

## VISUAL CUES IN MATE RECOGNITION IN THE DAMSELFLY *ISCHNURA ELEGANS* VANDER LINDEN (ZYGOPTERA: COENAGRIONIDAE).

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*This paper is dedicated to Philip S. Corbet on the occasion of his 70th birthday.*

Received 10 January 1998; revised 05 November 1998; accepted 19 January 1999

Keywords: Female colour forms, Odonata, *Ischnura elegans*, visual cues, sex recognition

### Abstract

Of the three recognised female morphs of *I. elegans*, only two occurred in Jagotin, Kiev Province, Ukraine. Andromorphs and *infuscans* together constituted 99.8% of females in the population, and only 0.2 % were *infuscans-obsolata*. The present paper is an experimental study testing male responses to female and male models. Three questions were asked: (1) Is the colour of the model an important cue in mate recognition by males? (2) What is the area of male field of view, responsible for mate recognition? (3) Which is the preferred direction, from which each model elicits the maximal rate of copulatory responses? All colour forms of females regularly occurred *in copula* with males throughout the day. The *violacea* and andromorph female models were preferred by males. However, the manner of model presentation strongly influenced male response: copulatory responses were rare when models were presented above the male. Copulatory behaviour with a male model resulted in nearly 70% of cases when the approach was from behind, which was significantly more frequent than with female models. Among female models, the andromorph and grey-green females of the form *infuscans* were recognised as a female more frequently from behind than the *violacea* and brown females of *infuscans*. The role of different visual cues in mate recognition is discussed.

### Introduction

Colour polymorphism of mature females is common among coenagrionids (Fincke, 1987). One morph is coloured like a male (androchrome), whereas other morphs are coloured differently (gynochrome). The biological significance of this phenomenon has been previously discussed by many authors (Johnson, 1975; Robertson, 1985; Hilton, 1987; Hinnekint, 1987; Conrad & Pritchard, 1989; Cordero, 1989; 1992; Thompson, 1989; Forbes, 1991; 1994; Cordoba-Aguilar, 1992; Fincke, 1994a; 1994b; Forbes *et al.*, 1995; 1997; Cordero & Andres, 1996; Cordero *et al.*, 1998). There are different hypotheses about the advantages for females to be polymorphic, however, the question which cues males use for the morph recognition is still unresolved.

Some authors have examined the attractiveness of different colour morphs to males using experiments with living tethered females of *Ischnura graellsii* (Cordero, 1989) and *I. denticollis* (Cordoba-Aguilar, 1992) or with freshly-killed females of *Enallagma boreale* pinned on a stem between clumps of vegetation (Forbes, 1991). In the first and the second cases the male responses to the complex mixture of morphological and behavioural stimuli produced by living models have been recorded. In the third experimental arrangement only copulatory responses have been taken into account. Forbes & Teather (1994) have carried out the series of experiments testing the attraction of female morphs of *E. ebrium* to conspecific males and *vice versa*. However, basic knowledge about mechanisms of visually guided mating behaviour in coenagrionid males is sparse.

*Ischnura elegans* is a species with complex female polymorphism. There are three colour morphs, each with several age-related colour forms (Parr, 1973a). Askew (1988) mentions that in the Ukraine he failed to find any rufescens or infuscans-rufescens individuals among hundreds examined. Indeed, we have found only about 0.2 % of these forms, and thus, they were not included in this study. In spite of this, males have to recognise three colour forms of sexually mature females, among which andromorphs are hardly distinguishable from the male. Several comprehensive studies have been done on the ecology of this species, in particular on its emergence patterns, age groups (Parr, 1973a), survivorship, local movements and dispersal (Parr, 1973b), and multiannual cycles (Hinneking, 1987). The mating frequencies of the three female morphs have been studied by Parr & Palmer (1971).

The present paper is based on experiments with freshly-killed individuals, which served as models and were presented to mature males of the damselfly *I. elegans*. This experimental setup enabled us to record any individual response of a male to male models and models of female colour forms without any influence of behaviour of the model, such as the frequency of wing beat, flight type, or wing and abdominal displays. Three questions about male precopulatory behaviour were asked. (1) Is the colour of the andromorph female an important factor in mate recognition by males? (2) What is the area of male field of view responsible for sex recognition? (3) Which is the preferred direction, from which each model elicits the maximal rate of tandem responses of a male? It is believed here that the study of mechanisms of visually guided behaviour may aid in understanding diverse aspects of mate choice in Zygoptera.

## Methods

Field observations and experiments were carried out in July-August, 1993 at moist meadows near Supoy Lake (Kiev Province, Central Ukraine), where *Ischnura elegans* (Vander Linden) were numerous. Other damselfly species, such as *Lestes sponsa* (Hansemann), *Enallagma cyathigerum* (Charpentier), *Erythromma najas* (Hansemann), also occurred in this habitat.

During three sunny days (10-13 August), 202 pairs in copula were captured from a study area whose dimensions were 30 x 30 m. Only females in copula were recorded. The time of each capture was recorded and the pair divided. Females were recorded as

one of four colour forms: blue (andromorph), brown and grey (*infuscans*), and violet (*violacea*, the immature stage of both *infuscans* and andromorphs). ‘Brown’ included those specimens of the form *infuscans* whose thorax colouration was brown, yellowish-brown, or reddish-brown. ‘Grey’ included specimens of the form *infuscans* with pale or olive thorax colouration. ‘Violet’ was the form *violacea*. There were few specimens with transitional colouration (such specimens were not used in experiments).

The experiments were carried out between 10:00 and 17:00 h. In experiments, the five types of model were used: blue, brown, grey, and violet females, and blue males. The wings of the models were intact. Freshly prepared models were used for 1-2 hours only. Thin rod (1.5 m long) with the model connected through a little holder to the rod tip was held in front of males perching on the vegetation. Models were presented only in profile. After 10-20 presentations to different males a new randomly chosen model was used. Each model was shown to the male only once at a level somewhat below the position of the perching male (in other experiments the models were also presented at a level somewhat above the position of the perching male; see below). To minimise repeated presentations to the same male individuals, an experimentator moved 3-4 m away after every single presentation.

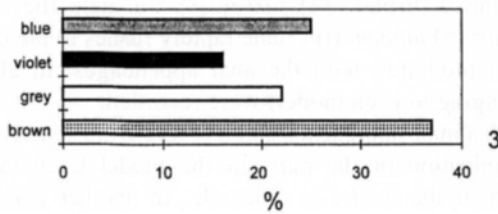
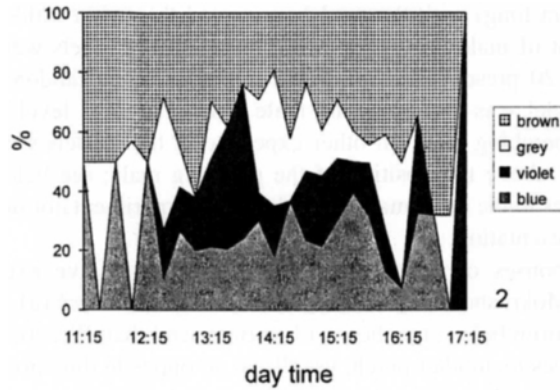
Behavioural responses of males were scored as one of five exclusive responses (see Frantsevich & Mokrushov, 1984; Gorb, 1992; 1998): (1) *attack* (a) - a male suddenly rushes at the model from below, touches it a few times and then flies away; (2) *escape* (e) - a male rapidly moves to another perch, usually in an opposite direction from the model; (3) *indifference* (i) - a male continues to fly without direction change or to perch, sometimes demonstrating a threat display; (4) *survey* (s) - a male flies around the model without attempting to pair; (5) *tandem* (t) - male rapidly rushes to the model, settles upon it and tries to grasp its prothorax with the anal appendages. In all, 1487 responses (an average of 250 belonging to each model) were recorded.

The direction at which a male approached a model was evaluated visually. This variable was valuable for determination of the parts of the model body that were the most important in recognition of the model as a female. In another experiment, we tested the area of the male field of view responsible for sex recognition. Female models were shown to the male at two levels: i) below the position of the perching male, and ii) above the position of the perching male.

## Results

### *Occurrence of female colour forms in copula during daytime*

The peak of occurrence of females in copula at the study area was recorded between 14:00 and 16:00 (Fig. 1). Females from copulated pairs (37.5% of all copulations) were mainly brown coloured individuals (Fig. 3). The various colour forms of females regularly occurred throughout the day. No colour form showed any particular preference for copula at specific times of the day, except that *violacea* did not mate in the morning (Fig. 2).



Figures 1-3. Copulatory activity of *I. elegans* at Supoy Lake. Fig. 1. Number of pairs in copula captured at the experimental site (pooled over three days). Fig. 2. Percentage of female colour forms captured in copula at the experimental site. Fig. 3. Percentage of female colour forms among pairs in copula. Charts based on data on 202 pairs in copula.

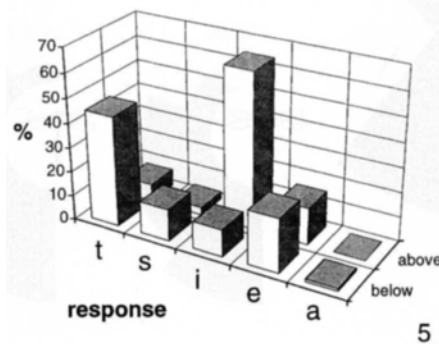
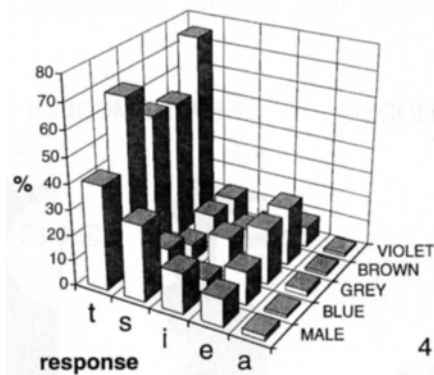
**Male preference of colour form of models**

Males demonstrated sexual response significantly more often to female models than to male models (male:  $t=40,8\%$ ,  $n=287$ ; female:  $t=63,0\%$ ,  $n=998$ ;  $\chi^2=39,90$ ,  $df=1$ ,  $p<0,001$ ). *Violacea* ( $t=76,5\%$ ,  $n=234$ ) and andromorphs ( $t=68,0\%$ ,  $n=275$ ) were more attractive than brown ( $t=54,4\%$ ,  $n=250$ ) and grey ( $t=55,6\%$ ,  $n=239$ ) forms of *infuscans* (Fig. 4) (violet-grey:  $\chi^2=21,92$ ,  $df=1$ ,  $p<0,001$ ; violet-brown:  $\chi^2=23,59$ ,  $df=1$ ,  $p<0,001$ ; blue-grey:  $\chi^2=9,19$ ,  $df=1$ ,  $p=0,002$ ; blue-brown:  $\chi^2=10,30$ ,  $df=1$ ,  $p=0,001$ ). However, there were no

significant differences between responses to the blue and violet females ( $\chi^2=2,83$ ,  $df=1$ ,  $p=0,092$ ). Males distinguished brown and grey models from male models (grey-male:  $\chi^2=10,13$ ,  $df=1$ ,  $p=0,001$ ; brown-male:  $\chi^2=8,50$ ,  $df=1$ ,  $p=0,004$ ). Males can also distinguish blue females from males (blue:  $t=68,0\%$ ,  $n=275$ ; male:  $t=40,8\%$ ,  $n=287$ ; blue-male:  $\chi^2=36,77$ ,  $df=1$ ,  $p<0,001$ ).

#### *Model location and its recognition by males*

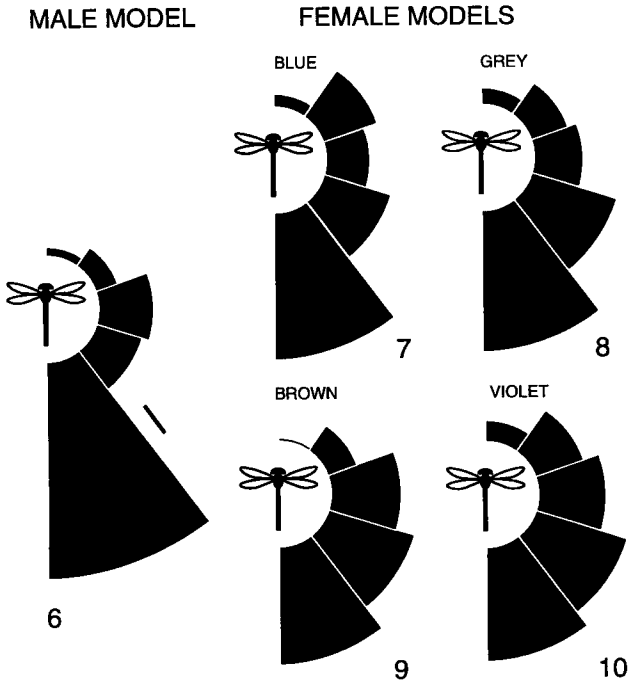
The same models, which were presented above or below perching males, elicited different responses of males. When models were presented above the male, sexual response was observed very seldom ( $t=6,1\%$ ,  $n=100$ ) (Fig. 5). However, the high percentage of sexual responses was recorded when the model was presented below the perching male ( $47,2\%$ ,  $n=120$ ). There were significant differences in male responses in experiments with different type of model presentations ( $\chi^2=37,23$ ,  $df=1$ ,  $p<0,001$ ).



Figures 4-5. Male responses to models. Fig. 4. Models of male and female colour forms (blue male,  $n=287$ ; blue female,  $n=275$ ; brown female,  $n=250$ ; violet female,  $n=234$ ; grey female,  $n=239$ ). Fig. 5. Male responses to female models under different experimental conditions. *Above*: female models presented against the background of the sky above perching males. *Below*: those presented against a background of vegetation below perching males.

*Directionality of the male approach to the model*

Some males recognised models as a female without a previous survey and immediately after recognition rushed towards it. Usually, males first flew around the model (*survey*) and then seized the model from some point. Presumably, this point is the area, from which the male has recognised the model as a female. In most observed cases, it was located behind the model. Tandem formations with a male model resulted from such a position of the male in nearly 70% of tandem responses (Fig. 6). There were significant differences in the orientation of tandem responses (from behind/from other directions) between male and all female models (male-violet:  $\chi^2=22,59$ ,  $df=1$ ,  $p<0,001$ ; male-blue:  $\chi^2=8,30$ ,  $df=1$ ,  $p<0,004$ ; male-grey:  $\chi^2=9,41$ ,  $df=1$ ,  $p=0,002$ ; male-brown:  $\chi^2=17,03$ ,  $df=1$ ,  $p<0,001$ ; male-female:  $\chi^2=20,14$ ,  $df=1$ ,  $p<0,001$ ). Among female models, the blue and grey models were recognised as females more often from this position than the violet and brown ones, but the differences were not significant (blue-violet:  $\chi^2=4,53$ ,  $df=1$ ,  $p=0,033$ ; blue-grey:  $\chi^2=0,12$ ,  $df=1$ ,  $p=0,725$ ; blue-brown:  $\chi^2=2,52$ ,  $df=1$ ,  $p=0,112$ ; grey-brown:  $\chi^2=1,40$ ,  $df=1$ ,  $p=0,237$ ; grey-violet:  $\chi^2=2,73$ ,  $df=1$ ,  $p=0,098$ ; brown-violet:  $\chi^2=0,14$ ,  $df=1$ ,  $p=0,710$ ) (Figs 7-10).



Figures 6-10. Number of sexual responses of males from different directions (in percent): blue male (6),  $n=108$ ; blue (7),  $n=167$ ; grey (8),  $n=129$ ; brown (9),  $n=132$ ; violet females (10),  $n=173$ . Scale=10%. Only tandem responses have been taken into account.

## Discussion

### *Visual cues in odonate behaviour*

Previous authors has demonstrated that different dragonfly species use different visible morphological features to recognise conspecific individuals. The present work helps to understand the basic mechanisms involved in a variety of behavioural situations. Most odonate males can distinguish males from females visually by morphological structures and colour patterns. Experiments with models of female parts have supported the conclusion that presence of abdomen and wings are the most important cues for female recognition in most species studied. Body size is important for *Libellula pulchella* (Pezalla, 1979), *Nesciothemis nigeriensis* (Parr & Parr, 1974), *Ischnura elegans* (Krieger & Krieger-Loibl, 1958); body colouration for *Erythemis simplicicollis* (Andrew, 1966), *Orthetrum albistylum* (Ito, 1960), *Plathemis lydia* (Jacobs, 1955), *N. nigeriensis* (Parr & Parr, 1974), *Pachydiplax longipennis* (Johnson, 1962; Robey, 1975), *Platycnemis pennipes* (Buchholtz, 1956), *I. elegans* (Krieger & Krieger-Loibl, 1958); wing coloration for *E. simplicicollis* (Andrew, 1966), *Calopteryx* spp. (Heymer, 1973; De Marchi, 1990; Hooper, 1995), *Perithemis tenera* (Jacobs, 1955), *Megaloprepus caerulatus* (Fincke, unpublished data); and abdomen shape for *Cordulia aenea* (Ubukata, 1983). Males of *Sympetrum* species use all these characters to recognise conspecifics and to distinguish rivals and mates (Frantsevich, 1982; Mokrushov, 1987). The visual cues of *Coenagrion puella* are mainly connected with abdomen colour pattern and both head and thorax colour (Gorb, 1998).

### *Male visual field responsible for sex recognition*

This paper shows that the manner of model presentation in field experiments may strongly influence male response. Males recognised models much better, when the model was located below the male against a grass background. This result may be explained by the fact that pairing sites in *I. elegans* are preferably located in vegetation. Males are adapted to wait perching in vegetation or actively search for females flying among vegetation. The same behaviour has been observed in males of some *Lestes* species (Mokrushov, pers. comm.). On the base of these results we hypothesise that non-receptive females avoid males by flying over vegetation. Receptive females flying in the vegetation would have higher chances of being captured by males. However, these hypotheses need to be tested by field experiments.

In contrast to *I. elegans*, males of some *Sympetrum* species are adapted to recognise females flying above perching males against a sky background (Frantsevich & Mokrushov, 1984). *S. sanguineum* males tend to occupy perches just above the ground in order to have better chances of detecting and recognising individuals flying over them (Gorb, 1994). Such differences in visual areas responsible for sex recognition are closely connected to searching and perching strategies of the male.

### *Orientation of male tandem response*

This study has evaluated direction from which a male recognises an object as female. Our data show that sexual response to the male model is mainly directed from behind and somewhat from above the model. The orientation of the response shows to which part of the model a male is attracted (Gorb, 1997). It may be suggested, that *I. elegans* males fail to distinguish sex of models viewed from behind. Males recognised models much precisely from one side. Presumably, both the colour pattern of the thorax, and abdomen shape are better distinguishable from one side of the model than from above and behind. Our previous experiments on *C. puella* have shown that sexual responses have been usually directed to the female part in the case of models of female parts and those of male-female chimerae. Even models with some male parts have elicited many sexual responses directed to female parts of the model (Gorb, 1998). Thus, coenagrionid males can recognise females by the presence of parts composing whole image of the female and by the presence of one female part (head, thorax) separately as well. Actually, only one part of female body can be sufficient to elicit a sexual response, which is rather unusual for odonate males.

### *Colour, pattern and behaviour in mate recognition*

Sex recognition in Zygoptera, and damselfly mating behaviour in general, are based on the complex of two types of releasers: morphological and behavioural. The behavioural releasers, such as displays, may often play a crucial role in mate choice among Coenagrionoidea (Utzeri, 1988; Gorb, 1992). On the basis of data obtained from experiments, in which living ischnuran females were presented to conspecific males, previous authors have concluded that gynochrome females (i.e. non male-like in pattern and colour) are always more attractive to males (*I. verticalis* - Fincke, 1987; *I. graellsii* - Cordero, 1989; *I. denticollis* - Cordoba-Aguilar, 1992; *I. elegans* - Cordero *et al.*, 1998). In experiments reported above, freshly-killed females were used as models to test male responses only to morphological cues. This allowed us to examine the role of body colouration without behavioural influences. Previous experiments on dead models of males and females of *I. elegans* have shown that all female colour morphs and males were equally (highly) attractive to males (Cordero *et al.*, 1998). This study demonstrates variations in attractiveness even between different colour forms of andromorphs and *infuscans* females of *I. elegans*. The greater attractiveness of violet and blue models of *I. elegans* may be explained simply by the fact that the patterns in blue + black or in violet + black contrast better and are visually more easy-to-recognise ones than the brown + black, grey + black patterns. The blue colour of an andromorph is not a key stimulus repelling males. This supports the results obtained with another polymorphic damselfly, *Enallagma ebrium* in experiments which tested responses of an individual male to different female morphs (Forbes & Teather, 1994). However, our data on dead models of *Coenagrion puella* have revealed a higher attractiveness of gynochrome females than androchrome females (Gorb, 1998). Similar results have been obtained for the damselfly *Nehalennia irene* (Forbes *et al.*, 1997).



It seems that living androchrome females are in most cases less attractive to males than other polymorphs. It can be hypothesised that there is some particular kind of behaviour of androchrome females that makes living females less attractive. Recently Forbes *et al.* (1997) have shown that androchrome females of *N. irene* were more likely to chase males, whereas gynochrome females rarely showed refusal displays. It has been suggested that gynochrome females may be greater targets of sexual aggression than androchromes while at the pond's edge, and that androchrome females more often frequent that habitat (Forbes *et al.*, 1997). It has been previously evaluated that all female polymorphs have similar survivorship, but they differ in mating frequency: old *infuscans-obsolata* of *I. elegans* stored significantly more sperm in their spermatheca than old androchromes, suggesting that they had mated more often (Cordero *et al.*, 1998).

## Acknowledgement

I thank two anonymous reviewers who helped to improve an early version of the manuscript.

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