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Volatile cues can drive the oviposition behavior in Odonata

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ABSTRACT

Selection for the oviposition site represents the criterion for the behavioral process of habitat selection for the next generation. It is well known that in Odonata the most general cues are detected visually, but laboratory investigations on the coenagrionid *Ischnura elegans* showed through behavioral and electrophysiological assays that adults were attracted by olfactory cues emitted by prey and that males of the same species are attracted by female odor.

The results of the present behavioral and electrophysiological investigations on *I. elegans* suggest the involvement of antennal olfactory sensilla in oviposition behavior. In particular, *I. elegans* females laid in the laboratory significantly more eggs in water from larval rearing aquaria than in distilled or tap water. Moreover, the lack of preference between rearing water and tap water with plankton suggests a role of volatiles related to conspecific and plankton presence in the oviposition site choice. *I. elegans* may rely on food odor for oviposition site selection, thus supporting the predictions of the “mother knows best” theory. These behavioral data are partially supported by electroantennographic responses. These findings confirm a possible role of olfaction in crucial aspects of Odonata biology.

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1. Introduction

Oviposition represents a critical habitat selection by the female for the next generation and represents the last step in the hierarchical manner that the species use to respond to the features of their habitat. Among the different hypotheses on how natural selection should shape oviposition preferences, the “mother knows best” principle suggests that females among herbivore insects prefer to oviposit on hosts that increase offspring survival (Scheirs et al., 2000; Mayhew, 2001). In this regard, the capability to find the right oviposition site requires the development of fine sensory systems.

Among aquatic insects such as Odonata, some species (all Zygoptera, Anisozygoptera and the aeshnid Anisoptera) with a cutting ovipositor lay their eggs endophytically while exophytic oviposition is inherent to the anisopterans with reduced ovipositor, designed to drop the eggs in water or to attach them superficially onto water plants or other periaquatic objects (Corbet, 1999). It is well known that the most essential cues are detected visually by Odonata e.g. attraction of females to oil ponds and other

shiny surfaces is a response to the horizontal polarization of light reflected from them (Horváth et al., 1998; Bernáth et al., 2002), a property shared with inland water surfaces which many aquatic insects use to locate oviposition sites from a distance (Bernáth et al., 2001). Some species that prefer standing water, such as *Orthetrum* species, can choose between “dark” or “bright” ponds (as perceived by the human eye) using the degree of polarization of the reflected light as visual cue (Bernáth et al., 2002).

Odonata can also rely on non-visual cues for certain aspects of their behavior (Corbet, 1999). Odonata that develop preferentially in running waters, such as *Calopteryx* species, have been demonstrated to use the flow rate to select their oviposition sites (Gibbons and Pain, 1992). In *Lestes sponsa* and *Lestes barbarus*, which oviposit inside vegetable tissues, the position of the eggs in the clutch is controlled by mechanoreceptors located at the basis of the stylus in the ovipositor (Matushkina and Lambret, 2011). In the ovipositor valves of *Aeshna cyanea* a high number of different mechanoreceptors have been described, and, as suggested for other damselflies (Matushkina and Gorb, 2007; Matushkina et al., 2016), they have been hypothesized to be used to evaluate the stiffness of the plant where the dragonfly aims to lay eggs (Rebori et al., 2013c).

Typical gustatory sensilla have been described on the valves of the endophytic ovipositor of *Aeshna cyanea* and *Ischnura elegans*, and they are considered potentially important to explore the

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vegetable tissues during oviposition, to select a suitable site for egg laying (Rebora et al., 2013b).

Although Odonata mostly rely on vision, ultrastructural (Rebora et al., 2008, 2009; Piersanti et al., 2010) and electrophysiological (Piersanti et al., 2011, 2014b, 2016; Rebora et al., 2012) investigations of their antennae revealed the presence of olfactory and thermo-hygroreceptors located in pits on the latero-ventral side of the flagellum. In addition, a neuroanatomical investigation of the brain of the dragonfly *Libellula depressa* revealed the existence of an antennal lobe lacking glomerular structures but revealing spherical knots that probably represent the functional connections between the afferent sensory neurons and the antennal lobe interneurons (Rebora et al., 2013a). Evidences of the use of the antennal olfactory sensilla in Odonata have been given by recent laboratory investigations demonstrating, by means of behavioral and electrophysiological assays, that adults of the damselfly *I. elegans* are attracted by olfactory cues emitted by prey (Piersanti et al., 2014a) and that males of the same species are attracted by female odor (Frati et al., 2015).

The aim of the present research is to investigate the potential involvement of olfactory antennal sensilla in Odonata oviposition, by means of behavioral (two-choice bioassays) and electrophysiological (EAG) assays.

As in some previous investigations by our research group (Piersanti et al., 2014a,b, 2016; Frati et al., 2015), the model species is the coenagrionid *I. elegans*.

2. Methods

2.1. Insects

Ichnura elegans is a damselfly that can be reared in the laboratory (Piersanti et al., 2015) and can be successfully used for behavioral assays in enclosed and artificial conditions. Females of this species typically oviposit alone, not in tandem as the other coenagrionids (Corbet, 1999). They are aggressive toward males or females that encroach on their oviposition sites, reserving an oviposition site temporarily for their own exclusive use (Miller, 1987), and lay eggs in almost all living or decaying vegetable matter that can be reached by the cutting endophytic ovipositor (personal observations).

I. elegans was reared at 25 ± 2 °C, a LD 16:8 h photoperiod and 60–80% RH conditions, as described by Piersanti et al. (2015). F0 field founders were males and females collected in late summer along shoreline vegetation in a small artificial pond for fish farming, close to the Trasimeno Lake (Umbria, Central Italy). The obtained larval stages were reared in aquaria and fed ad libitum with *Artemia salina* nauplii and freshwater plankton (*Daphnia* sp., *Cyclops* sp.). After emergence, males and females were placed together (~50 individuals), reared in insectaries (50 × 50 × 50 cm wooden cages covered with bee netting) with 1:1 sex ratio and fed ad libitum with *Drosophila melanogaster* flies. The internal walls of these cages were lined with aluminium foil, which reflects light and minimises escape behavior. Numerous plants of *Vicia faba* minor were placed inside the insectaries to increase humidity. Insectaries and aquaria were provided with artificial solar illumination (36 W/94 Philips TLD, The Netherlands). For the experiments, only insects belonging to the F1 generation were employed.

The insectaries used for behavioral experiments (behavioral insectaries) were the same as those used for rearing, with sexually mature adults of the same age (about 10 days after emergence) and with a 1:1 sex ratio. *V. faba* minor plants were covered with a net to avoid oviposition in the stems. The insectaries were humidified 2–3 times per day with a common water sprayer for garden.

2.2. Behavioral assays

To assess whether *I. elegans* females responded to volatiles from different kinds of waters, two-choice bioassays were performed. The following water types were considered: distilled water (DW); larval rearing water (RW); aged tap water (TW) and aged tap water plus plankton (TW+P).

RW was obtained mixing 200 ml of water from 3 different aquaria in which *I. elegans* larvae were regularly reared. Each aquarium was constituted as described by Piersanti et al. (2015). TW was obtained exposing water to the air for at least 24 h to remove the chlorine.

To obtain TW+P, tap water was placed in an aquarium identical to those used for larval rearing, supplemented with freshwater plankton (*Daphnia* sp., *Cyclops* sp.) with a density similar to that provided in the aquaria used for larval rearing.

TW and TW+P were maintained under the same illumination conditions as in the RW aquaria. They were used after a minimum of 3–4 days. In RW and TW+P used in the bioassays, larvae and plankton were not present because the upper aquarium plastic compartment, with the bottom replaced with a nylon net, was raised and the water, collected in the lower compartment, was used.

In the behavioral experiments, two-choice bioassays were conducted using single and double Petri dishes. For the single-Petri dishes assays, two plastic Petri dishes (9 cm diameter) were placed inside the behavioral insectary at 20 cm distance from each other. These Petri dishes were provided with a disk of filter paper on the bottom, to give *I. elegans* females a suitable substrate for embedding the eggs, and they were filled with 20 ml of water. A wooden stick was placed over each Petri dish as perch. The insectary was maintained under controlled conditions (25 ± 2 °C, a LD 16:8 h photoperiod and 60–80% RH) and after 24 h the filter paper disks from the Petri dishes were removed. Considering that one-two days after the oviposition are needed for eggs darkening, filter paper disks with eggs were maintained in water for at least two days after oviposition before counting them under a stereomicroscope (Zeiss Stemi SV8). At each bioassay, the position of the two Petri dishes, containing different water types, was inverted inside the behavioral insectary. All the water types in the experimental Petri dishes were completely transparent, so we can exclude any bias in the results due to visual stimuli. The following two-choice tests were carried out: DW vs. RW (n = 14); TW vs. RW (n = 11); TW+P vs. RW (n = 12). From one to three experiments per day were carried out with different insectaries.

To verify possible bias in the results of previous experiments due to the potential interference in water choice by the use of gustatory sensilla located on the female ovipositor of *I. elegans* (Rebora et al., 2013b), double-Petri dishes assays were conducted. Two Petri dishes (14 cm diameter) were filled with 220 ml of DW and RW respectively, to deliver different volatile cues. Inside each of them, a smaller Petri dish (9 cm diameter), filled with 20 ml of DW (Fig. 1) and containing a disk of filter paper, was placed to provide two identical substrates to the ovipositor. One wooden stick was placed over each Petri dish as perch. The two-double Petri dishes were placed inside the behavioral insectary for the bioassays following the same procedure explained above. The number of replicates was 29.

2.3. Electroantennography

For EAG recordings, just mated females were employed. The EAGs were carried out to evaluate female antennal responses towards DW, RW, TW and TW+P. On the basis of previous recordings (Piersanti et al., 2014b), ammonia (28% in H₂O) (Sigma-Aldrich, St. Louis, MO, U.S.A.) was chosen as reference

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