VARIATION IN ATTRACTION OF MALE *ENALLAGMA EBRIUM* (HAGEN) TO TWO FEMALE MORPHS (ZYGOPTERA: COENAGRIONIDAE)

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Variation in attraction of male *E. ebrium* to models of 2 ♀ colour morphs was studied at a site in Ontario, Canada, where 85-97% of females were green; the other females were blue, i.e. coloured like males. Mate-searching males were equally attracted to ♀ morphs in one experiment, contrary to studies on other Zygoptera. However, more mate-searching males failed to respond positively to the ♂-like morph when females were pinned near 'control' males; such failures appear to be errors in recognition of ♂-like females. Time of day (an index of intensity of mate-searching by males of this sp.) did not account for variation in the number of males that failed to respond positively to females of either morph. Moreover, males that were quite 'interactive' with other model males were not more likely (than less interactive males) to form tandem sooner with females of either morph. Thus, it was not possible to identify factors that could explain variation in differential male attraction to morphs. The possibility that female colour is a selectively neutral trait cannot be discounted.

INTRODUCTION

Female polymorphisms have been described in several coenagrionid damselflies (Odonata: Zygoptera) including species of *Ischnura* (JOHNSON, 1975; ROBERTSON, 1985; HINNEKINT, 1987; CORDERO, 1989), *Coenagrion* (THOMPSON, 1989), *Argia* (CONRAD & PRITCHARD, 1989), *Enallagma* (GARRISON, 1978; ASKEW, 1988; FORBES, 1991a) and *Nehalennia* (Forbes, Richardson & Baker, unpubl.). Typically, one female morph is coloured, and sometimes patterned, like the conspecific male [i.e. the homeo-

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chrome (WALKER, 1953), andromorph (JOHNSON, 1975), or androchromotype (HILTON, 1987)], whereas one or more other morphs are coloured unlike the male (i.e. the heterochrome, heteromorph or gynochromotype). In those species studied, morph type is heritable (JOHNSON, 1966; CORDERO, 1990a).

Several hypotheses exist to explain the coexistence of two or more female morphs within populations of damselflies. These hypotheses can be grouped into two broad categories. First, there are hypotheses (reviewed by CORDERO, 1992) which predict that different selection pressures act on female morphs [e.g., a greater predation rate on brighter male-like morphs by visual predators, and a lower incidence of costly interactions between that morph and heterospecific (JOHNSON, 1975) or conspecific males (ROBERTSON, 1985)]. Second, FINCKE (in press) proposed that morph colour or pattern are selectively neutral traits, regardless if conspecific males are more attracted to one morph over another. Under this scenario, morph ratios are determined largely by genetic drift.

To test predictions of the various hypotheses, researchers have examined how heterospecific males (DE MARCHI, 1990; FORBES, 1991b; CORDERO, 1992) and conspecific males (ROBERTSON, 1985; CORDERO, 1989, 1990b; CON-RAD & PRITCHARD, 1989; FINCKE, in press; FORBES, in press) respond to different female morphs to determine whether males might exert differential selection on morphs through interference. Researchers have varied in their approaches, however, from observing male responses to pinned (live or dead) females (CONRAD & PRITCHARD, 1989; FORBES, 1991a), to observing male responses to live tethered females (FINCKE, in press) or to pinioned females (FORBES, in press). Other researchers have observed natural interactions between males and different female morphs (ROBERTSON, 1985; CORDERO, 1992). Despite variation in methods used, some generalizations have emerged. First, males of an *Ischnura* species seem not to recognize male-like females as 'females' as easily as they distinguish other female morphs (review by CORDERO, 1992). And second, males are more attracted to the more common female morph; in fact, degree of male attraction to a particular morph relates to the proportion of that morph in the population (FINCKE, in press).

Although some generalizations have emerged, there are some inconsistencies between studies. For example, conspecific males are not always attracted to the most common female morph. Males showed no significant differences in their degree of attraction to female morphs in two damselfly species (*Argia vivida* and *Calopteryx splendens*). In *A. vivida*, > 65% of females were male-like, although the proportion of male-like females varied somewhat between two study populations (CONRAD & PRITCHARD, 1989). In *C. splendens*, male-like females accounted for only 10-15% of all females in the populations studied (DE MARCHI, 1990).

It is also not clear whether differential male attraction to female morphs (when it occurs) translates into differential selection on female morphs. In two popula-

tions studied, female morphs were not observed to differ in lifetime reproductive success (FINCKE, 1988; THOMPSON, 1989), despite the fact that males were more attracted to the more common female morph in Fincke's study population (FINCKE, in press). Other authors, however, have viewed interference from males as a strong selective force in odonates (CORBET, 1980). In a study on *I. graellsii*, male-like females were believed to benefit from avoiding excessive harassment by mate-searching males at high population densities, but to suffer from a mating disadvantage at low population densities (CORDERO, 1992). Thus, differential male attraction could, in theory at least, be both beneficial and detrimental to particular morphs depending on other factors, e.g., population density.

No study has examined whether there is substantial within-species variation in differential male attraction to morphs and whether such variation (if it exists) is explained by factors such as time of day (which could relate to a male's intensity of mate-searching) or to other factors such as the incidence and intensity of interactions between males. In fact, studies on conspecific male responses to female morphs have been confined to a few experiments conducted at or near the pond's edge (FORBES, 1991a; FINCKE, in press). This paper addresses the extent of variation in differential male attraction to female morphs in *Enallagma ebrium* and whether degree of differential male attraction to morphs is affected by the aforementioned factors.

STUDY SPECIES

Like males of other species of *Enallagma* (FINCKE, 1982), male *E. ebrium* show intense 'scramble' competition for access to mates. Male *E. ebrium* forage as well as search for mates at rendezvous sites; the number of foraging flights relates to time of day (FORBES, 1991a). We believed that time of day would influence a male's likelihood of encountering a receptive female (see below) and thus his intensity of mate searching. Mate-searching intensity could affect whether males respond, in a sexual manner, equally to male-like colours versus colours that were not male-like.

Mature *E. ebrium* females are either colored like males (blue) or are green, over much of their head, thorax, and sides of their abdomen. Female morphs do not differ in size (FORBES, 1991a). Both morphs of *E. ebrium* are patterned alike along the dorsum of their entire abdomen (with large continuous dark brown to black regions) and are quite dissimilar from *E. ebrium* males (which have much smaller black regions separated by blue areas, WALKER, 1953, p. 102).

The sequence of sexual behaviours, from initial 'capture' of a female through copulation to egg deposition by the female, lasts 1.5-3.0 h for *E. ebrium* (FORBES, 1991a). The wheel position lasts from 20-58 min (x̄ time=29.4 min, S.D.=8.5

min) for those *E. ebrium* pairs (n=31) in which males were observed to translocate sperm from their genital pore to their second abdominal segment (FORBES, 1991a). Sperm translocation by males indicates that the pair has just formed (ROBERTSON & TENNESSEN, 1984).

STUDY AREA AND METHODS

Field work was done from 15 June-23 July 1992 at Two-Island Lake (TL): a large marsh (described by FORBES, 1991c) that is near Chaffey's Locks, Ontario, Canada (44°34'N; 79°15'W). *E. ebrium* and *E. vernale* were present at TL. *E. boreale* was absent from this site, although *E. ebrium* and *E. boreale* co-occur at sites near TL (FORBES, 1991b).

Proportions of mature females of each morph were censused on 9 days (beginning at 13:00-14:00 h) by walking slowly near the marsh edge in an area of forest-edge habitat (ca 10 m x 65 m). We recorded morph type for each female seen either in tandem or in the wheel position with a male [see MILLER & MILLER (1981) for a description of such positions in the related *E. cyathigerum*].

E x p e r i m e n t   1 — Attraction of *E. ebrium* males to morphs

To compare level of attraction of mate-searching *E. ebrium* males to both types of conspecific females, two females (one blue and one green) were killed by thoracic compression and pinned (ca 3-5 cm apart) on a grass stem (see FORBES, 1991b) that was positioned horizontally on a clump of grass at the edge of TL. Each female model was pinned such that they were at a 45° to the grass stem and parallel to one another. Care was taken to ensure the abdomens of both females were straight. Females returning from oviposition, and females in tandem with males, curl their abdomens with the approach of mate-searching males; such abdomen curling is one of a suite of female rejection behaviours in *Enallagma* (FORBES, 1991a). We decided against using live tethered females (cf. DE MARCHI, 1990; FINCKE, in press) because we could not control the female's position adequately.

The purpose of this experiment was to determine whether *E. ebrium* males were more attracted to the more abundant morph (as generally predicted for damselflies). All males that responded by forming tandem with a female model were netted and marked, as described by FORBES (1991b). Subsequent responses of marked males were excluded from analyses. In total, 14 females of each morph were pinned with a female of the other morph type and positioned in sets of two at the marsh edge. Responses of 3-10 *E. ebrium* males per set of pinned females (123 different males in total) were recorded.

E x p e r i m e n t   2 — (a) Male attraction to morphs pinned near males and (b) influence of time of day on differential male attraction

For this experiment, pinned damselflies were placed on vegetation over land exactly as described above except that a pinned male was substituted for one of the female models. In total, 80 models were used: 20 blue females, 20 green females, and 40 'control' males. We always placed two sets of pinned damselflies close to one another (3-5 m apart). One set had a male and a male-like female; the other had a male and a green female. Responses of mate-searching males to control males or to the female model were recorded until 5 males responded positively for each set of pinned damselflies. Positive responses occurred if a male grasped a model male or female and attempted to form, or formed, tandem. In addition, some males hovered within 2-4 cm of a set of pinned damselflies. Males that showed positive responses and males that hovered near models (but then flew away) were

netted, marked and released.

Because we recorded responses of males to each of two sets of damselflies (that were placed within 5 m of one another and that were watched within 15 min of one another), we could compare whether more males hovered near either set of pinned damselflies, but failed to show positive responses. The order of observation of sets was alternated for each group of pinned damselflies. In other words, if we first observed male responses to the set with a male-like female, then for the next group of 2 sets, we first observed male responses to the set with a green female. Finally, we determined whether time of day (from 13:00 to ca 15:30 h) influenced the number of males that failed to respond positively. Previous studies showed that after 15:00 h, males often encountered females that had finished ovipositing. Such females were not receptive.

Experiment 3 — Responses of individual males to morphs

We also investigated whether individual males responded equally to conspecific females of both morphs, when female models were presented directly to males. This experiment was done because any differences in male attraction to female morphs (found in previous experiments) could potentially be explained by males being less willing to mate with females of one morph rather than those females being less easily distinguished by males. For this experiment, each of two females (one blue and one green) was killed and pinned at the end of one of two 20-25 cm grass stems (each 3 mm in diameter). Presentations were made by slowly pushing a model female head on toward, and perpendicular to, the focal male's thorax (from ca 0.5 m away). Model females were then situated within 1 cm of the focal male for ca 1-2 s before being slowly pulled back. Each presentation took ca 5 s.

We recorded whether focal males remained perched, or flew at, or flew away from, the model female. Males that flew at the model female would either hover above the model without contacting it, grasp the model's thorax with its legs, or grasp and form tandem with the model. Each focal male was presented with one female morph up to 3 times (or until the male formed tandem with the model female). Then, the male was allowed to remain perched undisturbed for 10-20 s before being presented with a model female of the other morph type. Thus, the experiment allowed us to determine whether males were more likely to form tandem with one morph at an earlier presentation. Order of presentation of morphs was alternated between males.

Experiment 4 — Interactions between males and responses to morphs

We predicted that males that show little interaction with other males should be less likely to engage male-like females than more 'interactive' males. Thus, we examined whether male responses to females of either morph depended on the males' previous interactions with model males. For each focal male, we first presented a model conspecific male [as described above for model females (Experiment 3)] 3 times. We recorded whether focal males remained perched, flew away from, or flew at, the model male. We noted whether focal males that flew away from the model male attempted to forage [see FORBES, (1991c) for a description of foraging by male *E. ebrium*]. Males that flew at the model male either hovered near it, grasped it with their legs, or attempted to form tandem with it. We scored model-directed responses as positive responses (up to 3 positive responses per male were possible) and flights away from the model as negative responses. After being presented with a model male 3 times, the focal male was then presented with a model female of either morph up to 3 times, or until the focal male formed tandem with the model female.

RESULTS

CENSUSES OF FEMALE MORPHS

Male-like females accounted for 2.9-15% of all females at TL (Tab. I). With the exception of one female, all females censused were paired to males. Because pairs are slow flying and include bright males, it is unlikely that one morph was more likely than the other to be sighted.

EXPERIMENT 1 — Attraction of *E. ebrium* males to morphs

More males formed tandem with the blue than with the green model for 6 sets of pinned females (Tab. II). The reverse was true for 4 sets, whereas in the remaining 4 sets, equal numbers of males formed tandem with green and blue females (Tab. II, p > 0.05, Binomial test; ZAR, 1984). There also was no significant mean difference in numbers of males responding to either female morph ($\bar{x}$ difference = 0.86 males, paired t=0.80, p=0.43). Thus, males *E. ebrium* were not more attracted to the male-like morph as found for *E. boreale* (FORBES, in press) nor were they more attracted to the more common (green) morph, which accounted for 85-97% of all females at TL.

Table I

Numbers and percent of male-like (blue) females and numbers of green females of *E. ebrium* seen paired to males or seen as single females (in parentheses) during censuses at TL

Date	No. blue	% blue	No. green	Total
15 June	1	3.8	25	26
20 June	1	2.9	33	34
29 June	1	3.0	32	33
4 July	3	15.0	17	20
13 July	1	3.2	35	36
18 July	2	6.9	27	29
19 July	3(1)	10.0	27	30
20 July	2	6.1	31	33
21 July	3	10.3	26	29

Table II

Numbers of conspecific male *E. ebrium* that formed tandem with male-like (blue) females versus green females for each of 14 sets of pinned females used in Experiment 1

Date	Pair No.	No. males forming tandem with blue	green	% males forming tandem with blue
25 June	1	0	3	0
	2	7	3	70
	3	2	2	50
26 June	4	9	1	90
	5	3	7	30
	6	6	4	60
	7	2	8	20
28 June	8	6	4	60
	9	9	1	90
4 July	10	5	5	50
	11	4	5	44
	12	6	4	60
	13	3	3	50
13 July	14	5	5	50

EXPERIMENT 2 — (a) Male attraction to morphs pinned near males and
(b) influence of time of day on differential male attraction

On each of 20 occasions when a green female was pinned with a control male,
all 5 males that responded positively (100 males in total) formed tandem with
the model female. On the 20 occasions in
which a male-like female was used, only
1 of 100 males that responded positively
attempted to form tandem with the model
male; the remaining males formed tandem
with the model female. Clearly, *E. ebrium*
males easily distinguished between males
and females of either morph.

We also recorded and marked a number
of males that hovered near (within 2-4 cm
of) sets of pinned damselflies, but that did
not respond positively. Significantly more
males failed to respond positively (i.e.,
hovered nearby) when a male-like female
was pinned with a male ($\bar{x}$=3.05 males)
than when a green female was pinned with
a male ($\bar{x}$=1.00 males; paired t=3.69,
df=19, p=0.002). However, time of day
was not significantly correlated with the
number of males that failed to show posi-
tive responses, regardless if a male-like
female (Spearman r=-0.186, N=20,
p>0.05) or a green female (Spearman
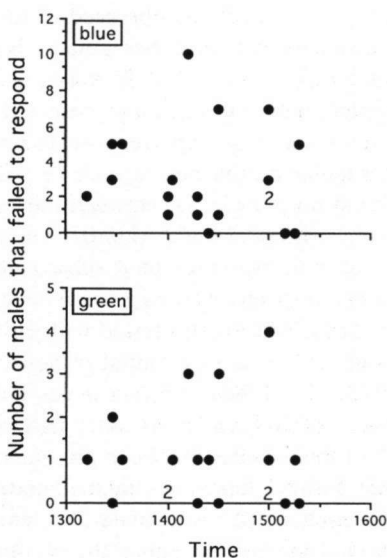r=-0.086, N=20, p>0.05) was pinned with
a male (Fig. 1).

Fig. 1. Number of males that failed to respond positively to sets of pinned damselflies (i.e. a male pinned with either a blue or green female model) versus time of day when experiments were conducted. Numbers in graphs refer to multiple observations for 2 failed responses (upper panel) or for 0 failed responses (lower panel).

EXPERIMENT 3 — Responses of individual males to morphs

Forty-eight of the 50 males tested formed tandem with both female morphs
when females were presented directly to them. The remaining 2 males formed
tandem with the green female but not with the blue female. Three males formed
tandem with the blue female on an earlier presentation that with the green female,
while the reverse was true for 6 males (p>0.05, Binomial test). Thus, individual
males showed no significant tendency to fail to respond (or to respond at a later
presentation) to either morph when females were presented directly to males.

EXPERIMENT 4 − Interactions between males and responses to morphs

Seventeen males (or 24.3% of 70 males tested) were observed to forage during presentations with model males. Because foraging males may be less responsive to conspecifics, we first examined whether there was an association between whether a male was observed to forage and whether that male had been tested subsequently with either a male-like female or a green female. There was no such association: 29 of 53 males that did not forage, and 6 of 17 males that did forage, were subsequently presented with a male-like female (χ^2=1.94, p=0.16). This result was expected because males were chosen for presentation with a particular morph before their responses to model males were scored. We also found no association between the number of positive responses made by focal males to model males (i.e. 0-1 versus 2-3 positive responses) and whether that focal male was presented subsequently with a male-like female (19 versus 16 males, respectively) or a green female (18 versus 17 males, respectively; χ^2=0.057, p=0.81). Thus, males tested with either green females or male-like females were quite similar in their initial responsiveness to model males.

Only 3 of 70 E. ebrium males failed to form tandem with the model female on 1 of 3 presentations, after first being presented with a model male 3 times (2 of those males had been presented with a male-like female). Of the 67 males that formed tandem with the model female, 44 formed tandem on the first presentation (22 with male-like females and 22 with green females) while 23 formed tandem on either the second or third presentation (11 with male-like females and 12 with green females). Thus, males showed no differences in their likelihood of forming tandem with male-like females or green females, after having 'interacted' 3 times with conspecific males (χ^2=0.07, p=0.79). Again, these females were presented directly to males.

We also examined whether males that differed in their number of positive responses to model males differed in their likelihood of forming tandem with a model female of either morph on either the first, second, or third presentation. We found that focal males that showed 0-1 versus 2-3 positive responses to model males were equally likely to form tandem with model male-like females on the first (11 versus 11 males), second (5 versus 3 males) or third (2 versus 1 males) presentation (χ^2=0.55, p=0.95; number of males forming tandem on the second or third presentation were pooled to ensure expected frequencies were > 5, ZAR 1984). We also found that such males were equally likely to form tandem with green females on the first (11 versus 11 males), second (3 versus 5 males) or third (3 versus 1 males) presentation (χ^2=0.00, p=1.0). Thus, focal males that were quite interactive with model males were no more responsive to male-like females than males that were less interactive; the same held true for males responding to green females.

DISCUSSION

E. ebrium males did not show differential attraction to female morphs when two females were pinned near one another or when females were presented directly to males. The percent of males that formed tandem with the male-like female in the first experiment was quite variable (ranging from 0-90% of all males tested per set of pinned females, Tab. I). This first result was surprizing especially given that we (unpubl.) found that male *E. ebrium* at another site (near Guelph, Ontario) were more attracted to green than to blue females (green females accounted for ca 70% of all females in that population). And in another experiment near TL, FORBES (1991b) found that *E. ebrium* males were more attracted to green than to blue *E. boreale* females. These differences between studies are difficult to reconcile given that the experimental protocols of each study were identical.

In another study, FORBES (in press) showed that male *E. boreale* were more attracted to male-like females than to green females. The relative proportion of male-like females in the present study species (6.9% of 261 females sampled over all days) is substantially less than the relative proportion of male-like females for *E. boreale* from a nearby site (67.8% of 485 females censused over all days: FORBES, in press; χ^2=244, p<0.0001). Yet male *E. ebrium* were not less attracted to the rare morph as generally predicted. It appears that between and within species, there is considerable variation in differential male attraction to morphs that is not easily explained by variation in frequency of particular morphs.

By comparison, our second result was quite similar to previous findings on *Enallagma*, i.e. males readily distinguished between other males and females of either morph (cf. FINCKE, in press) and more males failed to respond positively to sets of damselflies with a male-like female and male than to sets with a green female and male. The implication of this finding is that single male-like females would receive less male attention than green females, at least under some circumstances. Nonetheless, male-like females that are willing to mate or remate (on a given day) are certainly likely to pair with males as are green females (cf. FINCKE, in press). This type of pairing with males, however, differs from situations in which females (returning from oviposition) pair with males. In the latter case, *E. ebrium* females attempt to avoid 'extra' pairings with males by showing a bouncing flight or by perching flat against grass stems. If females are captured by males then they remain perched while the male attempts to fly away or they refuse to 'genital touch' (ROBERTSON & TENNESSEN, 1984) with males and turn their heads from side to side. We refer to these occurrences as failed invitations.

We witnessed 20 such failed invitations over five days (from 15:00-16:00 h). Eleven involved green females, 6 involved blue females and 3 involved teneral females. Three of those females were captured and found to contain fewer than

20 mature eggs confirming that they had already oviposited that day (cf. FORBES & BAKER, 1991). 11 of the failed invitations were timed because males were observed to clasp females (in the remaining 9 instances, males and females were already in tandem when discovered). The mean times for males to dissociate from females was 5.1±3.7, 2.5±2.4, and 7.5±3.5 minutes for green, blue, and teneral females, respectively. Although the data are too few to make meaningful comparisons, the results do suggest that females of both morphs need not remate if they are unwilling to do so and that they can reject males in a substantially shorter period of time than that required for another copulation (which lasted 29.4 min on average). The very fact that mature females returning from oviposition avoid 'extra' pairings with males and refuse to remate suggests that such pairings are disadvantageous to females (males may exert selection on females). Whether either morph is more disadvantaged by interference from males is not known for this species.

From the male's perspective, the likelihood of encountering a receptive female should dictate how vigorously males mate search and perhaps how tenaciously they hold on to 'unwilling' females. We expected that time of day should influence how 'motivated' males were and how likely they were to investigate conspecifics at close range. However, time of day did not explain significant variation in the number of males that fail to respond positively to sets of damselflies, although we generally found that more males failed to respond positively to male-like females than to green females when females were pinned near control males. We believe that such failed responses are simply errors in detecting or recognizing females (rather than individual males preferring to form tandem with only particular females) because we found that individual males would readily form tandem with females of either morph when females were presented directly to males.

Finally, focal males showed considerable variation in their interactions with other males. This variation in the number of positive responses to other males (and in tendency to forage) was not associated with the likelihood of a male being presented with a male-like female versus a green female. Thus, we could determine whether males showing similar levels of responsiveness were equally likely to form tandem with females of either morph. Overall, males responded equally to both female morphs (that were presented directly to them) after having interacted with other males. And males that were found to be quite interactive with model males were no more likely to form tandem with model females (of either morph) at an earlier presentation than were less interactive males.

Taken together, our results suggest that variation in differential male attraction to female morphs exists (between studies and between esperimental protocols described in this study). Although variation in male responsiveness to other males also exists, such variation does not translate into variation in differential male attraction to female morphs. Thus, we failed to identify factors responsible for variation in differential male attraction to morphs. Whether differential male

attraction (when it occurs) results in differential selection on female morphs is still an unanswered question. It is possible that for some species, differential male attraction is detrimental under certain situations (e.g. for females returning from oviposition). Other experiments are needed that vary the degree of male attraction to morphs and then examine indices of short-term fitness of females. Such experiments are difficult until factors accounting for variation in differential male attraction are identified. Until such factors are identified, the possibility that female colour is a selectively neutral trait for *E. ebrium*, as generally suggested for damselflies by FINCKE (in press), cannot be discounted.

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M. Forbes & K.L. Teather

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