AT	Beynon (1999)
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## Lestidae

<i>Lestes sponsa</i>	<i>Sympetrum striolatum</i> (Charpentier)	T (t)	Paine (1991a, 1991b)
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Table 6. Distribution of mistakes with heterospecific females, among female polymorphic Zygoptera species and their monomorphic congeners for genera in which there are  $\geq 4$  North American and/or European species. Each species is represented only once even though its males were known to make mistakes with multiple species ( $p$  values are for 2-tailed Fisher exact tests). For example, of the 29 species of *Argia* in the sample, unique mistakes were reported for one monomorphic, and three polymorphic species. The mean  $\pm$  s.d. number of mistake types/species is in parentheses. \*:  $p < 0.05$ , \*\*:  $p < 0.001$ , Student's  $t$ -test.

Genus	Proportion of total making mistakes with a heterospecific		$p$
	Monomorphic species	Polymorphic species	
<i>Calopteryx</i> <sup>1</sup>	2/8 (0.25 $\pm$ 0.46)	1/1 (2.0**)	0.33
<i>Lestes</i>	8/20 (0.80 $\pm$ 1.28)	1/1 (8.0**)	0.43
<i>Argia</i>	1/15 (0.07 $\pm$ 0.26)	3/14 (0.43 $\pm$ 0.65)	0.33
<i>Coenagrion</i>	0/1 (0)	4/14 (0.43 $\pm$ 0.85)	1.0
<i>Enallagma</i>	2/17 (0.24 $\pm$ 0.66)	9/18 (1.33 $\pm$ 2.03*)	0.03
<i>Ischnura</i>	0/4 (0)	7/15 (1.27 $\pm$ 2.60)	0.24
<i>Nehalennia</i>	1/4 (0.25 $\pm$ 0.50)	1/1 (1.0)	0.40
<i>Platycnemis</i>	0/3 (0)	1/1 (2**)	0.25

<sup>1</sup> Andromorphs were known from only a few populations of the polymorphic species.

ovipositions were not observed, probably because mechanical differences in congeners reduce the probability of hybridization in coenagrionids (Paulson 1974; Robertson & Patterson 1982). Nevertheless, interspecific tandems were not uncommon in our study. Not only do these tandems waste a female's time, tandem pairs may suffer considerable predation risk (e.g. Rehfeldt 1990).

To the extent that density and sex ratio vary, even over the course of a day, a shift between two alternative male decision rules over ecological time may be common. Because habitat structure, population density, sex ratio, and morph frequency are predicted to affect per capita mating attempts toward females and males (Fincke 2004), controlled experiments that vary these factors independently should help define more precisely, how each affects the decision rule used by males and the consequence of the rule for male search efficiency.

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### REFERENCES

- Banks, M.J. & D.J. Thompson, 1985. Lifetime mating success in the damselfly *Coenagrion puella*. *Animal Behaviour* 33: 1175-1183.
- Bell, W.J., 1991. Searching behavior. Chapman & Hall, London.
- Bedjanič, M., 1994. Odonatna favna Turnovih ribnikov (Rače, Slovenija). *Exuviae* 1: 1-4.
- Beynon, T.G., 1999. An unusual mismatch. *Journal of the British Dragonfly Society* 15: 17.
- Bick, G.H. & J.C. Bick, 1957. The Odonata of Oklahoma. *The Southwestern Naturalist* 2: 1-18.
- Bick, G.H. & J.C. Bick, 1963. Behavior and population structure of the damselfly, *Enallagma civile* (Hagen) (Odonata Coenagrionidae). *The Southwestern Naturalist* 8: 57-84.
- Bick, G.H. & J.C. Bick, 1981. Heterospecific pairing among Odonata. *Odonatologica* 10: 259-270.
- Bick, G.H. & L.E. Hornuff, 1965. Behavior of the damselfly *Lestes unguiculatus* Hagen (Odonata: Lestidae). *Proceedings of the Indiana Academy of Sciences* 75: 110-115.
- Bick, G.H. & L.E. Hornuff, 1966. Reproductive behavior in the damselflies *Enallagma aspersum* (Hagen) and *Enallagma exsulans* (Hagen) (Odonata: Coenagriidae). *Proceedings of the Entomological Society, Washington* 68: 78-85.
- Bick, G.H., J.C. Bick & L.E. Hornuff, 1977. An annotated list of the Odonata of the Dakotas. *Florida Entomologist* 60: 149-166.
- Bilek, A., 1963. Ein Freiland-Hybrid der Gattung *Agrion* Leach (= *Coenagrion* Kirby) (Odonata, Agrionidae). *Nachrichtenblatt Bayerischer Entomologen* 12: 56-58.

- Clausen, W., 1990. Weitere Libellenbeobachtungen aus dem nördlichen Ostwestfalen. *Natur und Heimat* 50: 49-53.
- Corbet, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Cornell University Press, Ithaca.
- Cordero, A., 1989. Reproductive behaviour of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 237-244.
- Cordero, A. & J.A. Andrés, 2001. Estimating female morph frequencies and male mate preferences of polychromatic damselflies: a cautionary note. *Animal Behaviour* 61: F1-F6.
- De Marchi, G. 1990. Precopulatory reproductive isolation and wing colour dimorphism in *Calopteryx splendens* females in southern Italy (Zygoptera: Calopterygidae). *Odonatologica* 19: 243-250.
- Dunkle, S.W., 1990. *Damselflies of Florida, Bermuda and the Bahamas*. Scientific Publishers, Gainesville.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *American Naturalist* 126: 1-25.
- Fincke, O.M., 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behavioral Ecology and Sociobiology* 10: 293-302.
- Fincke, O.M., 1985. Alternative mate-finding tactics in a non-territorial damselfly (Odonata: Coenagrionidae). *Animal Behaviour* 33: 1124-1137.
- Fincke, O.M., 1986a. Underwater oviposition in a damselfly (Odonata: Coenagrionidae) favors male vigilance, and multiple mating by females. *Behavioral Ecology and Sociobiology* 18: 405-412.
- Fincke, O.M., 1986b. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). *Evolution* 40: 791-803.
- Fincke, O.M., 1994. Female dimorphism in damselflies: failure to reject the null hypothesis. *Animal Behaviour* 47: 1249-1266.
- Fincke, O.M., 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, R. Jödicke, E.I. Malikova, D.R. Paulson & M. Watanabe, 2005. The frequency of female-specific color polymorphisms in Holarctic Odonata: why are male-like females typically the minority? *International Journal of Odonatology* 8; in press.
- Forbes, M.R., 1991. Female morphs of the damselfly *Enallagma boreale* Selys (Odonata: Coenagrionidae): a benefit for androchromatypes. *Canadian Journal of Zoology* 69: 969-970.
- Forbes, M.R. & K.L. Teather, 1994. Variation in attraction of male *Enallagma ebrium* (Hagen) to two female morphs (Zygoptera: Coenagrionidae). *Odonatologica* 23: 103-114.
- Garman, P., 1917. The Zygoptera, or damselflies, of Illinois. *Bulletin of the Illinois Laboratory of Natural History* 12: 411-587.
- Garrison, R.W., 1979. Population dynamics and systematics of the damselfly genus *Enallagma* of the Western United States (Odonata: Coenagrionidae). Ph.D. Thesis, University of California, Berkeley.
- Gorb, S.N., 1998. Visual cues in mate recognition by males of the damselfly *Coenagrion puella* (L.) (Odonata: Coenagrionidae). *Journal of Insect Behavior* 11: 73-92.
- Hilton, D.F.J., 1983. Mating isolation in two species of *Nehalennia* (Zygoptera: Coenagrionidae). *Odonatologica* 12: 375-379.
- Hilton, D.F.J., 1987. A terminology for females with color patterns that mimic males. *Entomological News* 98:221-223.

- Hinnekin, B.O.N., 1987. Population dynamics of *Ischnura e. elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia* 146: 3-31.
- Jödicke, R., 1996. Die Odonatenfauna der Provinz Tarragona (Catalunya, Spanien). In: Jödicke, R. (ed.) "Studies on Iberian dragonflies", *Advances in Odonatology, Supplement 1*: 77-111.
- Jödicke, R., 1997. Binsenjungern und Winterlibellen Europas. Lestidae. Westarp, Magdeburg.
- Jödicke, R., U. Krüner, G. Sennert & J.T. Hermans, 1989. Die Libellenfauna im südwestlichen niederrheinischen Tiefland. *Libellula* 8: 1-106.
- Jurzitza, G., 1966. Über interspezifische Paarungsversuche bei Odonaten. *Beiträge zur Naturkundlichen Forschung in Südwestdeutschland* 25: 71-72.
- Johnson, C., 1964. The inheritance of the female dimorphism in the damselfly, *Ischnura damula*. *Genetics* 49: 513-519.
- Johnson, C., 1975. Polymorphism and natural selection in ischnuran damselflies. *Evolution Theory* 1: 81-90.
- Kellicott, D.S., 1895. Catalogue of the Odonata in Ohio. Part I. *Journal of the Cincinnati Society of Natural History* 17: 195-216.
- Kunath, G., 1991. Interessante Fehlkoppelungen bei Kleinlibellen (Zygoptera). *Libellula* 10: 155-156.
- Lindeboom, M., 1996. Fortpflanzungsbiologie der Gebänderten Prachtlibelle *Calopteryx splendens* (Calopterygidae, Odonata). Dissertation, Albert-Ludwigs-Universität Freiburg.
- Loibl, E., 1958. Zur Ethologie und Biologie der deutschen Lestiden (Odonata). *Zeitschrift für Tierpsychologie* 15: 54-81.
- Miller, M.N. & O.M. Fincke, 1999. Cues for mate recognition and the effect of prior experience on mate recognition in *Enallagma* damselflies. *Journal of Insect Behavior* 12: 801-814.
- Moore, B.P., 1953. A curious instance of attempted cross-pairing in the Zygoptera. *The Entomologist's Monthly Magazine* 89: 277.
- Paine, A., 1991a. Brief notes and observations. *Journal of the British Dragonfly Society* 7: 25-26.
- Paine, A., 1991b. Brief notes and observations. Mixed pairings. *Journal of the British Dragonfly Society* 7: 44.
- Paine, A., 1996. Notes and observations. Mixed pairing. *Journal of the British Dragonfly Society* 12: 62.
- Parr, M.J., 1976. Some aspects of the population ecology of the damselfly *Enallagma cyathigerum* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica* 5: 45-57.
- Paulson, D.R., 1974. Reproductive isolation in damselflies. *Systematic Zoology* 23: 40-49.
- Paulson, D.R. & R.A. Cannings, 1980. Distribution, natural history and relationships of *Ischnura erratica* Calvert (Zygoptera: Coenagrionidae). *Odonatologica* 9: 147-153.
- Peters, H.P.J., 1988. Exuviae als graadmeter voor succesvolle voortplanting in de Overasseltse- en Hatertse vennen. Peters, Nijmegen.
- Rehfeldt, G.E., 1990. Anti-predator strategies in oviposition site selection of *Pyrrhosoma nymphula* (Zygoptera: Odonata). *Oecologia* 85:233-237.
- Robertson, H.M., 1985. Female dimorphisms and mating behaviour in a damselfly, *Ischnura ramburii*: females mimicking males. *Animal Behaviour* 33: 805-809.
- Robertson, H.M. & H.E.H. Patterson, 1982. Mate recognition and mechanical isolation in *Enallagma* damselflies (Odonata: Coenagrionidae). *Evolution* 36: 243-250.
- Ryan, M.J., J.H. Fox, W. Wilczynski & A.S. Rand, 1990. Sexual selection and signal evolution: the ghost of biases past. *Nature* 343: 66-67.

- Scheffler, W., 1970. Die Odonatenfauna der Waldmoore des Stechlin-See-Gebietes. *Limnologica* 7: 339-369.
- Sherratt, T.N., 2001. The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecology Letters* 4: 22-29.
- Siroť, L.K. & H.J. Brockman, 2001. Costs of sexual interactions to females in Rambur's fork-tail damselfly, *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Animal Behaviour* 61: 415-424.
- Steiger, S., 1988. Untersuchungen zur Populationsentwicklung von *Coenagrion puella* L. Schriftenreihe Bayerisches Landesamt für Umweltschutz 79: 131-136.
- Stoks, R., 1994. Eerste Belgische voortplantingswaarneming van *Lestes barbarus* (Fabricius, 1798). *Gomphus* 10: 84-87.
- Stoks, R., 1995. Inleidende etho-ecologische studie van *Lestes sponsa*. Eindverhandeling, Universiteit Antwerpen
- Stoks, R., 2000. Components of lifetime mating success and body size in males of a scrambling damselfly. *Animal Behaviour* 59: 339-348.
- Tennessee, K.J., 1975. Reproductive behavior and isolation of two sympatric coenagrionid damselflies in Florida. Ph.D. Thesis, University of Florida, Gainesville.
- Thompson, D.J., 1989. Lifetime reproductive success of andromorph females of the damselfly *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 209-213.
- Timm, W., 1906. Verzeichnis der in der Umgegend von Hamburg vorkommenden Odonaten. *Insekten-Börse* 23: 134-135, 140, 147-148, 151, 155.
- Tümpel, R., 1922. Die Geradflügler Mitteleuropas. Zweite Auflage. Perthes, Gotha.
- Utzeri, C. & C. Belfiore, 1990. Tandem anomali fra odonati (Odonata). *Fragmenta Entomologica* 22: 271-287.
- Utzeri, C., E. Falchetti & R. Raffi, 1987. Adult behaviour of *Lestes barbarus* (Fabricius) and *L. virens* (Charpentier) (Zygoptera, Lestidae). *Fragmenta Entomologica* 20: 1-22.
- Van Gossum, H., R. Stoks & L. De Bruyn, 2001. Reversible frequency-dependent switches in male mate choice. *Proceedings of the Royal Society, London (B)* 268: 83-85.
- Waage, J.K., 1975. Reproductive isolation and the potential for character displacement in the damselflies, *Calopteryx maculata* and *C. aequabilis* (Odonata: Calopterygidae). *Systematic Zoology* 24: 24-36.
- Walker, E.M., 1953. The Odonata of Canada and Alaska. Volume 1. University of Toronto Press, Toronto.
- Weichsel, J.I., 1985. Copulation between the damselflies *Hetaerina americana* (Fabricius) and *Calopteryx maculata* (Palisot de Beauvois) (Zygoptera: Calopterygidae). *Odonatologica* 14: 57-64.
- Wesenberg-Lund, C., 1913. Odonaten-Studien. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 6: 155-228, 373-422.
- Williamson, E.B., 1920. Notes on Indiana dragonflies. *Proceedings of the Indiana Academy of Science* 30: 99-104.