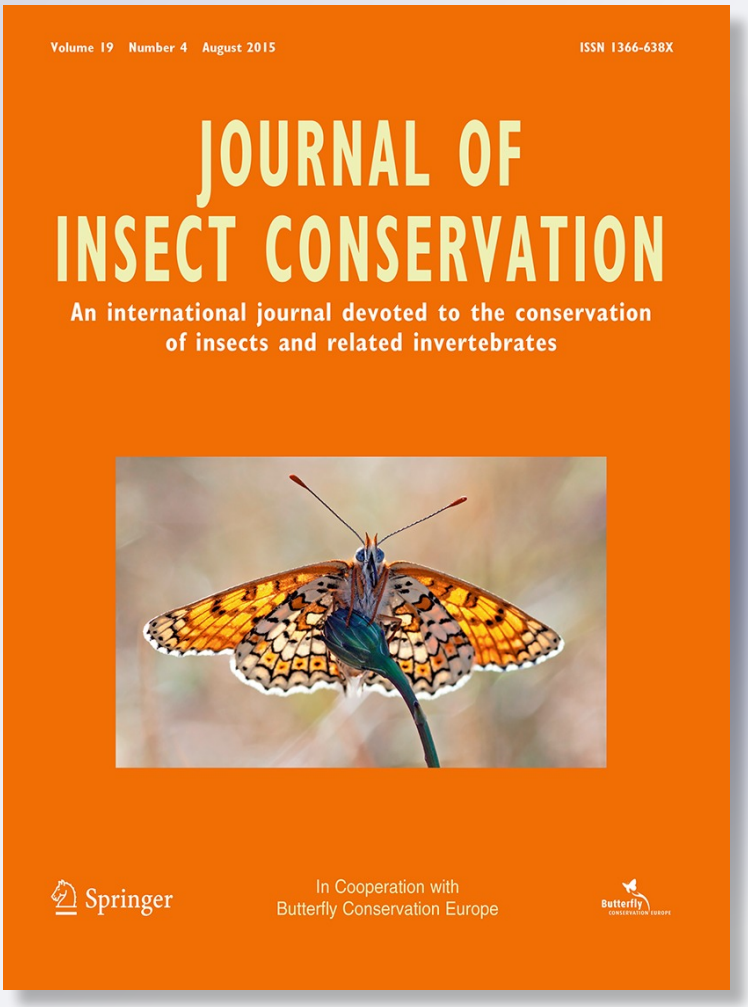
Plant preference during oviposition in the endangered dragonfly Lestes macrostigma *(Odonata: Zygoptera) and consequences for its conservation*

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Journal of Insect Conservation
An international journal devoted to the conservation of insects and related invertebrates

ISSN 1366-638X
Volume 19
Number 4

J Insect Conserv (2015) 19:741-752
DOI 10.1007/s10841-015-9796-z



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ORIGINAL PAPER

Plant preference during oviposition in the endangered dragonfly *Lestes macrostigma* (Odonata: Zygoptera) and consequences for its conservation

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Received: 12 February 2015 / Accepted: 24 July 2015 / Published online: 23 August 2015
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Abstract Biotic and abiotic features impact the breeding success of animals and thereby induce selection pressures for habitat selection. Little is known about the plant selection by predatory insects which lay their eggs within plants. In previous work, we have highlighted that during oviposition males of *Lestes macrostigma*—an endangered dragonfly species—prefer to land on *Bolboschoenus maritimus* and dead shoots of *Juncus maritimus* but disfavour living shoots in that species, and that females seem to prefer dead material during substrate examination. In this study we assessed behavioural preference in females during substrate examination, substrates suitability for oviposition, the effort females had to make to lay their eggs and their resulting oviposition rate. We show *L. macrostigma* has a preference for *B. maritimus* and, albeit to a lesser extent, for dead substrates. No clear trend appeared regarding substrate suitability. Females had to make a greater effort to lay an egg within living shoots of *J. maritimus*. By contrast, this effort was less in *B. maritimus* and dead shoots of *J. maritimus* and the oviposition rates were higher for these two types of substrate. We hypothesize that these preferences are relevant in the selection of oviposition substrates which are more likely to be flooded earlier by rainfall, reducing risk of egg desiccation and increasing hatching success. With regard to conservation, *B. maritimus* and *J. maritimus* should be encouraged by wildlife managers especially in habitat restoration programs which aim to increase the number of suitable breeding sites for the species.

Keywords Fitness · Endophytic oviposition · Oviposition site choice · Oviposition rate · Oviposition substrate · Substrate examination

Introduction

The reproductive success of animals strongly depends on several biotic and abiotic breeding site features (Clutton-Brock 1988). These features can have, for instance, an impact on egg mortality, hatching success, larval development or survival, and thus have strong consequences in terms of fitness. Hence, breeding habitat selection strategies should have been selected for in many taxa. Organisms, especially those which do not provide direct parental care to their progeny, show oviposition site selection with different strategies regarding food accessibility for larvae, desiccation risk and thermal stress, intraspecific competition, predation risk, etc. (e.g. Anura: Rudolf and Rödel 2005; Chelonia: Restrepo et al. 2006; Diptera: Kershenbaum et al. 2012; Gastropoda: Kano and Fukumori 2010; Lepidoptera: Thompson and Pellmyr 1991; Odonata: Buskirk and Sherman 1985).

In dragonflies (Odonata), habitat and oviposition site selection from vegetation is an important feature which can have dramatic consequence on their conservation (Thompson et al. 2003, Wildermuth 2008). Many dragonflies (Zygoptera, Anisozygoptera, Anisoptera: Aeshnidae)

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are endophytic egg-layers which use a cutting ovipositor to deposit their eggs within the plant tissues (Corbet 2004). Unlike in phytophageous insects, such as Lepidoptera but also Coleoptera and Diptera (see Thompson and Pellmyr 1991 for a review), little attention has been paid in predatory dragonflies to their relationship with plant species during oviposition site selection, which clearly does not affect the food regime of larvae (Martens 1992; Grunert 1995; Guillermo-Ferreira and Del-Claro 2011). Oviposition site selection in endophytic egg-laying dragonflies can be divided into several steps: after the initial choice of the oviposition substrate, the process goes on with the choice of ovipositor insertion site within this substrate and egg deposition per se (Martens 2001; Lambret et al. 2015). There is evidence that many dragonfly species show clear preferences in selecting plant species or parts of plants for oviposition (e.g. Matushkina and Gorb 2004). The substrate state (i.e. whether it is green/living or dry/dead) is also subject to selection by females (Martens 2001; McMillan and Arnold 2004).

Lestes macrostigma (Eversmann, 1836) is a noteworthy damselfly species in that it is restricted to brackish waters, has a very fragmented distribution area and a strong conservation status from European to regional scales (Lambret et al. 2009, 2015). Increasing the knowledge of *L. macrostigma* habitat requirements is of primary consequence for the management of its breeding sites (Grunert 1995; Dupont 2010). An important facet of the association of *L. macrostigma* with brackish waters is the regular presence of *Bolboschoenus maritimus* (L.) Palla a plant species into which oviposition is most often reported (see Table 1). In previous work we showed that *L. macrostigma* has a preference for shoots of *B. maritimus*, which are living although often partially surrounded by a dead leaf, from the first step of oviposition site selection, namely the initial choice. During this initial step, the male chooses the landing site and the female chooses to examine the plant substrate or to fly to another (Lambret et al. 2015). Other plant species were also recorded as oviposition substrates, such as *Juncus maritimus* Lam., of which *L. macrostigma* also prefers dead shoots over living shoots (Lambret et al. 2015).

Here, we expected the preference for specific substrates to be consistent during the whole life cycle because this preference should indicate a selection pressure on egg development and survival which should transpose to the individual fitness level (Sawchyn and Gillot 1974; Siva-Jothy et al. 1995). The aim of this study was first to define whether the plant preferences after the initial choice of landing site, namely ovipositor insertion site selection and egg-deposition, are in accordance with the initial choice. Second, it was to define how this preference may affect individual fitness. Thus, for different combinations of plant species and state (hereafter: types of shoot), we assessed in females: (a) how often they tried to oviposit, (b) how often they found a suitable place to lay one egg, (c) the effort they had to make to lay one egg (i.e. time and number of movements of both the ovipositor valves and the abdomen; see Matushkina and Lambret 2011) and (d) their resulting oviposition rate. With regards to conservation, and considering both the initial preference for *B. maritimus* over other types of shoots and the favouring of dead over living material, we focused our attention on the results in *B. maritimus* compared to other types of shoot, but also on living shoots of *J. maritimus* compared to other types of dead substrate.

Methods

Study sites, timing and weather conditions

The study took place in the National Natural Reserve of the Marais du Vigueirat (Fig. 1), a protected area of the Camargue (Southern France), at five different sites: the Baisse des Marcels (43°29′27″N/04°48′22″E), the Clos des Montures (43°30′04″N/04°47′28″E), the Trou du Héron (43°30′51″N/04°47′01″E), the Roubine du Héron (43°30′49″N/04°47′01″E) and the Rizières de l'Étourneau (43°30′52″N/04°46′30″E). These sites are hereafter named BdM, CdM, TdH, RdH and RizEt, respectively. The BdM is a brackish temporary swamp of which a detailed description of habitat and management is published elsewhere (Matushkina and Lambret 2011; Lambret and Stoquert 2011): its vegetation mainly consists of *B. maritimus* and *J. maritimus* but also low densities of *J. subulatus* Forssk and *Phragmites australis* (Cav.) Steud. The habitat of the CdM and the RizEt resembles that of the BdM but *J. maritimus* is far less abundant in the RizEt. By contrast, the TdH and the RdH are two brackish temporary ponds which are filled only by rainfall. The vegetation of their surroundings is more halophilous than that of the other sites and available host-plants consist of *P. australis*, *J. acutus* L., scattered *J. maritimus* and, in some years, small numbers of *B. maritimus*.

Data were gathered between May 14th and June 20th, 2011. Oviposition behaviour was studied mainly when it reached its maximal intensity between ca 10:30 and 13:00, solar time (Lambret and Stoquert 2011). One female (out of 38) was, however, studied at 14:00 solar time.

Because meteorological conditions affect Odonata activity (Joseph and Lahiri 1989; Pilon et al. 1995; Robinson and Frye 1986) days with rain and/or with cloud coverage over 25 % were avoided. Air temperature and wind speed were recorded every 15 min by a Davis Vantage Pro meteorological station which was set in the

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Table 1 Plant species used by *L. macrostigma* for oviposition across its breeding range according to the literature

Country	Region (site)	References	*Bolboschoenus* (*Scirpus*) *maritimus*	*Carex stenophylla*	*Juncus acutus*	*Juncus maritimus*	*Juncus* sp.	*Phragmites australis*	*Schoenoplectus* (=*Scirpus*) *lacustris*	*Tamarix gallica*
Austria	Burgenland (Neusiedler See)	Stark (1980)	Oviposition						Oviposition	
	Niederösterreich (Sankt Pölten-Land)	Schweighofer et al. (2010)	Oviposition							
Bulgaria		Marinov (1997, 2005) and com. pers.	Oviposition							
France	Charente Maritime	e.g. Jourde (2009)	Oviposition							
	Lanquedoc-Roussillon (around Montpellier)	Cassagne-Mejean (1965)					Oviposition			
	Loire Atlantique	Meurgey (2006)	Oviposition							
	Camargue	Lambret et al. (2015)	Oviposition		Oviposition	Oviposition		Oviposition		Oviposition
	Vendée	Machet (1990)	Oviposition							
Greece	Lesbos Island	T Termaat pers. com.	Habitat							
Hungary	Great Hungarian plain (Kecskemét, Szeged)	Ujhelyi (1959); AF Kalmár pers. com	Habitat						Habitat	
Italy	Sardinia	C Vanappelghem pers. com.					Habitat			
Romania	Transylvania (Ocna Sibiului)	Plattner (1967)	Habitat						Habitat	
Russia	Siberia (Omsk)	Kosterin (1996), com. pers.	Habitat							
Spain	Doñana	Cano-Villegas and Conesa-García (2009), Ferreras-Romero et al. (2005)	Oviposition							
Ukraine	Donetsk	Martynov and Martynov (2007), A Martynov pers. com.		Oviposition						

When breeding evidence was reported but with no information regarding oviposition, the plant species is quoted as being present in the habitat

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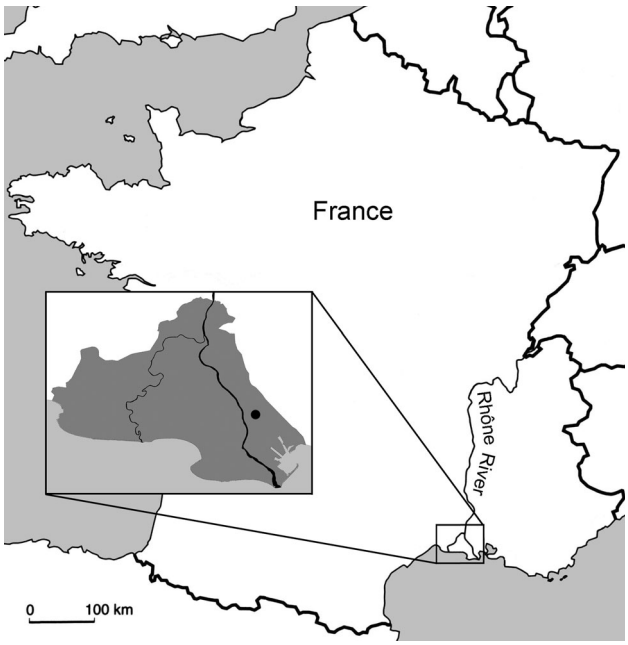


Fig. 1 Location of the National Natural Reserve of the Marais du Vigueirat (*black dot*) within the Camargue, i.e. the Rhône River's delta (*dark grey*)

protected area: over the sampling days, between 09:30 and 13:00 (solar time), the mean air temperature was 26.2 °C (SE = 0.18; min = 18.8; max = 32.4; n = 240) and the median of wind speed was 3.1 m/s (25 % percentile = 1.8; 75 % percentile = 4; min = 0.4; max = 9.8; n = 240).

Oviposition behaviour

Oviposition behaviour in *L. macrostigma* has been already partly described (Matushkina and Lambret 2011; Lambret et al. 2015). We hereafter provide further details which are useful for a general understanding of assessments. After copulation, the female usually remains with its mate and flies from one shoot to another searching for a suitable oviposition substrate. Most of the time, once the tandem has landed on a shoot, the female bends its abdomen in so as to lean the ovipositor against the plant surface and palpates the material by one or several touches. This is believed to be an examining phase to find a suitable place to insert the valves of its ovipositor inside the plant tissue (e.g. Grunert 1995; Lutz and Pittman 1968; Martens 2001; Matushkina and Lambret 2011). After egg deposition, the female removes its cutting valves from the hole and walks ca 2 mm back along the shoot and starts to deposit a new egg and so on, producing an egg clutch (see definition below) after which the female starts to search for another suitable oviposition site. For such, the female sometimes walks a few mm laterally or several cm onward along the shoot. Otherwise, the pair flies to another shoot after the female has failed several times to deposit an egg. The pair also flies to another shoot after an intermediate landing (see below).

Definitions and measured variables

- Intermediate landing: alighting on a shoot during which time the female does not bend its abdomen until take off.
- Examination and/or insertion site (hereafter EIS): place where the female palpates the substrate. An EIS can turn into a failed egg deposition (palpation only or incomplete ovipositor insertion) or into a successful egg deposition. EIS changes as soon as the female walks so that a shoot can bear several EIS.
- Insertion time (hereafter *T*): time from the protrusion of the ovipositor valves into the plant tissue until its removal, disregarding if the egg deposition failed or succeeded (see *Assessments* for measurement details). Females sometimes remained in a fixed position after the ovipositor had entirely protruded into the shoot, although the duration required for protrusion per se in such a case was comparable to others during actual egg deposition. Egg flow may stop during oviposition (Martens 1992) which could explain the few extreme *T* values we recorded. Although we give these extremely long durations in the results (see *Egg-laying speed and abdominal swings*), we did not include these data in the subsequent analysis.
  We made four close-up field videos of females during protrusion: these revealed that the ovipositor valves were moving continuously during *T*. (Lambret, unpublished results, 2011). We therefore assume that *T* was a good indicator of the effort provided by the female to lay one-egg regarding ovipositor valves moving.
- Number of swing(s) (hereafter *Ns*): number of abdominal swings from side to side during protrusion (Matushkina and Lambret 2011).
- Duration of stay (hereafter *D*): total duration from landing on the shoot to take off (see *Assessments* for measurement details).
- Egg clutch: a series of eggs which are deposited in a straight line backward along the substrate (Matushkina and Lambret 2011). A new egg clutch is differentiated as soon as the female walks in another direction more than ca 2 mm without palpation.
- Number of eggs (hereafter *No*): total number of eggs deposited by a monitored female in the same shoot.

Assessments

Oviposition site selection was assessed by direct observation of egg-laying females. We described their behaviours

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on a digital recorder Sony® ICD-B500 and measured the duration of each of them from the digital records using Syntrillium® Cool Edit Pro 2.0 software.

Females were found by randomly walking and searching among the vegetation where they usually perch. If our approach had disturbed the animal, we waited two minutes before starting the observation. Each female was then monitored with close-focus binoculars Zeiss® Victory T*FL 10 × 42 during the ca 30 subsequent minutes. Monitoring of females lasted 34.58 ± 7.33 min (mean ± SD, n = 38); the duration varied due to e.g. a separation of the tandem or a long egg clutch (see below). To avoid the bias associated with observing the same animal multiple times, i.e. pseudo-replication (Hurlbert 1984), females were caught at the end of the monitoring and marked with an alfa-numeric code on one of the forewings using a permanent marker Stabilo® OHPen S; however, one female was prematurely lost and could not be marked. At TdH and RdH, female marking was made one day before the monitoring, because the vegetation was very dense and *L. macrostigma* so numerous that they were more likely to be lost during the observation than at other sites.

Each time the female landed on a shoot, we identified the shoot to the species and its state, i.e. living or dead. When a shoot was decaying, but still actually green and yellow, it was recorded as living; this was especially the case in *B. maritimus* for which all shoots were living. We recorded whether landing was an intermediate landing or followed by substrate palpation. In the latter case, we counted the number of EIS and for each of them the number of palpation touches and whether the egg deposition was a failure or a success. Various authors have reported as difficult the assessment of whether an egg is deposited or not (e.g. McMillan and Arnold 2004; Martens 1992). Martens (1992, 2001) also indicates that eggs are deposited after longer incisions. It was clear in our study, as we always observed females from the side to see how deep each protrusion was, that an egg was actually deposited only if the ovipositor was protruded entirely, whatever the subsequent length of stay in this position. We checked this field observation by dissecting three shoots after observation of oviposition behaviour and checking actual egg deposition (Lambret, unpublished results, 2011). For each egg clutch, we calculated the failure rate i.e. the number of protrusions which resulted into failure to deposit an egg divided by the total number of protrusions. We finally recorded *T* for the total number of EIS for each egg clutch and *D*.

Based on these previous assessments, we calculated for each type of shoot the "resulting" oviposition rate (OR). We used the mean number of eggs per shoot (*No*), *D* (see above), the mean duration of intermediate landings (*D*il), the probability that a shoot was not palpated (*P*il). Given these parameters OR was obtained from the formula:

$$\mathrm{OR} = \frac{No}{D + D\mathrm{il}\ P\mathrm{il}\ /(1 - P\mathrm{il})}$$

Statistical analysis

For all variables but OR, differences between types of shoot were tested by using Generalized Linear Mixed Models. Mixed models were used to take into account the pseudo-replication induced by the fact that some behaviours are quantified several times for the same females. A "female" random effect was thus included in all models. Depending on the tested variable, we used binomial error (for all variables that were success/failure) or Gaussian error (for all counts or duration variables that were log-transformed in order to normalise the residuals of the models). Overall significances were tested by analysis of deviance. Contrast analyses were performed in order to assess whether the differences between pairs of shoots were significant or not for the target modelled variables. More specifically we systematically tested the differences between *B. maritimus* and each of the other types of shoot, and subsequently between living shoots of *J. maritimus* and the other types of dead shoots (i.e. these of *J. maritimus*, *J. acutus* and *P. australis*). Although running any statistical test to detect significant difference(s) between ORs was impossible because it results from a calculation of several estimated parameters, we obtained their 95 % confidence intervals by a bootstrap procedure. We then looked for overlapping between each other assuming that a difference between two ORs was significant when the respective 95 % confidence intervals did not overlap. The bootstrap procedure consisted here of randomly sampling the raw data of each landing on a shoot with replacement as many landings as observed, then summing the number of deposited eggs and dividing it by the sum of the *D*. This procedure was performed 10,000 times for each type of shoot. It allowed us to calculate the expected distribution of the OR and their 2.5 and 97.5 % quantiles were then used as confidence intervals.

Unless otherwise stated, results are given as mean with their lower and upper 95 % confidence intervals between square brackets. All analyses were performed with R 2.13 (R Core Team 2013), more specifically with library lme4 (Bates et al. 2014).

Study sites differed in their composition in types of shoot. Therefore we did not consider the effect of study sites for the analysis as we assessed that it was overlapped by the effect of types of shoot.

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Results

Substrate examination

During substrate examination females had a preference for living *B. maritimus* and dead substrates:

They bent their abdomen more or less frequently with respect to type of shoot (GLMM with binomial error, $X^2_8 = 146.68$, $P < 0.001$; Fig. 2). Abdomen bending on *B. maritimus* shoots was significantly more frequent [76.33 % (68.45–82.73)] than on dead and living shoots of *J. maritimus* [respectively: 56.11 % (48.08–63.83), 38.43 % (31.86–45.45), Table 2(a)], living shoots of *P. australis* [63.49 % (54.81–71.38), $z = -2.259$, $df = 1$, $P = 0.024$], living shoots of *J. subulatus* [45.63 % (30.96–61.10), $z = -3.567$, $df = 1$, $P < 0.001$] and leaves [10.83 % (5.66–19.73), $z = -8.028$, $df = 1$, $P < 0.001$]. In contrast, abdomen bending frequency on *B. maritimus* shoots was not significantly different than on dead shoots of *J. acutus* and of *P. australis* [respectively: 80.35 % (70.92–87.28), 68.46 %, Table 2(a)] and on shoots of *T. gallica* [67.95 % (48.23–82.84), $z = -0.915$, $df = 1$, $P = 0.360$]. Abdomen bending on living shoots of *J. maritimus* was significantly less frequent than on dead shoots of *J. maritimus*, *J. acutus* and *P. australis* [Table 3(a)] and than on living shoots of *P. australis* and shoots of *T. gallica* (respectively: $z = 4.749$, $df = 1$, $P < 0.001$; $z = 2.872$, $df = 1$, $P = 0.004$); by contrast it was not significantly different than on living shoots of *J. subulatus* ($z = 0.849$, $df = 1$, $P = 0.396$) and was significantly more frequent than on leaves ($z = -4.188$, $df = 1$, $P < 0.001$).

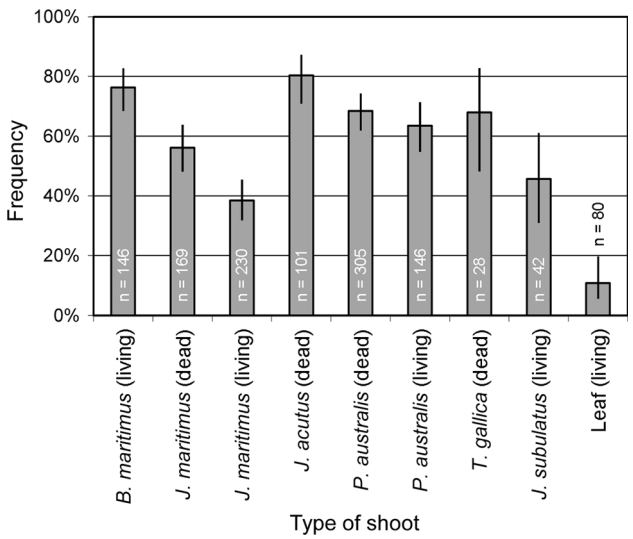


Fig. 2 Mean and 95 % confidence interval of frequency of abdominal bending by *L. macrostigma* females (substrate examination) by type of substrate

Considering shoots into which females did not lay any egg, albeit belonging to a type of shoot into which oviposition was possible (see below), the duration of stay of females significantly differed regarding types of shoot (GLMM with Gaussian error after log-transformation, $X^2_4 = 22.15$, $P < 0.001$; Fig. 3a). They stayed significantly longer on *B. maritimus* shoots [mean = 13.69 s (10.89–17.21)] than on dead and living shoots of *J. maritimus* [respectively: mean = 8.29 s (6.76–10.17), mean = 9.91 s (8.23–11.93), Table 2(a)]. They stayed significantly less time on living shoots of *J. maritimus* than on dead shoots of *J. acutus* and *P. australis* and longer on living than on dead shoots of *J. maritimus* although with low significance [Table 3(a)]. When we focused only on shoots which had been palpated but which were not appropriate for egg-laying, the duration of stay of females also significantly differed regarding the type of shoot (GLMM with Gaussian error after log-transformation, $X^2_4 = 19.91$, $P < 0.001$; Fig. 3b). They stayed significantly longer on *B. maritimus* shoots [mean = 43.75 s (32.97–58.06)] than on dead and living shoots of *J. maritimus* and dead shoots of *P. australis* [respectively: mean = 23.37 s (17.46–31.27), mean = 25.93 s (19.13–35.15), mean = 18.66 s (14.26–24.42), Table 2(a)] and longer than on dead shoots of *J. acutus*, albeit with low significance [mean = 29.34 s [20.48–42.02], Table 2(a)]. There was no significant difference in this duration of stay between living shoots of *J. maritimus* and dead shoots of *J. maritimus*, *J. acutus* and *P. australis* [Table 3(a)]. By contrast, the number of palpations per EIS was similar whatever the type of shoot (GLMM with Gaussian error after log-transformation, $X^2_4 = 3.73$, $P = 0.44$): *B. maritimus* mean = 3.28 times (2.23–4.66), dead shoots of *J. acutus* mean = 4.99 times (68.45–82.73), dead shoots of *J. maritimus* mean = 3.40 times (2.54–4.48), living shoots of *J. maritimus* mean = 3.93 times (2.87–5.28)and dead shoots of *P. australis* mean = 4.24 times (3.27–5.42).

Substrate suitability

The suitability of *B. maritimus* for oviposition was contrasted:

Females never oviposited into *J. subulatus*, *T. gallica*, living shoots of *P. australis* and leaves of any species. Focusing on species into which oviposition was possible – namely *B. maritimus*, living and dead shoots of *J. maritimus*, dead shoots of *J. acutus* and of *P. australis*– they had a preference for *B. maritimus* shoots: the rate of shoots into which at least one egg had been laid significantly differed regarding type of shoot (GLMM with Binomial error, $X^2_4 = 35.13$, $P < 0.001$, Fig. 4a) and the highest rate was observed for *B. maritimus* [30.46 % (21.24–41.58)].

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Table 2 Contrast analyses between *B. maritimus* and the other types of shoot (i.e. oviposition substrate) for the oviposition parameters in *L. macrostigma* which were significantly different regarding all types of shoot

		B. maritimus	Dead *J. maritimus*	Living *J. maritimus*	Dead *J. acutus*	Dead *P. australis*	Corresponding figure
(a) Substrate examination	Abdomen bending	1	$z = -3.603$ $P < 0.001$	$z = -6.667$ $P < 0.001$	$z = 0.715$ $P = 0.474$	$z = -1.575$ $P = 0.115$	2
	Duration of stay #1	1	$t = -3.736$ $P < 0.001$	$t = -2.551$ $P < 0.001$	$t = 0.764$ $P = 0.445$	$t = -0.193$ $P = 0.847$	3a
	Duration of stay #2	1	$t = -3.312$ $P = 0.001$	$t = -2.702$ $P = 0.007$	$t = -1.720$ $P = 0.086$	$t = -4.394$ $P < 0.001$	3b
(b) Substrate suitability	Shoot	1	$z = -3.03$ $P = 0.001$	$z = -4.091$ $P < 0.001$	$z = -0.837$ $P = 0.403$	$z = -5.543$ $P < 0.001$	4a
	EIS	−1	$z = 3.831$ $P < 0.001$	$z = 4.305$ $P < 0.001$	$z = 2.917$ $P = 0.003$	$z = 0.489$ $P = 0.62$	4b
(c) Egg deposition effort	Speed	1	$t = 2.255$ $P = 0.024$	$t = 3.891$ $P < 0.001$	$t = 7.830$ $P < 0.001$	$t = 1.273$ $P = 0.213$	5
	Abdominal swings	1	$t = 1.315$ $P = 0.194$	$t = 3.144$ $P = 0.003$	$t = 2.492$ $P = 0.018$	$t = 2.415$ $P = 0.022$	6
(d) Oviposition rate		1	1	−1	−1	−1	7

Rank attributed to *B. maritimus* if behaving on this type of shoot: (1) confers an advantage compared to other types of shoot, (−1) is less advantageous than on another type of shoot. Duration of stay #1 and #2 correspond respectively to all shoots observed and only to shoots which have been palpated. For each test $df = 1$. Oviposition rate is based on a combination of previous results and statistical analyses *per se* were not possible; ranks are attributed according to the same reasoning as above. Sample sizes are the same as in corresponding figures

Table 3 Contrast analyses between living shoots of *J. maritimus* and the other types of dead shoot (i.e. oviposition substrate) for the oviposition parameters in *L. macrostigma* which were significantly different regarding all types of shoot

		Living *J. maritimus*	Dead *J. maritimus*	Dead *J. acutus*	Dead *P. australis*	*B. maritimus*	Corresponding figure
(a) Substrate examination	Abd. bending	−1	$z = 3.421$ $P < 0.001$	$z = 6.606$ $P < 0.001$	$z = 7.002$ $P < 0.001$	$z = 6.606$ $P < 0.001$	2
	Duration of stay #1	−1	$z = -1.894$ $P = 0.059$	$z = 2.772$ $P = 0.006$	$z = 2.313$ $P = 0.021$	$z = 2.551$ $P = 0.011$	3a
	Duration of stay #2	0	$z = -0.588$ $P = 0.557$	$z = 0.518$ $P = 0.605$	$z = -1.665$ $P = 0.097$	$z = 2.702$ $P = 0.007$	3b
(b) Substrate suitability	Shoot	0	$z = 0.545$ $P = 0.586$	$z = 2.801$ $P = 0.005$	$z = -2.046$ $P = 0.041$	$z = 4.094$ $P < 0.001$	4a
	EIS	1	$z = -0.176$ $P = 0.860$	$z = -1.122$ $P = 0.262$	$z = -2.188$ $P = 0.029$	$z = -4.529$ $P < 0.001$	4b
(c) Egg deposition effort	Speed	0	$z = -2.179$ $P = 0.030$	$z = 5.553$ $P < 0.001$	$z = -0.140$ $P = 0.889$	$z = -3.891$ $P < 0.001$	5
	Abdominal swings	−1*	$z = -1.952$ $P = 0.057$	$z = -0.225$ $P = 0.823$	$z = 0.441$ $P = 0.663$	$z = -3.144$ $P = 0.003$	6
(d) Oviposition rate		0	1	0	0	1	7

Rank attributed to living shoots of *J. maritimus* if behaving on this type of shoot: (1) confers an advantage compared to other types of dead shoot, (−1) is less advantageous than on another type of dead shoot, (0) corresponds to both or none of previous assertions; −1* is given when almost significant. Contrast analyses regarding living shoots of *J. maritimus vs B. maritimus* are given again for a full understanding but are not considered for ranking living shoots of *J. maritimus*. Duration of stay #1 and #2 correspond respectively to all shoots observed and only to shoots which have been palpated. For each test $df = 1$. Oviposition rate is based on a combination of previous results and statistical analyses *per se* were not possible; ranks are attributed according to the same reasoning as above. Sample sizes are the same as in corresponding figures

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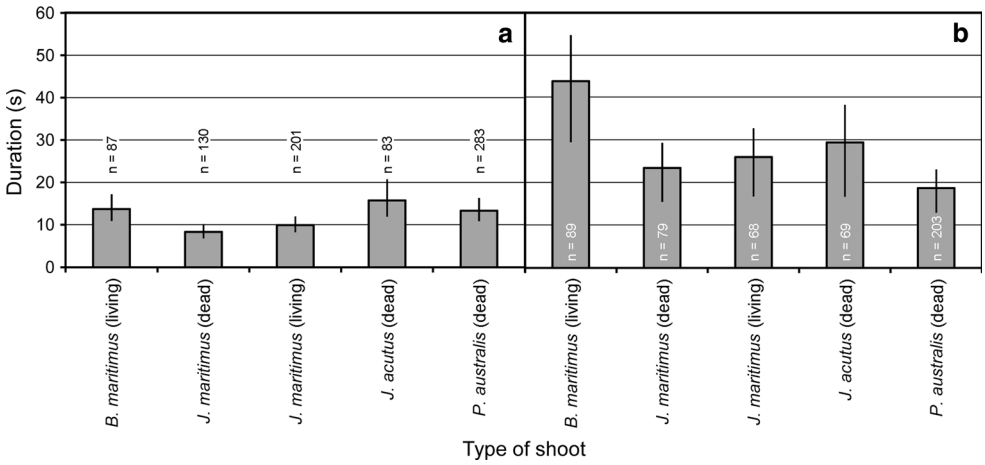


Fig. 3 Mean and 95 % confidence interval of duration of stay of *L. macrostigma* females on shoots within which egg-laying has not been observed although they belong to a plant species/state combination for which oviposition is possible: **a** on all shoots observed; **b** only on shoots which have been palpated. Note that a female stays longer when she decides to palpate the substrate

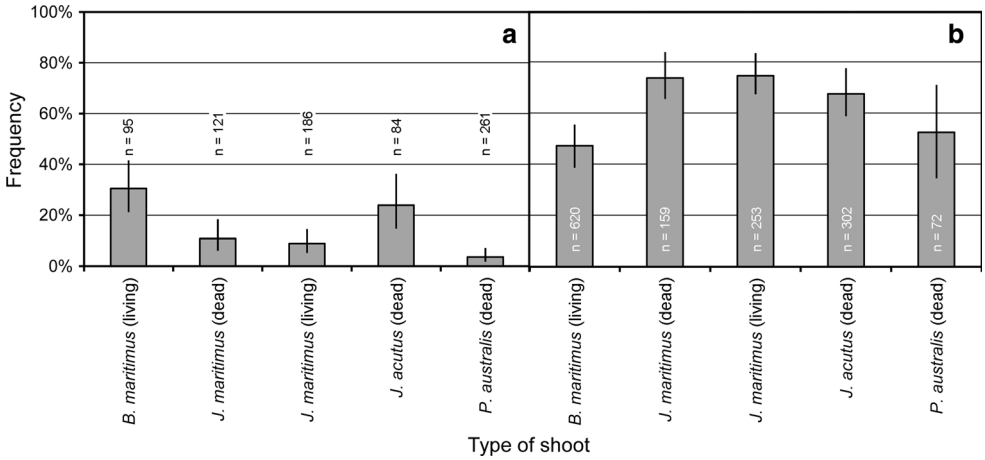


Fig. 4 Mean and 95 % confidence interval of suitability of oviposition substrates of *L. macrostigma* females regarding the different types of shoot: **a** rate of shoots appropriate to oviposition; **b** focusing on shoots which were appropriate to oviposition, rate of EIS appropriate for the deposition of one egg

The contrast analysis revealed that this rate was significantly higher than all other rates [*J. maritimus* dead shoots: 10.83 % (6.13–18.41), *J. maritimus* living shoots: 8.89 % (5.27–14.61), *P. australis*: 3.65 % (1.81–7.20), Table 2(b)] except for *J. acutus* dead shoots [23.91 % (14.76–36.33), Table 2(b)]. The difference in this rate between living shoots of *J. maritimus* and the different types of dead shoots was shown to be significantly higher than in *P. australis* dead shoots [Table 3(b)], significantly lower than in *J. acutus* dead shoots [Table 3(b)] and was not significantly different than in *J. maritimus* dead shoots [Table 3(b)].

Focusing on shoots which were selected for oviposition: the rate of EIS recorded for the deposition of one egg varied significantly regarding types of shoot (GLMM with Binomial error, $X_4^2 = 26.68$, $P < 0.001$, Fig. 4b). Contrast analysis showed that this rate was similar in *B. maritimus* [47.14 % (38.76–55.69)] and in dead shoots of *P. australis* [52.43 % (33.87–70.34), Table 2(b)]; on the other hand, it was significantly lower than in *J. acutus* dead shoots [67.44 % (57.32–76.16), Table 2(b)], *J. maritimus* dead and living shoots [respectively: 73.67 % (63.52–81.81), 74.57 % (65.70–81.78), Table 2(b)]. In other words, it was more difficult for females to find an appropriate place (i.e. appropriate EIS) to deposit one egg in *B. maritimus* than in other species. Additionally, this rate of EIS was similar in living shoots of *J. maritimus* to dead shoots of *J. maritimus* and *J. acutus* [Table 3(b)] but was significantly higher than in dead shoots of *P. australis* [Table 3(b)].

No significant differfence in clutch size was detected between types of shoot (GLMM with Binomial error, $X_4^2 = 0.74$, $P = 0.95$): *B. maritimus* mean = 2.79 eggs (2.00–3.91), dead shoots of *J. acutus* mean = 3.62 eggs (2.24–5.86), dead shoots of *J. maritimus* mean = 3.71 eggs (2.39–5.74), living shoots of *J. maritimus* mean = 3.34 eggs (2.08–5.37) and dead shoots of *P. australis* mean = 2.31 eggs (1.15–4.65). Meanwhile, the greatest clutch size was observed in a living shoot of *J. maritimus*: 53 eggs were laid (the greatest clutch size observed in a shoot of *B. maritimus* reached 22 eggs).

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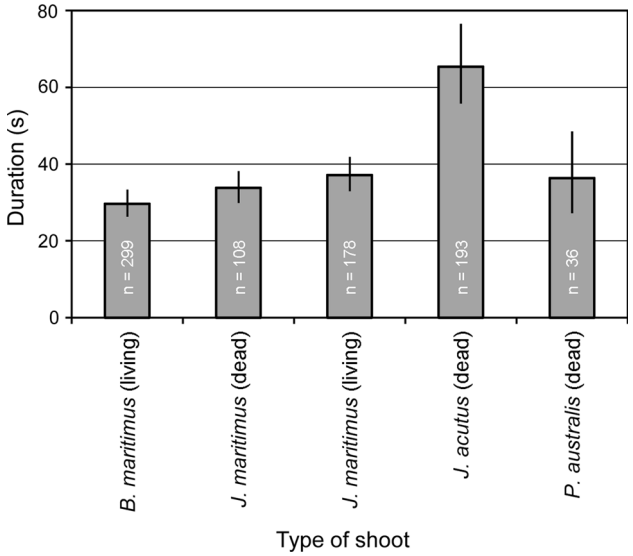


Fig. 5 Mean and 95 % confidence interval of time needed for *L. macrostigma* females to lay one egg by type of shoot

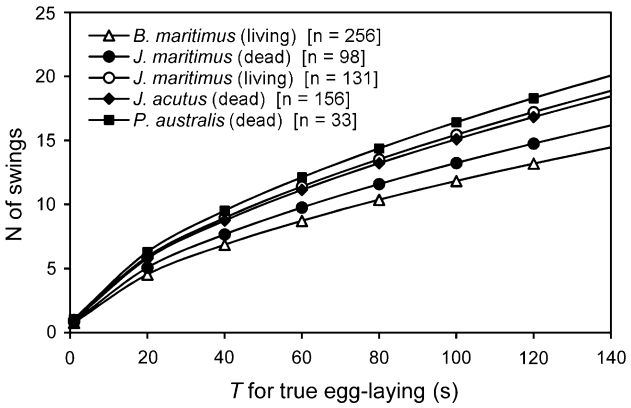


Fig. 6 Number of abdominal swings in *L. macrostigma* with respect to egg-laying time for each type of shoot

Egg-deposition speed and abdominal swings

During one egg clutch in *B. maritimus*, we witnessed one female which stayed apparently motionless after actual protrusion on three occasions: *T* lasted 40, 42 and 47 s when the actual time for protrusion was, respectively, 29, 17 and 15 s. During the other protrusions of this egg clutch, *T* lasted in average 28.11 s (min = 23, max = 39, SE = 1.116, n = 19). As this female stayed apparently motionless for 11, 25 and 32 s (much longer than the couple of seconds usually observed in all other egg depositions), we have not been able to identify if an egg had actually been deposited. We did not retain these three data for subsequent analysis.

T differed significantly regarding the type of shoot (GLMM with Gaussian error after log-transformation, $X^2_4 = 48.17$, $P < 0.001$; Fig. 5). *T* in *B. maritimus* shoots [mean = 29.63 s (26.33–33.36)] was significantly shorter than in *J. maritimus* living and dead shoots and than in *J. acutus* dead shoots [respectively: mean = 37.16 s (32.93–41.92), mean = 33.80 s (29.88–38.22), mean = 65.36 s (55.77–76.60), Table 2(c)]; it was not significantly shorter than in *P. australis* [mean = 36.33 s (27.18–48.57), Table 2(c)]. The difference in *T* between living shoots of *J. maritimus* and the different types of dead shoot was shown to be significantly lower than in *J. acutus* dead shoots, significantly higher than in *J. maritimus* dead shoots and was not significantly different than in *P. australis* dead shoots [Table 3(c)].

Focusing on successful egg-laying data: the longer *T* the higher the *Ns* (F^1_{588} $F^1_{588} = 384.21$, $P < 0.001$; Fig. 6). More importantly regarding plant preference, *Ns* also depended on the type of shoot ($F^4_{48} = 3.623$, $P = 0.012$). According to the contrast analysis, for a certain value of *T*, females had to swing their abdomen significantly fewer times when laying eggs into *B. maritimus* than in living shoots of *J. maritimus*, dead shoots of *J. acutus* and of *P. australis* [Table 2(c)]; by contrast, this difference was not significant compared to dead shoots of *J. maritimus* [Table 2(c)]. For the same *T*, *Ns* was almost significantly higher in living than in dead shoots of *J. maritimus* but was not significantly different than in dead shoots of *J. acutus* and *P. australis* [Table 3(c)].

Oviposition rate

ORs were the highest in dead shoots of *J. maritimus* and in *B. maritimus* [respectively, 54.27 eggs/h (38.70–66.02) and 49.37 eggs/h (38.97–60.05); Fig. 7]: these were more than twice the OR of the other types of shoot. Based on the 95 % CI, we assume that, on the one hand, there was no significant difference between the OR of dead shoots of *J. maritimus* and of *B. maritimus* because the 95 % CI of one includes the mean value of the other [Fig. 7; Tables 2(d), 3(d)]. On the other hand, the OR of these two types of shoot were both significantly higher than in living shoots of *J. maritimus* and dead shoots of *J. acutus* and of *P. australis* because the 95 % CI of the former do not overlap the 95 % CI of the latter [respectively, 21.19 eggs/h (5.85–34.36), 21.22 eggs/h (12.33–27.88) and 8.59 eggs/h (2.17–16.63), Fig. 7; Tables 2(d), 3(d)].

Discussion

Lestes macrostigma can oviposit in various plant species (Table 1) and some of its populations are permanent in habitats where *B. maritimus* is absent. However, this damselfly exhibits a true behavioural preference for *B.*

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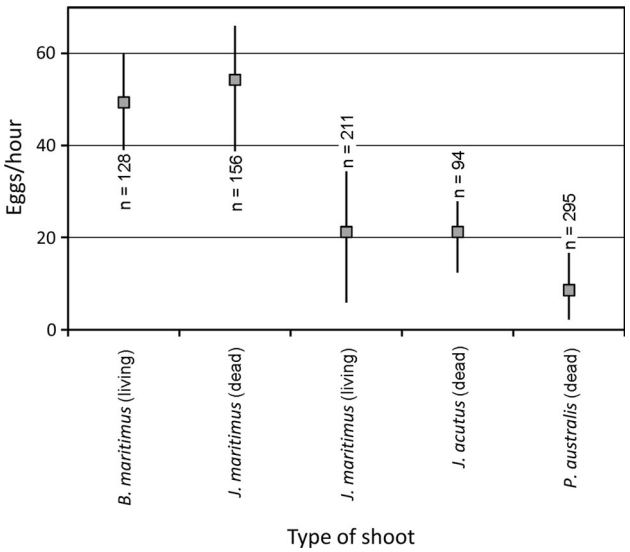


Fig. 7 Oviposition rate and 95 % confidence interval of *L. macrostigma* by type of shoot

maritimus [Table 2(a)]. This preference consists of a higher abdominal bending rate by females (substrate examination to find a place to lay eggs) and longer stays on this type of shoot during oviposition. This preference may be related to the better performance the female exhibits within this oviposition substrate: first, even though it is harder for females to find an appropriate EIS on a *B. maritimus* shoot than on other types of shoot, we observed a higher rate of shoots which are appropriate for egg laying in this species [Table 2(b)]; and second, females have to make less effort (i.e. swings of the abdomen and movements of ovipositor valves) to protrude into plant tissues and lay their eggs [Table 2(c)]. As a consequence, the OR—which synthesizes our different results—is higher in *B. maritimus* than in other types of shoot except in dead shoots of *J. maritimus* [Fig. 7; Table 2(d)].

The behavioural preference of females is strongest in *B. maritimus* compared to the other types of shoot [Table 2(a)], and for the different types of dead shoot, as living shoots of *J. maritimus* are clearly disfavoured [Table 3(a)]. If the suitability of living shoots of *J. maritimus* is higher than in the different types of dead shoot [Table 3(b)], the corresponding performances of females show an opposite trend [Table 3(c)]. The OR in living shoots of *J. maritimus* is low whilst the OR in one of the dead substrates, i.e. *J. maritimus*, is high and even greater than that in *B. maritimus* despite not being significantly different [Fig. 7; Tables 2(d), 3(d)].

Regarding these different oviposition features, it seems especially time and energy efficient for the females to lay eggs in *B. maritimus*; and also in one dead substrate: dead shoots of *J. maritimus*. In summary: choice and investment by the female (i.e. behavioural preference) are consistent with their oviposition fitness performance, and especially OR: (1) high preference and high performance in *B. maritimus*, (2) high preference of dead shoots and high performance in one of them, namely dead shoots of *J. maritimus*, and (3) disfavour and low performance in living shoots of *J. maritimus*.

Consistency with initial choice and fitness advantages for adults

Lambret et al. (2015) hypothesized that plant preference during oviposition site selection in Odonata was consistent along the reproductive life cycle, i.e. from the first step of oviposition until hatching of eggs. We here emphasize that the preference of *L. macrostigma* males for *B. maritimus* and dead substrates during the initial choice (i.e. when landing on the substrate) is in total accordance with the OR of females in *B. maritimus* and in one of the dead substrates, dead shoots of *J. maritimus*. Ovipositing in *B. maritimus* and dead shoots of *J. maritimus* gives direct advantages to the adult: the higher OR in these types of shoot are synonymous with a reduction of the duration of the oviposition bout. This reduces the predation risk and increases the time available for foraging (Lambret et al. 2015). This should increase *L. macrostigma* progeny because females continue to lay eggs throughout their adult lives (Corbet 2004; Cordero 1991).

Reasons for choice of *Bolboschoenus maritimus* versus *Juncus maritimus*

Shoots of *B. maritimus* are subject to a higher behavioural preference from the female (Table 2a) than dead shoots of *J. maritimus* although both oviposition substrates provide a similar high ovipositing efficiency (i.e. OR). The spatial and temporal distribution of plant species within a vernal pond is directed by the pond depth gradient and the duration of flooding (Grillas et al. 2004). Within the temporal and brackish waters where *L. macrostigma* breeds, *B. maritimus* grows in the lowest part of the shallow marshes while *J. maritimus* usually grows at an upper level of shallow marshes and on the banks of the deepest ponds.

The preference of *L. macrostigma* for *B. maritimus* rather than dead shoots of *J. maritimus* is likely to reflect advantages for eggs: lower parasitism rate and/or better survival during diapauses and/or better access to conditions necessary for postdiapause development and/or a higher hatching rate (Sawchyn and Gillot 1974; Siva-Jothy et al. 1995; Reinhardt and Gerighausen 2001). In *L. macrostigma*, shoots containing eggs need to be flooded for successful egg development and the sooner the flooding of the egg-clutch the higher the hatching rate (Lambret, unpublished data, 2014). In the Camargue, temporary ponds

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are re-flooded again by the first substantial fall rains. We expect that, considering the spatial distribution of plants (see above) and since the ponds' lower zone is flooded sooner than its upper zone and banks, laying eggs in *B. maritimus* should increase the chance of egg-clutches being flooded earlier, increasing progeny survival and therefore breeding success.

Reasons for selection of dead shoots versus living shoots of *Juncus maritimus*

For one of the dead substrates—dead shoots of *J. maritimus*—ovipositing efficiency is as high as in *B. maritimus* while it is low for the two other types of dead substrate, namely dead shoots of *J. acutus* and of *P. australis* [Fig. 6; Tables 2(d), 3(d)].

On the one hand, the different types of dead shoot are preferred by females compared to living shoots of *J. maritimus*, which are disfavoured [Table 3(a)]. On the other hand, although ovipositing efficiency is higher in dead shoots of *J. maritimus* than in dead shoots of *J. acutus* and of *P. australis*, the latter two are preferred to the former during the first steps of oviposition (Figs. 2, 3a). This could reveal that females are able to recognize living shoots of *J. maritimus* quickly and to disfavour, i.e. not to select, this type of shoot because of the relatively low oviposition efficiency. By contrast, females seem unable to distinguish among the different types of dead substrate because dead shoots of *J. acutus* and of *P. australis* are preferred despite their relatively low oviposition efficiency.

Lestes macrostigma typically oviposits within vertical shoots (Matushkina and Lambret 2011). According to the expected selection pressure process described above, dead shoots may be selected over the living shoots of *J. maritimus* because vertical dead material is more likely to break and be closer to the dry ground than living material. Thereby, when temporary ponds are flooded again, eggs which have been laid in such dead material have a higher chance of being flooded earlier and hence reducing desiccation risk.

Implications for conservation and management

Our results show the importance of maintaining a well developed population of *B. maritimus* within *L. macrostigma* habitat for its conservation. For wildlife managers this means paying special attention to grazing pressure and scheduling since this plant is preferentially eaten by cattle (Mesléard et al. 1999). Alternatively, in the deepest ponds where *B. maritimus* does not develop, maintaining some patches of *J. maritimus* or else of *J. acutus* (targeting the dead shoots of both species) at the edge of *L. macrostigma* ponds can also facilitate breeding. Finally, if some habitat is to be restored or created for *L. macrostigma* conservation (Lambret 2011, 2013) ecological engineering should take into account these plant substrate preferences, especially if sowing seeds (Muller et al. 2013).

Acknowledgments We would like to thank the Amis des Marais du Vigueirat for the access to the National Natural Reserve. We are grateful to Marc Solari who kindly translated the paper of Horst Grunert into French, making easier the use of this work for our study, and to Imogen Rutter for improving the language of our manuscript.

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