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# The conspicuousness of colour cues in male pond damselflies depends on ambient light and visual system

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The colours of male coenagrionid damselflies have been interpreted by some as intraspecific signals that reduce intrasexual harassment by advertising the unprofitability of pursuing conspecific males as potential mates. As visual cues, male colours should be conspicuous to other males under the specific light environments where males search for females. We tested this prediction by using spectroradiometry and two models of damselfly colour vision to determine the chromatic and achromatic contrast of males from six species of *Enallagma* damselflies with pond backgrounds under the ambient light conditions when each species was most active. The males of five species were active at the time when their colour was most conspicuous against aquatic vegetation. Three blue species were most active and attained their highest levels of contrast during midday, while species that became active in late afternoon or evening reflected longer wavelengths and increased in brightness contrast under low sun angles. A sixth species, *Enallagma pictum*, departed from this pattern. We propose that colour may serve as a signal of both sexual and species identity among males.



*Keywords*: colour vision; *Enallagma* damselflies; sensory drive; sexual signal; spectral reflectance

Sexual dichromatism is common among animals and often attributed to sexual selection for characteristics in one sex that reflect light as a conspicuous visual signal to members of the same or opposite sex (Silberglied 1984; Andersson 1994; Irwin 1994; Houde 1997). The utility of colour as a signal depends on the vision of the receiver and the light environment in which the sender and the receiver interact. A conspicuous colour will reflect the ambient light, provide strong contrast with the visual background and exploit the sensory characteristics of the receiver (Endler 1990, 1993). Spectrometry and quantitative measurements of colour have been useful in interpreting the evolution of sexual signals in vertebrates, their tactical design and their efficacy in the relevant environmental context (Endler & Théry 1996; Macedonia 2001; Fuller 2002; Gomez & Théry 2004; Leal & Fleishman 2004; Uy & Endler 2004; Doucet et al. 2007; Stuart-Fox et al. 2007). In this study, we applied similar techniques and a comparative approach to assess the conspicuousness of insect colours that are presumed to serve as intraspecific signals.

Damselflies (Odonata: Zygoptera) have been the subject of numerous studies of mating behaviour (Corbet 1999; Fincke et al. 2005). Research on the signal content of damselfly coloration has focused on the territorial and courtship behaviour of calopterygid damselflies (Grether 1996; Siva-Jothy 1999; Fitzstephens & Getty 2000; Cordoba-Aguilar et al. 2007) or the evolution of female polymorphism in coenagrionid damselflies (Cordero & Andrés 1996; Sherratt 2001; Van Gossum et al. 2001; Sirot et al. 2003; Fincke 2004; Fincke et al. 2005). Male coenagrionid damselflies practice scramble competition mating behaviour (e.g. Bick & Bick 1963; Bick & Hornuff 1966; Fincke 1982) and there is no evidence that females exert mate

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choice even though males are generally more colourful than females (Hafernik & Garrison 1986; Fincke 1997). Sherratt & Forbes (2001) proposed that male colour serves as a warning signal of the unprofitability of pursuing another male as a potential mate. When males are offered a choice of females or males mounted on dowels, they almost never show a sexual response towards the males (Fincke et al. 2007). In the genus *Enallagma*, most species have andromorphic females that resemble the males in coloration, and many species include heteromorphic females that differ from males in coloration. Competing hypotheses based on a cost of harassment to females have proposed that, by mimicking male signals, andromorphs are less harassed (Robertson 1985; Sherratt 2001; Sherratt & Forbes 2001) or are maintained by negative frequency-dependent selection exerted by males that learn the colour of an appropriate mate (Miller & Fincke 1999; Fincke 2004; Svensson et al. 2005). Despite the emphasis on male colour in hypotheses about the content of female signals, there has not been an assessment of the conspicuousness and design of male signals to conspecifics.

As signals of sexual identity, the colours of male damselflies should reflect the ambient light and contrast with the background that is visible to conspecifics when they interact. We assessed the relative conspicuousness of male damselflies under two alternative models of odonate colour vision. Furthermore, sensory drive theory predicts that congeneric species that are active under different light conditions should show different colour signals that maximize conspicuousness in their respective environments (Endler 1992). We tested this prediction by comparing the conspicuousness of males in six species of *Enallagma* damselflies that differed in colour and activity period.

## METHODS

### Study Subjects

We selected six damselfly species for study that represented the range of adult colours occurring in North American *Enallagma*. All of the males showed one colour on over 60% of the body surface as well as black stripes and bands. *Enallagma aspersum*, *E. basidens*, *E. geminatum*, *E. signatum* and *E. vesperum* were observed and collected from June through August at four open-water ponds in Licking County in central Ohio, U.S.A. We observed and collected *Enallagma pictum* at Cumberland Pond and Whitesbog, New Jersey, U.S.A., where it co-occurred with four of the other congeners.

### Activity of Male Damselflies

To determine the light conditions under which male damselflies were active, we conducted hourly censuses of males at the six ponds between 0800 and 2100 hours (Eastern Daylight Time, EDT) on eight dates between late June and early August in 2001, 2005 and 2007. Since damselfly activity is depressed under overcast conditions, censuses were conducted only under cloudless skies. Transects across the ponds and parallel to the shore were surveyed at the start of each hour from a fisherman's float tube. We used binoculars to visually identify species by their size and specific colour pattern and counted all males within 10 m of the transect line. It was also noted where males hovered or perched on aquatic vegetation.

### Ambient Light Spectra

Pond damselflies are illuminated directly by the sun and indirectly by diffuse light reflected from the sky, pond surface or surrounding vegetation. The spectra of ambient light sources change with the time of day and angle of the sun. We recorded irradiance spectra between 350 and 700 nm at 1 nm intervals with a LI-1800-11 remote cosine receptor connected by a quartz fibre optic cable to a LI-COR 1800 portable spectroradiometer (LI-COR Instruments, Lincoln, NB, U.S.A.). Before it was taken into the field, the spectroradiometer and receptor were calibrated with a lamp of known spectral energy distribution (LI-1800-02). For simplicity, we measured direct sunlight and sidewelling light over a 180° solid angle at locations where males were most active by holding the probe 10 cm above and parallel to the pond surface at 90° and 180° relative to due north. Concurrent with the day-long censuses of adult activity, we recorded irradiances hourly between 0900 and 2100 hours at the five ponds. Irradiance spectra were expressed in $\mu mol/m^2/s/nm/sr$ and pooled by hour for analysis. Because of the activity patterns of the observed species, mean irradiances ($N = 25$) at midday (1100–1400 hours) and late in the day (1800–2000 hours) were used in subsequent calculations of damselfly and background radiances.

### Reflectance Spectra of Damselflies and Visual Backgrounds

Spectral reflectances, at 1 nm intervals between 350 and 700 nm, were obtained from live males of each *Enallagma* species using an Ocean Optics SD2000 spectrometer (Ocean Optics, Inc., Dunedin, FL, U.S.A.), a WS-1 diffuse reflectance standard, and a PS-2 xenon light source. Males were restrained on their sides on a two-axis stage (Thorlabs, Inc., Newton, NJ, U.S.A.) and illuminated at a working distance of 2–4 mm. We focused the coaxial probe on the meso- and metapleural surface of the thorax. Reflectance spectra were also recorded from the abdominal segments of the specimens and found to be similar to those measured from the thorax in all but *E. vesperum*. Spectra were also collected from vegetation on the pond surface and shore that provided the dominant visual background for pond damselflies. The reflectances of 20 specimens of *Nuphar* sp., *Potamogeton* sp. and *Spirogyra* sp. were pooled to produce spectra of aquatic vegetation on which male damselflies perched over water. We also obtained spectra from the shoreline vegetation to calculate sensitivity factors for damselfly photoreceptors (see below).

### Colour Vision of *Enallagma* damselflies

An estimate of the conspicuousness of a colour signal, free of human bias, requires knowledge of the spectral