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Role of visual and non-visual cues in damselfly mate recognition

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In many species of damselflies, sexual conflict in the form of male harassment is thought to explain the widespread existence of female-limited color polymorphisms. With a few exceptions, the majority of investigations into these mating systems have assumed that male damselflies primarily use visual cues to detect and recognize their mates. Recently, laboratory studies have demonstrated that damselflies orient to olfactory signals from prey and that males orient to chemical cues from conspecific females. However, to date there are no field experiments which explicitly test the role that chemical cues play in sex recognition. Here we used a field experiment on *Enallagma civile* damselflies to test if free flying males detect and recognize females in the absence of the use of visual cues through the use of non-visual signals. In the absence of visual cues males did not exhibit positive responses toward female conspecifics, whereas when both visual and non-visual cues were present, males readily detected females and often tried to mate with them. Although it is possible that non-visual cues may be involved during close contact, our results emphasized that visual cues take center stage in damselfly mate recognition in the field environment. Because the field environment is the context in which selection acts on natural populations, results of this study have implications for our understanding of how selection on visual cues acts to maintain female-limited color polymorphism in damselflies whose males must search for potential mates.

Keywords: chemoreception; dragonfly; *Enallagma civile*; Odonata; sensory biology

Introduction

Identifying the sexual cues that organisms utilize to detect and recognize their conspecific mates is crucial to understanding mating behaviors, which in turn can provide insight into mechanisms of evolution that may lead to speciation (e.g. Andersson, 1994; Kaneshiro, 1980; Ryan, 1990). Numerous studies on the mating systems of mate-searching damselflies that exhibit female-limited color polymorphisms (Fincke, Jodicke, Paulson, & Schultz, 2005), have led to a better understanding of sexual selection and sexual conflict (Córdoba-Aguilar & Cordero-Rivera, 2008). Color polymorphisms in damselfly populations are thought to have evolved as different female strategies to alleviate sexual conflict in the form of male harassment. A common explanation is that male-like andromorph females mimic the blue males, and hence they avoid sexual harassment (e.g. Gosden & Svensson, 2009; Sherratt, 2001; Sirot, Brockmann, Marnis, & Muschett, 2003). More recently, in *Enallagma* damselflies, the male mimicry advantage was found to be balanced by an additional anti-harassment strategy of the green or brown

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heteromorphs. Heteromorphs avoided male detection through camouflage against green or brown vegetation, but, once detected, were easily recognized as mates, whereas the andromorph females mimicked males in their coloration, were easily detected, but once detected, were more difficult for males to recognize as "female" (Fincke, 2015). These findings on signal "apparency" (i.e. the ease of detection and recognition of a signal) assume that males use primarily visual cues in locating females.

Odonates are generally believed to rely nearly exclusively on their powerful vision to interpret their surroundings (Corbet, 1999). A recent genetic study emphasizes one aspect of their incredible vision: there are as many as 30 active opsin genes in some odonate eyes, many times that of most animals (Futahashi et al., 2015). Field research also supports damselflies' reliance on visual cues, particularly in mate recognition. An in-depth field study on *Coenagrion puella* (Linnaeus, 1758) damselflies by Gorb (1998) tested models that manipulated color and morphological features of females. In chimeras with mixed male and female parts, males' tandem responses increased the more female parts the model displayed, with males preferentially seizing the parts of the models with female anatomy. Color was also found to be significant, as tandem responses were recorded more with models exhibiting the light green color of heteromorph females. Males of the damselfly genus *Enallagma* are also known to synchronize their activity with sunlight; one study found that males were most active when the direct overhead sun provided the greatest contrast between their blue bodies and the green foliage (Schultz, Anderson, & Symes, 2008). By standing out as blue males, males can avoid harassment by other males searching for females.

Nevertheless, the importance of the visual system in damselflies does not preclude the possibility of chemical cues supplementing visual information. The cuticular hydrocarbons of insects play a particularly important role in conspecific recognition, as most species have a unique hydrocarbon profile (Howard & Blomquist, 2005). Within-species, sex-specific hydrocarbons or differences in relative abundance of hydrocarbons are also widespread (Howard & Blomquist, 2005), as in various species of ladybug beetles (Pattanayak et al., 2014), in *Formica fusca* ants (Chernenko, Holman, Helanterä, & Sundström, 2012), and several species of tsetse flies (Nelson & Carlson, 1986). Finally, studies on species such as the butterfly *Bicyclus anynana* and the wolf spider *Schizocosa uetzi* caution against focusing strictly on a single sensory modality when studying behaviors as important as mating. In a series of laboratory experiments, Costanzo and Monteiro (2007) found that *Bicyclus anynana* females would mate with males that displayed the correct visual stimuli but lacked olfactory signals; however, females preferred males that exhibited both visual and olfactory signals. A damselfly male's decision to attempt tandem may also be reinforced by olfactory cues. In the case of wolf spiders, while females required vibratory signals to mate, they were more receptive to males with more visual ornamentation (Hebets, 2005). By analogy, it is possible that chemical cues could be important in damselfly mating, even if they are subordinate to visual cues.

Compared with other insects, odonates have very short antennae. However, recent laboratory evidence demonstrated that the chemoreceptors of odonate antennae are more active than previously thought. Piersanti et al. (2014) demonstrated that *Ischnura elegans* (Vander Linden, 1820) responded to chemical cues of fruit fly prey by coupling behavioral assays with electrophysiological data from microelectrodes placed into the cuticle of the antennae. Another study by some of the same authors demonstrated that in the absence of visual cues, male *I. elegans* oriented preferentially toward both andromorph and heteromorph females, with males preferring the scent of andromorphs over heteromorphs; electroantennography however, indicated that the two female morphs elicited similar, but stronger responses than did the males (Frati, Piersanti, Conti, Rebora, & Salerno, 2015). That study suggests potential complications of conclusions based solely on experimental manipulation of visual cues. Because damselfly mating behaviors have been molded by natural selection in the field environment, field studies which test males'

ability to discern females based on nonvisual cues are necessary to understand the degree to which olfaction may play a role in a male's detection and recognition of potential mates.

Here we use a wild population of the damselfly species *Enallagma civile* (Hagen, 1861; Zygoptera: Coenagrionidae) to test the hypothesis that damselfly males require visual cues to detect (i.e. sense as present) and/or recognize (i.e. correctly identify) female conspecifics under natural conditions.

Material and methods

Our study population was *Enallagma civile* that live around the artificial ponds at the University of Oklahoma's Aquatic Research Facility in Norman, OK, USA (35.2200° N, 97.4400° W). Female damselflies were captured using an insect net and stored in small mesh insectaries (dimensions: 28 cm^3) until used in a trial. Because intermediate female color morphs predominated at the site throughout the study, all females used in the trials were of the intermediate morph. Intermediate morphs exhibit a blend of andromorph and heteromorph coloration; the underside of the thorax and abdomen is andromorphic blue, while the head and the upper half of the thorax is green like a heteromorph (Figure 1a). Like those of heteromorphs and andromorphs, the upper part of the intermediate morphs' abdomen is black.

Behavioral assay: male response to non-visual sexual cues

To assess whether damselfly males detect and recognize female conspecifics in the absence of visual cues, tests exposing males to visual and non-visual stimuli were performed. Trials were conducted on sunny days during September and early October 2015 between the hours of 11:30 and 15:30.

The setting for each replicate was two adjacent meter-squared plots marked off near the eastern edge of a small artificial pond (with an area of approximately 285 m^2) surrounded by high grasses. Each replicate in the experiment consisted of two treatments observed simultaneously, one per quadrat, a control treatment in which both visual and non-visual cues were present and an experimental treatment that obscured visual cues. A short window of opportunity for male activity necessitated observing the two treatments simultaneously. The trials were conducted in sets of two replicates, one with the control in the northern square, and one with the control in the southern square. The two-meter square plots used in each set of two replicates varied in their positions along the length of the pond. Both treatments used a modified version of the damsel-on-a-dowel technique (Fincke, Fargevieille, & Schultz, 2007). Using household glue (Duco Technology Inc.,
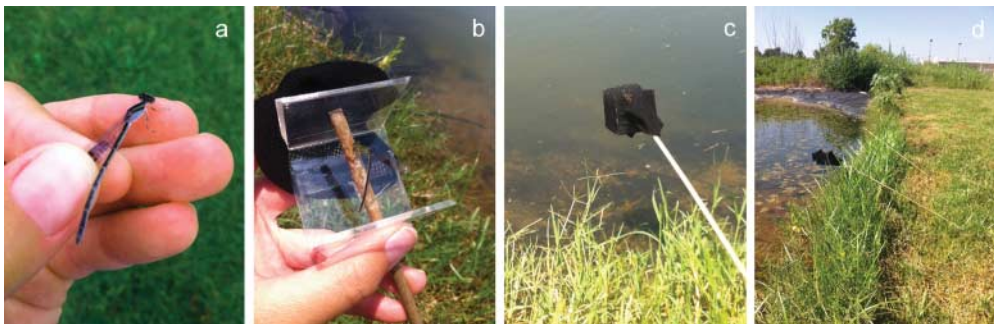

Figure 1. (a) Intermediate morph female; (b) experimental treatment box open on three sides; (c) covered experimental box; (d) field setup of control and experimental (quadrat markers not shown).

Henderson, NV, USA) live, sexually mature females were fixed by their legs in a perched position about 2.0 cm from the end of a wooden dowel (90 cm long, 4.76 mm in diameter). A unique female was used for each trial.

The difference between the two treatments was the sensory cues assumed to be available to passing males. In the non-visual cue treatment, the female on the dowel was placed inside half a plastic 5 cm^3 box that had three sides open to the air and a 6 mm hole drilled into the middle of one side for the dowel to pass through (Figure 1b). The side of the plastic box provided a structure onto which was secured a piece of previously washed, black fishnet pantyhose (Figure 1c). The pantyhose was assumed to prevent the males from detecting the female visually, while allowing any chemical cues to pass through via the three open sides of the box. The control (i.e. visual and non-visual cues) was simply an unobstructed female on a bare dowel, where both chemical and visual cues were assumed available to a passing male. The wooden dowels were placed in the ground at approximately a 35° angle such that the glued female was in the center of the meter-square plot, approximately even with the top of the grass. Dowels and damselflies were oriented westward toward the pond. To maximize male interactions with females, the end of the dowel was placed at the edge of the vegetation adjacent to the water (Figure 1d).

For a total of 10 min the most extreme of a passing male's behavior was noted. In increasing order of interest, behaviors were scored as "fly-by" in which a male passed within 10 cm of a female, hover, grab or perch after grab, or tandem (Fincke, 2015). Here we conservatively consider fly-by and hover as non-sexual behaviors. A fly-by indicated that a male was within the sensory range of being able to detect an individual, whereas a hover provided unambiguous evidence that a male detected an individual of interest. In contrast, grab and tandem were considered sexual responses and an indication that a male recognized a female as a potential mate. Note, however, that for the experimental treatment, the most extreme response that a female might elicit from a male was a grab or perching on the panty hose; it was impossible for a male to take the hidden female in tandem. When possible, males scored as exhibiting a sexual or non-sexual response were caught and held in a mesh insectary (dimensions: 28 cm^3) until the end of the trial. They were then marked on the wing and released about 30 meters away at the end of the trial. To account for variation in male abundance among replicates, the total number of males that passed through the meter square, but which never passed within 10 cm of the female (i.e. never exhibited any reaction to her) was also recorded. After the completion of each trial, females were marked on the wing with a permanent black marker to ensure that each female was used only once.

Statistical tests

The field experiment was analyzed using a general linear model (SAS version 9.3, SAS Institute Inc., Cary, NC, USA). The independent variables were treatment type (experimental or control). The dependent variables were the number of non-sexual and sexual reactions of males. Although we show the number of tandems by males in the control group, for comparison of the control and experimental treatments, these were pooled with grabs in analyzing sexual reactions. The total number of non-reacting males in a quadrat was entered as a covariate to account for variation in male abundance during trials.

Results

No marked male after release was ever found to react in another trial; all analyses below are on unique males. There was no interaction effect between non-reactive males passing through

the m^2 plot and non-sexual responses ($F_{1,38} = 1.09$, $p = 0.303$) nor between male density and sexual responses ($F_{1,38} = 1.83$, $p = 0.184$). Hence, the interaction term was eliminated in the analyses below.

Male non-sexual reactions

The number of non-sexual male reactions (i.e. a fly-by or hover response) did not differ between the visual control and the non-visual experimental treatments, accounting for the density of un-reacting males in the plot ($F_{1,39} = 1.90$, $p = 0.175$, Figure 2). Whereas 64.37% of the non-sexual reactions to the controls were "hover", none of the males' reactions to the non-visual treatment were hovers; all were "fly-bys" only (Figure 3). The proportion of non-sexual responses was not affected by the number of non-reacting males within the quadrat ($F_{1,39} = 0.03$, $p = 0.860$).

Male sexual reactions

As predicted, the number of male sexual responses was greater in the visual control treatment than in the non-visual experimental treatment ($F_{1,39} = 28.72$, $p < 0.0001$, Figure 2). In fact, there was no experimental replicate in which males grabbed at or perched on the netting covering the female (Figure 3). Across the two treatments, the proportion of sexual responses was not affected by the number of non-reacting males within the quadrat ($F_{1,39} = 0.63$, $p = 0.433$), Figure 4).
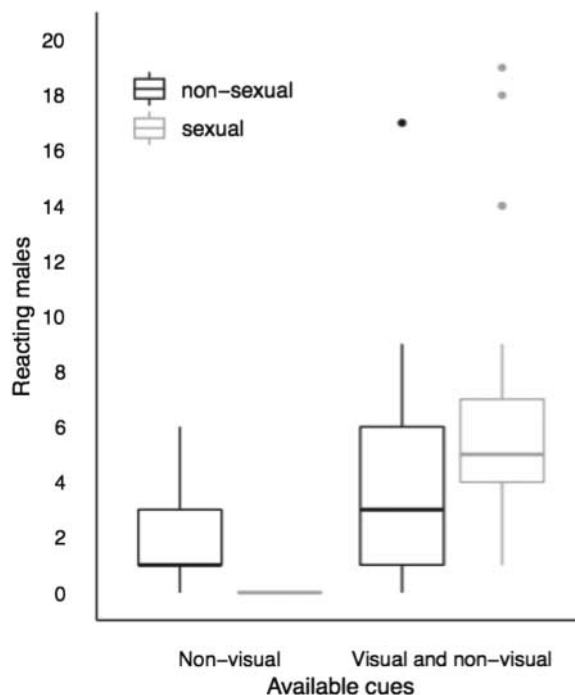

Figure 2. Male reactions in controls (visual and non-visual cues) and experimental treatment (only non-visual cues). Reactions were non-sexual (fly-by or hover) or sexual (grab, tandem for controls; grab or perching on netting for experimental). Median values are represented by the bars on each box.
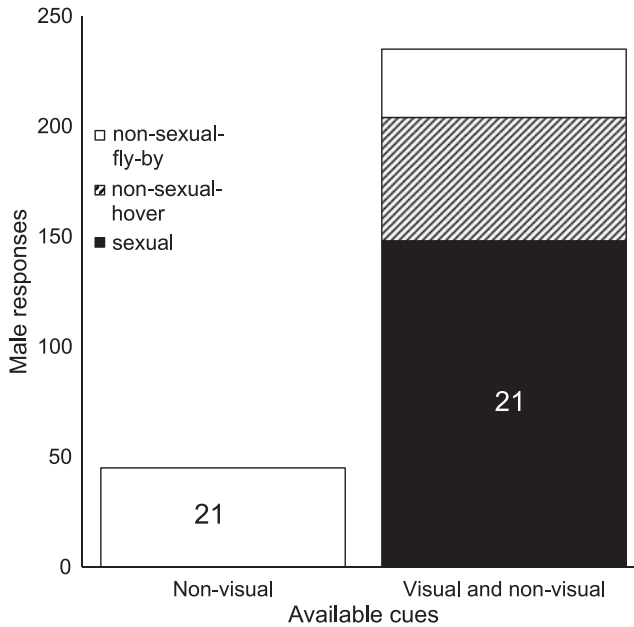
Figure 3.   Type and frequency of total male responses elicited in the field experiment (controls and experimental). In the "non-visual cue" treatment males could respond sexually with grab or perch but were precluded from using tandem and tandem attempts. Numbers refer to sample sizes for treatment and controls.
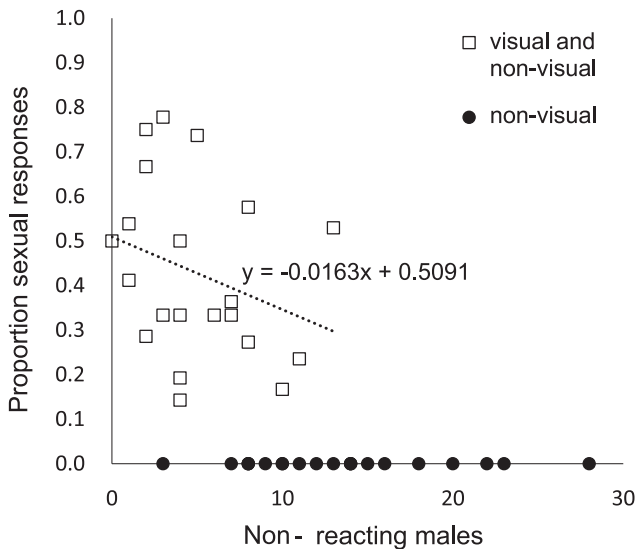

Figure 4.   Proportion of male sexual responses as a function of the number of non-reacting males in the m^2 plot. The number of non-reacting males within the quadrat and the proportion of sexual responses was a non-significant association.

Discussion

Our results supported the hypothesis that without visual cues, male *Enallagma civile* damselflies that encounter a female do not detect or recognize her in the field environment. First, in the experimental treatment, no passing male paused to hover, which would have unambiguously

indicted he detected an individual of interest. Nor did any male grab at or perch on the pantyhose that visually obscured the female, behaviors which would have indicated sexual interest. In contrast, in each of the visual controls, at least one passing male attempted to mate with the exposed female on the dowel. The non-sexual behaviors in the different treatments were more nuanced. While there was no overall difference in the number of non-sexual responses between the visual control treatment and the non-visual experimental treatment, the proportions of hover and fly-by within the total number of non-sexual responses varied by treatment (Figure 3). When presented with the female on the bare dowel, males often exhibited a hover response, pausing in the air in front of the female or perching on her dowel. In contrast, the only reactions to the female obscured by the pantyhose were fly-bys, indicating at best that the males encountered a female but offered no greater evidence that he detected her as an individual of interest or recognized her as a potential mate.

Our study is the first to test the ability of damselfly males to discern females using only non-visual cues in a field environment. Our results reinforce earlier experiments showing the importance of odonate vision to identify mates (Gorb, 1998) and to find prey (e.g. Pritchard, 1966; Sherk, 1978). The present study also formally tested and corroborated evidence found by Fincke (2015) that free flying *Enallagma hageni* (Walsh, 1863) males in the field were much less likely to detect females of either morph color when they were perched in shade (i.e. conditions that reduce their visual apparency) compared with detection of females perched in sun at the top of vegetation. Then, compared to blue females, green females were less likely detected against green vegetation. However, when perched on a dowel with two of the blue males, the blue female morph was less likely to be recognized as "female" relative to the green morph. Importantly, when disturbed by males, females of both morphs typically flew into shade, where they were not pursued by males. These findings are consistent with the more robust results of the current study in which the black pantyhose eliminated visual cues from females.

In contrast with our field results are those of Frati et al. (2015), which intriguingly demonstrated that under laboratory conditions, males registered and responded to the scent of conspecific females. Assuming that *Enallagma* and its sister genus *Ischnura* share similar neurophysiology, there are several possible explanations for the differences in the results between the two studies. First, the natural setting exposed damselflies to a wide range of scents simultaneously, diluting any potential chemical cues of conspecifics. Work with other insects such as hawkmoths has shown that background scents interfere with the insects' ability to distinguish and track floral odors (Riffell et al., 2014); thus it seems likely that olfactory mating signals would be weaker in the presence of background odors as well. In the behavioral assay component of the laboratory study, conspecific chemical cues were presented to the damselflies in cylindrical glass chambers, isolated from competing smells that would exist in field conditions. Similarly, the electroantennography portion of the study puffed purified air containing only damselfly scent extracts over the antennae of the males. A similarly strong olfactory signal, necessary to elicit a male response, may not be present in natural settings. In fact, the authors reported that during behavioral assay pilot tests males would not orient preferably to an odor source from only four females; eight individuals were needed to elicit a response. Damselfly females are often elusive in the wild and mark and recapture studies often reveal male-biased sex ratios. In a study conducted among *E. civile* in Oklahoma, for example, only 27% of marked females were recaptured compared to 70% of males (Bick & Bick, 1963). It therefore seems improbable that males in a field setting would encounter a sufficiently high female density, and thus level of female odor, as was used in the laboratory experiment of Frati et al. (2015).

Another potential complication of the laboratory experiment involves the artificial conditions in which the insects were raised. Experiments that increased *Enallagma* damselfly males' preference for a female color morph by increasing their exposure to that female morph illustrate that mating behaviors are not strictly innate, but are subject to a degree of plasticity (e.g. Miller &

Fincke, 1999; Fincke et al. 2007 for *Enallagma*; see Sánchez-Guillén et al. 2013 for *Ischnura elegans*). A study with honey bees found that associative strengths between sucrose and odors are reduced when multiple, different background odors are present (Smith, 1998). Extending the logic of these three studies, damselflies raised in aquaria and insectaries with few competing odors may learn from a young age to associate conspecifics with their odor more than damselflies that developed in conditions with many competing smells. A relatively increased sensitivity to conspecific odor might subtly alter mate-searching behaviors.

The discrepancies between the two studies could also be due to an effect of olfactory cues at short ranges, which Frati et al. (2015) caution against dismissing. The isolated and likely amplified chemical cues tested in Frati et al. (2015) may have elicited a male response only present in close range to females in the wild. If this were the case, damselflies would be comparable to insects such as emerald ash borers (*Agrilus planipennis*), which discern and locate females within 5 cm through the use of olfaction (Pureswaran & Poland, 2009). In the current study, females were placed in the middle of half a 5 cm^3 box covered with pantyhose (see Methods), allowing males the potential to get within about 3–4 cm of the female within. The males in Fincke (2015) also came within 10 cm of the females in shady position on the fern. The failure to elicit a male sexual response in the present study, and the reduced detection in Fincke (2015) offer strong evidence that olfaction alone is not sufficient to attract males to females; however, they leave untested potential synergistic effects of visual and olfactory modalities in damselfly mate recognition. Agrawal, Safarik, and Dickinson (2014) found such a system among fruit flies (*Drosophila melanogaster*), in which males first used vision when deciding to pursue a potential mate. While male sex pheromones prevented males from initiating the pursuit, the presence of female sex pheromones had no effect on the decision to chase the object. Once a male had decided to pursue an object, the detection of female conspecific chemical cues determined how much effort he would devote to continuing the chase. An analogous hierarchy of sensory modalities for mating male damselflies cannot be ruled out: visual cues may be essential for damselfly males to approach a potential mate, while short range chemical cues from the female might influence if he then attempts to mate with her.

In our study, we were unable to block chemical cues while allowing males access to only visual cues. In pilot tests, males failed to approach a visual cue only treatment that consisted of a female on a dowel inside a clear plastic box (non-glare glass boxes might have eliminated unnatural reflectance patterns). However, an experimental treatment that provided only visual cues could shed light on the possible role of olfaction over a short distance. For example, if males exposed to such a treatment had a greater number of hover responses than males exposed to a control with both visual and chemical cues available, one could argue that olfactory cues at a short distance to the female play a role in males' decision to attempt mating.

Because intermediate females represent the majority of the females at the study site beginning in early fall (see Fincke et al., 2007), we were unable to test for morph-specific differences in male reactions to visual and nonvisual cues. Because male *E. civile* do not seem to distinguish heteromorphs from intermediates (Moodie, 1995), likely the male reactions quantified here would also apply to heteromorphs. However, Frati et al. (2015) reported that the scent of *Ischnura elegans* andromorphs elicited a greater male behavioral (but not neurophysiological) response than did heteromorphs in the lab, suggesting that males in the field environment might also exhibit morph-dependent reactions. The behavior of *Enallagma hageni* in the wild is consistent with a male's use of the simple decision rule to identify potential mates of "if not blue, then female" (Xu, Cerreta, Schultz, & Fincke, 2014). Consistent with such a rule, Frati et al. (2015) posited that when a damselfly male is confronted with a conspecific whose color does not easily elucidate sex, males might then rely on scent to discriminate andromorph females at close range. In butterflies, odor is known to affect mate learning by females (Westerman & Monteiro, 2013). Thus, odor cues in damselflies might be important during the time that sexually immature

males learn to distinguish both female morphs from males (i.e. formation of the "decision rule" mentioned above). Alternatively, damselflies may use odor cues primarily to detect and recognize suitable prey as suggested by Piersanti et al., (2014) or during oviposition as suggested by Frati, Piersanti, Rebora, and Salerno (2016).

Although our study did not directly test all of the possible intricacies of olfaction in damselflies, the results nevertheless demonstrated for the first time under natural conditions that for male damselflies olfactory cues alone were insufficient to identify and locate mates. These results have implications for our understanding of female-limited color polymorphisms in damselflies, which are often ascribed as adaptations resulting from sexual conflict (e.g. Fincke, 2015; Fincke et al., 2005; Gosden & Svensson, 2009, but see Cooper, 2010). Whereas the sensory modality of vision remains key in mediating conspecific interactions in Odonates, further research is needed to understand more subtle roles that odor may play in decisions made by adults.

Acknowledgments

References

Agrawal, S., Safarik, S., & Dickinson, M. (2014). The relative roles of vision and chemosensation in mate recognition of *Drosophila melanogaster*. *The Journal of Experimental Biology*, *217*, 2796–2805. doi:10.1242/jeb.105817

Andersson, M. B. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Bick, G. H., & Bick, J. C. (1963). Behavior and population structure of the damselfly, *Enallagma civile* (Hagen) (Odonata: Coenagrionidae). *The Southwestern Naturalist*, *8*, 57–84. doi:10.2307/3669549

Chernenko, A., Holman, L., Helanterä, H., & Sundström, L. (2012). Cuticular chemistry of males and females in the ant *Formica fusca*. *Journal of Chemical Ecology, 38*, 1474–1482. doi:10.1007/s10886-012-0217-4

Cooper, I. A. (2010). Ecology of sexual dimorphism and clinal variation of coloration in a damselfly. *The American Naturalist*, *176*, 566–572. doi:10.1086/656491

Corbet, P. S. (1999). *Dragonflies: Behavior and ecology of Odonata*. Ithaca, NY: Comstock Publishing Associates.

Córdoba-Aguilar, A., & Cordero-Rivera, A. (2008). Cryptic female choice and sexual conflict. In A. Córboba-Aguilar (Ed.), *Dragonflies & damselflies: Model organisms for ecological and evolutionary research* (pp. 189–202). Oxford: Oxford Biology.

Costanzo, K., & Monteiro, A. (2007). The use of chemical and visual cues in female choice in the butterfly *Bicyclus anynana*. *Proceedings of the Royal Society of London B: Biological Sciences, 274.1611*, 845–851. doi:10.1098/rspb.2006.3729

Fincke, O. M. (2015). Trade-offs in female signal apparency to males offer alternative anti-harassment strategies for color polymorphic females. *Journal of Evolutionary Biology*, *28*, 931–943. doi:10.1111/jeb.12623

Fincke, O. M., Fargevieille, A., & Schultz, T. D. (2007). Lack of innate preference for morph and species identity in mate-searching *Enallagma* damselflies. *Behavioral Ecology and Sociobiology, 61*, 1121–1131. doi:10.1007/s00265-006-0345-3

Fincke, O. M., Jodicke, R., Paulson, D., & Schultz, T. D. (2005). The evolution and frequency of female colour morphs in Holartic Odonata: Why are male-like females typically the minority? *International Journal of Odonatology*, *8*, 183–212. doi:10.1080/13887890.2005.9748252

Frati, F., Piersanti, S., Conti, E., Rebora, M., & Salerno, G. (2015). Scent of a dragonfly: Sex recognition in a polymorphic Coenagrionid. *PLoS One*, *10*, e0136697. doi:10.1371/journal.pone.0136697

Frati, F., Piersanti, S., Rebora, M., & Salerno, G. (2016). Volatile cues can drive the oviposition behavior in Odonata. *Journal of Insect Physiology, 91–92*, 34–38. doi:10.1016/j.jinsphys.2016.06.007

Futahashi, R., Kawahara-Miki, R., Kinoshita, M., Yoshitake, K., Yajima, S., Arikawa, K., & Fukatsu, T. (2015). Extraordinary diversity of visual opsin genes in dragonflies. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, e1247–1256. doi:10.1073/pnas.1424670112

Gorb, S. (1998). Visual cues in mate recognition by males of the damselfly, *Coenagrion puella* (L.) (Odonata: Coenagrionidae). *Journal of Insect Behavior*, *11*, 73–92. doi:10.1023/A:1020818617066

Gosden, T. P., & Svensson, E. I. (2009). Density-dependent male mating harassment, female resistance, and male mimicry. *The American Naturalist*, *173*, 709–721. doi:10.1086/598491

Hebets, E. (2005). Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology*, *16*, 75–82. doi:10.1093/beheco/arh133

Howard, R. W., & Blomquist, G. J. (2005). Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Annual Review of Entomology*, *50*, 371–393. doi:10.1146/annurev.ento.50.071803.130359

Kaneshiro, K. Y. (1980). Sexual isolation, speciation, and the direction of evolution. *Evolution*, *34*, 437–444. doi:10.2307/2408213

Miller, M. N., & Fincke, O. M. (1999). Cues for mate recognition and the effect of prior experience on mate recognition in *Enallagma* damselflies. *Journal of Insect Behavior*, *12*, 801–814. doi:10.1023/A:1020957110842

Moodie, M. N. (1995). Evolution of female color morphs in damselflies. MS diss., University of Oklahoma.

Nelson, D. R., & Carlson D. A. (1986). Cuticular hydrocarbons of the tsetse flies *Glossina morsitans*, *G. austeni* and *G. pallidipes. Insect Biochemistry*, *16*, 403–416. doi:10.1016/0020-1790(86)90054-5

Pattanayak, R., Mishra, G., Omkar, C. S., Chanotiya, C. S., Rout, P. K., & Mohanty, C. S. (2014). Does the volatile hydrocarbon profile differ between the sexes: A case study on five aphidophagous ladybirds. *Archives of Insect Biochemistry and Physiology*, *87*, 105–125. doi:10.1002/arch.21184

Piersanti, S., Frati, F., Conti, E., Gaino, E., Rebora, M., & Salerno, G. (2014). First evidence of the use of olfaction in Odonata behavior. *Journal of Insect Physiology, 62*, 26–31. doi:10.1016/j.jinsphys.2014.01.006

Pritchard, G. (1966). On the morphology of the compound eyes of dragonflies (Odonata: Anisoptera), with special reference to their role in prey capture. *Proceedings of the Royal Entomological Society of London Series A, General Entomology*, *41*, 1–8. doi:10.1111/j.1365-3032.1966.tb01126.x

Pureswaran, D. S., & Poland, T. M. (2009). The role of olfactory cues in short-range mate finding by the emerald ash borer*, Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). *Journal of Insect Behavior*, *22*, 205–216. doi:10.1007/s10905-008-9166-8

Riffell, J. A., Shlizerman, E., Sanders, E., Abrell, L., Medina, B., Hinterwirth, A. J., & Kutz, J. N. (2014). Flower discrimination by pollinators in a dynamic chemical environment. *Science*, *344*, 1515–1518. doi:10.1126/science.1251041

Ryan, M. J. (1990). Signals, species, and sexual selection. *American Scientist*, *78*, 46–52.

Sánchez-Guillén, R. A., Hammers, M., Hansson, B., Van Gossum, H., Cordero-Rivera, A., Galicia Mendoza, D. I. & Wellenreuther, M. (2013). Ontogenetic shifts in male mating preference and morph-specific polyandry in a female colour polymorphic insect. *BMC Evolutionary Biology*, *13*, 116. doi:10.1186/1471-2148-13-116

Schultz, T. D., Anderson, C. N., & Symes, L. B. (2008). The conspicuousness of colour cues in male pond damselflies depends on ambient light and visual system. *Animal Behaviour*, *76*, 1357–1364. doi:10.1016/j.anbehav.2008.04.024

Sherk, T. E. (1978). Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes. *Journal of Experimental Zoology*, *203*, 61–79. doi:10.1002/jez.1402030107

Sherratt, T. N. (2001). The evolution of female-limited polymorphisms in damselflies: A signal detection model. *Ecology Letters*, *4*, 22–29. doi:10.1046/j.1461-0248.2001.00184.x

Sirot, L. K., Brockmann, H. J., Marnis, C., & Muschett, G. (2003). Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Animal Behaviour*, *66*, 763–775. doi:10.1006/anbe.2003.2279

Smith, B. H. (1998). Analysis of interaction in binary odorant mixtures. *Physiology & Behavior*, *65*, 397–407. doi:10.1016/S0031-9384(98)00142-5

Westerman, E. L., & Monteiro, A. (2013). Odour influences whether females learn to prefer or to avoid wing patterns of male butterflies. *Animal Behaviour, 86*, 1139–1145. doi:10.1016/j.anbehav.2013.09.002

Xu, M., Cerreta, A. L., Schultz, T. D., & Fincke, O. M. (2014). Selective use of multiple cues by males reflects a decision rule for sex discrimination in a sexually mimetic damselfly. *Animal Behaviour*, *92*, 9–18. doi:10.1016/j.anbehav.2014.03.016