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ORIGINAL ARTICLE

Initial preference for plant species and state during oviposition site selection by an odonate

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Abstract

Endophytic egg-laying odonates use an ovipositor to insert their eggs inside plant tissues. Before egg deposition, oviposition site selection consists of two crucial steps: (i) the initial choice, typically decided in species that oviposit in tandem within vertical substrates by the male when landing and then by the female by staying on the substrate or flying to another; and (ii) the insertion site choice, made by the female who uses her ovipositor to palpate the substrate. Some odonates prefer to deposit their eggs within specific plant species. Some are able to discriminate between living and dead substrates during the initial choice. However, the extent to which odonates discriminate among distinct plant species during the initial choice is unknown. We studied the initial site preference in *Lestes macrostigma* (Odonata: Lestidae) to determine whether the males and/or females show a distinct preference among five types of shoots when landing on or when palpating the substrate, respectively. Male *L. macrostigma* preferred to land on *Bolboschoenus maritimus* and dead *Juncus* spp. When focusing on *J. maritimus*, females preferentially palpated the substrate when the male landed on dead shoots. We suggest that the male preference for these substrates is consistent with that of the female during insertion site choice but also during egg deposition. Such behavior should reduce the duration of oviposition, with benefits of reducing the predation risk and increasing available time for foraging. The advantage in preferring these substrates should be linked to a selection pressure acting on egg development and/or survival.

Key words: behavior, damselfly, endophytic egg-laying, *Lestes macrostigma*, substrate choice.

INTRODUCTION

Choosing the site where a batch of eggs is laid is an essential aspect of an insect's life history since it directly impacts fitness by determining the survival prospects of offspring. Odonates use different modes of oviposition: (i) endophytic oviposition, where eggs are inserted into plant tissues by a female who is on the substrate itself; (ii) epiphytic oviposition, where groups of eggs are attached to the plant surface while the female is settled or in flight; and (iii) exophytic oviposition, where a resting or flying female deposits single or groups of eggs either into water or within or on sediment (Corbet 2004: table A.2.5). For species with endophytic oviposition, the site selection process begins with the choice of landing site, the "initial preference", which is then followed by the choice of insertion site and finally egg deposition (Waage 1987; Martens 2001). Oviposition site choice is associated with fitness in odonates, for example by affecting egg clutch size and egg deposition rate (Laplante 1975; Grunert 1995; Martens 2001) or egg survival (Siva-Jothy *et al.* 1995; Reinhardt & Gerighausen 2001). Hence it is expected that odonate species with endophytic oviposition should show clear preferences during egg deposition and select some specific plant species or certain parts of plants within which they deposit their eggs (e.g. Sawchyn & Gillot 1974; Reinhardt & Gerighausen 2001; Purse & Thompson 2009). Furthermore, an odonate species, *Coenagrion caerulescens* (Fonscolombe, 1838), which prefers to lay

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eggs in dead plant substrates, can discriminate between living and dead plant material during the "initial preference" phase (Martens 2001). This early assessment of substrate is assumed to reduce the (time and energy) costs associated with searching for a suitable oviposition site. However, whether an odonate exhibits a preference for a specific plant species during the choice of landing site and the choice of insertion site has never been assessed so far.

Mating behavior in odonates is characterized by a male seizing the female, and then both individuals forming a tandem where the male inseminates the female. In most damselfly species (Odonata: Zygoptera), the male remains then in that position during the endophytic oviposition to ensure his paternity, a strategy called "contact guarding" (Corbet 2004). The male is therefore in a forward position and assumed to drive the direction of flight (Laplante 1975). In species that typically lay their eggs in vertical plant material, the male takes the initiative in perching and is the first to land on the substrate (McMillan & Arnold 2003; P. Lambret, unpubl. data, 2011; G. Rüppell, pers. comm., 2013); in such species, males should therefore determine the initial choice of landing site. After landing, the female uses her ovipositor to palpate the substrate, presumably to examine the substrate for the suitability for oviposition (e.g. Grunert 1995; Martens 2001; Matushkina & Lambret 2011), and then to deposit eggs into the plant tissues (Jödicke 1997; Matushkina & Gorb 2002). However, just after landing, the female can either decide to keep its abdomen straight and to fly to another substrate (V. Cannevelle & P. Lambret, unpubl. data, 2009, 2010). Therefore, the female also proceeds to an initial choice.

Using an odonate model of endophytic oviposition within vertical plant material, we aimed to determine whether: (i) the male makes an initial site preference for specific plant species and/or the plant state (i.e. living or dead) when landing; (ii) the female prefers certain plant species and/or their states during her initial substrate palpation; and (3) the female's preference (if any) corresponds with any initial preference shown by the male.

Examining the behavior underlying oviposition site preference can be readily achieved using the damselfly *Lestes macrostigma* (Eversmann, 1836) (Lestidae) as it uses different plant material for oviposition and its reproductive behavior and ecology have been increasingly studied in the Camargue, southern France (Lambret *et al.* 2009; Lambret & Stoquert 2011; Matushkina & Lambret 2011). This species has been designated as "threatened" within Europe (Kalkman *et al.* 2010). While *L. macrostigma* nominally extends across a large South Palearctic range from the Portuguese coast and the Mediterranean to Siberia and Central Asia, its distribution is very fragmented and the species occurs very locally within Europe (Dijkstra & Lewington 2006). Adults are typically observed during spring and early summer, with the specific flying season depending on location and climate (Jödicke 1997; Dijkstra & Lewington 2006). In the Camargue, emergence typically begins during the first two weeks of May and lasts 2–3 weeks; adults are on the wing until late June or early July (Lambret 2010; D. Cohez & P. Lambret, unpubl. data, 2009–2013). The pre-reproductive period (sexual maturation) lasts for 2 weeks (Lambret 2010). Embryos develop in the plant tissues until larvae hatch the next spring (Schiel 2013; P. Lambret, unpubl. data, 2012). The distinctly localized occurrence of this species is probably due to the stenoecy of its larvae, which develop in brackish waters (Robert 1958; Plattner 1967). *Lestes macrostigma* has been most often reported to lay eggs into *Bolboschoenus maritimus* (L.) Palla (Cyperaceae) (e.g. Stark 1980; Lambret *et al.* 2009; Schweighofer *et al.* 2010) but also lay eggs within other plants, including living shoots of *Carex stenophylla* Wahlenb. and *Schoenoplectus lacustris* (L.) Palla (Cyperaceae), living and dead shoots of *Juncus maritimus* Lam. and dead shoots of *J. acutus* L. (Juncaceae), dead shoots of *Phragmites australis* (Cav.) Steud. (Poaceae) and finally, dead branches of *Tamarix gallica* L. (Tamaricaceae) (Stark 1980; Martynov & Martynov 2007; Lambret *et al.* 2009; Lambret 2011; P. Lambret, unpubl. data, 2010; A. Martynov pers. comm., 2014). As yet, no one has assessed whether there is active preference for certain plant species, or their condition, during oviposition in *L. macrostigma*.

MATERIALS AND METHODS

Study site

The study took place in the National Natural Reserve of the Marais du Vigueirat, a protected area of the Camargue (southern France), at the Baisse des Marcels (43°29′27″N, 04°48′22″E), a brackish temporary swamp of which habitat and management have been described in detail (Lambret & Stoquert 2011).

Vegetation description

During oviposition, *L. macrostigma* lands at the bottom of the vegetation (Matushkina & Lambret 2011) and thus, in *Juncus* species, either on stems (which bear an inflorescence) or on leaves (which do not). At the bottom, stems and leaves are similar. Hereafter, we use the term "shoots" to define both stems and leaves in *Juncus* species. In the other plant species, shoots are all

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stems. As far as shoots are approximately of the same thickness in all species, we assume that the relative number of each type of shoot was a good assessment of their relative abundance.

In order to compare the relative abundance of plant species and state onto which *L. macrostigma* lands to those available in the field, we gathered data on vegetation on 24 and 27 June 2013. A 0.5×0.5 m square was set at 25 plots, which were randomly selected using the software Quantum GIS (http://www.qgis.org/). Within each plot, we counted the total number of shoots of each species: *B. maritimus*, *J. maritimus*, *J. subulatus* and *P. australis*. We also recorded the state of each of these shoots. Although the base of the living shoots of *B. maritimus* were often partially surrounded by a dead leaf, such shoots were sorted as living. The distinction between dead shoots of *J. maritimus* and *J. subulatus* was impossible because these shoots did not differ in shape, diameter or color; corresponding data were thus recorded as "dead shoots of *Juncus* spp.". Data from dead and living shoots of *P. australis* were pooled because living shoots often bore dead leaves, which made impossible the distinction between both types during the oviposition behavior study (see below).

Oviposition behavior, timing and weather conditions

Data regarding oviposition were recorded between 27 June and 2 July 2013. Initial preference was studied between about 1100 and 1400 h (Lambret & Stoquert 2011). Because meteorological conditions affect Odonata activity, we did not record data during days with rain and/or with cloud coverage more than 25% and/or wind greater than 3 Beaufort (5.5 m/s) (see Lambret & Stoquert 2011).

The study site was randomly crossed by walking in order to search for ovipositing tandems. Once we found a tandem, we disturbed it and it flew to another shoot. We waited until it flew and landed on a subsequent shoot in order to oviposit again, a period during which we assume that the tandem recovered from disturbance. We considered this first landing after disturbance as the initial choice. From this step, and during each landing until the female bent its abdomen in for the first time in order to palpate the plant substrate, we recorded the plant species onto which the tandem had landed and the state of the shoot for *Juncus* spp. We also recorded the state of the place where the female was setting when the tandem landed on *B. maritimus* or *P. australis* and when the female landed on a different shoot than the male.

To avoid the bias associated with observing the same animal multiple times, i.e. pseudo-replication (Hurlbert 1984), the male and the female were caught at the end of each monitoring and marked on one of the forewings using a permanent marker (Stabilo OHPen S; Heroldsberg, Germany).

Data analysis

To define the available vegetation, generalized linear mixed models (GLMM) were used to estimate the frequency and their standard error of each type of shoot in the square plots. The model variables were the types of shoot that were converted in binomial variables (0 or 1 for each type of shoot), which were separately analyzed with the GLMM. GLMM were preferred to generalized linear models because several shoots were described in the same plot; they then could not be considered as independent measurements. The GLMM thus allows including in the model a "plot" random effect that aims at dealing with this non-independence.

Initial landing choice was tested by comparing the relative abundance of available shoots (obtained from the vegetation description study) to the relative abundance of shoots chosen by the male (obtained from the oviposition behavior study). A contingency table was made with the observed number of shoots of each sort with the two relative abundances described above as the main entrances, and a Chi-square test was used.

Female initial preference (i.e. probability to palpate the shoot), if any, was also modeled using a GLMM. Since the number of shoots of certain types was too small to include these types in the GLMM, this analysis was conducted on *J. maritimus* living and dead shoots only, assuming that among dead shoots, the rate of *J. subulatus* was negligible (see the vegetation composition results below). The response variable was the palpating behavior of the female (1 or 0 depending on whether the female palpated the substrate or not). Not every female palpated after the first landing of the tandem. Thus, since several landings could be recorded for a same tandem until the female palpated the shoot, we included in the model a "tandem" random effect to deal with the non-independence of the measurements of the same tandem. The covariates included in the models were the state of the shoot (living or dead) and the number of landings. These covariates were tested alone, in addition and in interaction. The best model was selected using the Akaike Information Criterion (AIC) and the relative performance of the models was assessed by the AIC weight (Burnham & Anderson 2002).

All analyses were conducted using R v2.13 (R Core Team 2013), especially with the lme4 package for the GLMM (Bates *et al.* 2014).

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RESULTS

Vegetation composition

The most abundant shoots in the studied area were living *J. maritimus* and dead *Juncus* spp. (Fig. 1). The relative abundance of the other shoots was much lower. We compared the frequency of each type of shoot estimated by a classic percentage with those estimated by the GLMM, which deals with the pseudo-replication effect of the square plots. While these classic and GLMM frequencies were almost similar for *B. maritimus*, dead shoots of *Juncus* spp. and living shoots of *J. maritimus* (2.1% *vs* 1.4%, 33% *vs* 32.6%, 56.5% *vs* 53%, respectively), the frequency of living shoots of *J. subulatus* and of *P. australis* were much lower when estimated with the GLMM than with the classic percentage (6.9% *vs* 0.5%, 1.5% *vs* 0.6%). If we assume that in *J. subulatus* dead shoots are distributed across the study area as living shoots are, this suggests that *B. maritimus* and *J. maritimus* were homogeneously distributed across the study area (no pseudo-replication effect of studied plots) while *J. subulatus* and *P. australis* were more spatially aggregated (i.e. relatively abundant but in some plots only). We assumed that the rate of dead shoots of *J. subulatus* compared to dead shoots of *J. maritimus* was similar to that found for living shoots. Since the frequency of living shoots of *J. subulatus* was almost negligible compared to that of *J. maritimus* we considered that the dead shoots of *Juncus* spp. were all *J. maritimus* in the subsequent analysis.

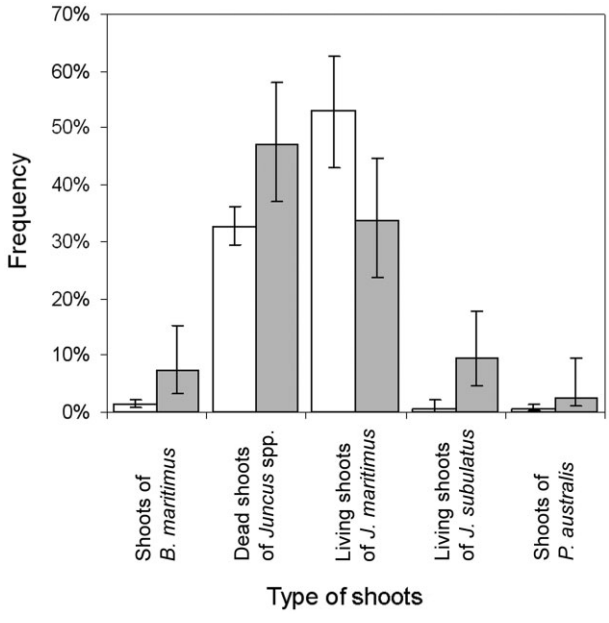


Figure 1 Frequencies of plant shoots which are present (white bars) and on which tandems of *Lestes macrostigma* (driven by the male) initially choose to land during oviposition (grey bars). Estimates are given with 95% CI.

Landing site choice

In total 84 initial landings were observed. Males showed a significant difference in landing site choice regarding the type of shoots (Chi-squared test: $\chi^2 = 23.69$, d.f. = 4, $P < 0.001$; Fig. 1). Contributions to the Chi-squared value indicated that this difference was first due to the preference for *B. maritimus* (42.24% of the χ^2 value) and second to the disfavor for living shoots of *J. maritimus* (31.85%); and third to the preference for dead shoots of *J. maritimus* (20.41%). Males also seemed to have a preference for living shoots of *J. subulatus*; however this species contributed poorly to the χ^2 value (3.80%). We assume that this can be due to an artifact in our behavior study: we might find more tandems in a part of the study area where *J. subulatus* was more abundant (spatial aggregation; see the vegetation composition results above).

First ovipositor contact

In all, 55 females landing in tandem on 91 shoots were observed. Landings on *P. australis* and living *J. subulatus* shoots were too rare to be included in the GLMM data set ($n = 2$ and $n = 7$, respectively). A total of nine landings on *B. maritimus* were recorded; females always palpated when they landed on a dead place ($n = 3$) but never bent the abdomen when they landed on living plant material ($n = 6$).

The selected best GLMM model for *J. maritimus* based on the AIC value included an additive effect of shoot state and the number of landings on the palpation probability (Table 1). It has an AIC weight of 54.9%; this model explains our data almost one and a half times better than the second best model. The estimates of the best GLMM model showed that the probability that the female palpated the substrate was higher for dead shoots

Table 1 Model comparison of the substrate palpation probability in *Juncus maritimus* by *Lestes macrostigma* female regarding the effect of the state of the shoot, of the number of landings and of their interaction

Model	AIC	Δ AIC	AIC weight
Landing + state	102.89	0	0.549
Landing + state + landing × state	103.69	0.80	0.368
Landing	106.74	3.85	0.080
State	113.88	10.99	0.002
Constant	115.27	12.38	0.001

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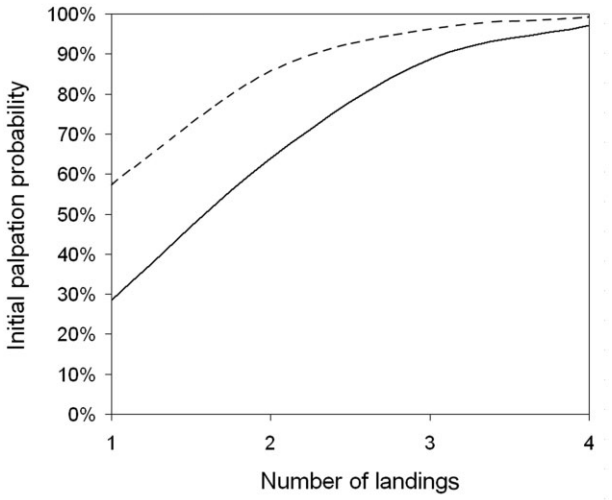


Figure 2 GLMM predicted probability that *Lestes macrostigma* females palpate the substrate during their initial choice regarding the number of landings during oviposition. Full and dotted lines correspond to living and dead shoots of *Juncus maritimus*, respectively.

than for living shoots (Fig. 2) and that this probability increased with the number of landings for both dead and living shoots. Female palpations occurred generally after the third landing.

DISCUSSION

Our results show that *L. macrostigma* males, who are driving the tandem flight during oviposition, landed preferentially on one plant species: *B. maritimus*. Assuming that the frequency of *J. subulatus* among dead shoots was negligible compared to *J. maritimus*, we highlight that they also landed preferentially on dead shoots of *J. maritimus* and disfavored living shoots of that plant species. We have not been able to assess whether females have a preference for any plant species during initial palpation (i.e. substrate examination). On the other hand, our results highlight their preference for dead material in *J. maritimus* and suggest the same trend in *B. maritimus*. Thus, the female's strategy could be to wait until the male lands on a dead shoot. However, we also highlight that the substrate examination by females is linked to the number of landings: our model shows that the probability of palpation increases with the number of landings also in living shoots of *J. maritimus*. In other words, at least at the fourth landing, the female bent its abdomen in order to palpate the substrate whatever the species and the state of the shoot. This decrease of preference by the female could reflect that preferred oviposition substrate is less available (e.g. Thompson & Pellmyr 1991). However, since males also prefer dead shoots of *J. maritimus* for initial landing, this situation happens very rarely (2.90% of the time).

Successive landings of the tandem and substrate palpation by the female represent a major part of the total time spent during oviposition (Bick & Bick 1961, 1970; Martens 1992; Grunert 1995; McMillan & Arnold 2003). Minimizing the duration of an oviposition bout should increase the time available for foraging and reduce the risk of detection by predators (Martens 2001). Indeed, after the daily oviposition bout, both males and females in *L. macrostigma* remain perched in the shade where they forage (Lambret & Stoquert 2011). Thus, from an evolutionary point of view, assuming first that both males and females benefit from a plant species and state preference and, second, that the female is the one of the tandem that finally selects the site where they lay their eggs, we expect that the male's preference for dead shoots of *J. maritimus* during initial choice has been selected by the female's preference for the same type of material during substrate palpation and egg-laying. Similarly, the initial preference of the male for *B. maritimus* could reveal that the female also prefers this plant species for oviposition, especially if the place where the female is settled is dead.

If ovipositing tandems select particular material, it implies a selection pressure, especially on egg development and survival (Sawchyn & Gillot 1974; Siva-Jothy *et al.* 1995). This pressure should transpose to the fitness of the egg-laying females, making the substrate preference consistent all along the *L. macrostigma* reproductive life cycle. Hence, we hypothesize that both egg deposition rate, considering the advantage of adults to minimize oviposition bouts, and hatching success are higher in *B. maritimus* and in dead shoots of *J. maritimus* than in other substrates (Martens 1992, 2001; Grunert 1995; Siva-Jothy *et al.* 1995). Studies are in progress to test these hypotheses.

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