Ecological aspects of underwater oviposition in *Lestes sponsa* (Odonata: Lestidae)

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Abstract. Underwater oviposition is a special subtype of endophytic oviposition and constitutes the predominant mode for certain species of Calopterygidae and Coenagrionidae. Very little is known about underwater oviposition in Lestidae and other dragonfly groups (e.g., Anisoptera). In July 2009, we recorded this specific behaviour in a population of *Lestes sponsa* in the Czech Republic (Moravia, Štramberk). We subsequently studied the frequency of this phenomenon at regional (16 sites surveyed in an area of ca 1,260 km^2) and local (proportions of eggs laid beneath and above the water's surface at three locations) levels. We examined further key environmental factors influencing underwater oviposition and certain ecological parameters (depth and time) of this behaviour in *L. sponsa*. The frequency of underwater oviposition on the regional scale was relatively low (< 20 %), but the frequency of this behaviour on a local scale was sometimes high. At those sites where underwater oviposition occurred, 4,759 (62 %) out of a total of 7,699 eggs were laid underwater. The main factors affecting underwater oviposition were transparency of the water column and type of submerged vegetation. Ovipositing pairs spent on average 338 seconds under the water at an average depth of 20 cm. Further research should focus on the benefits of this specific oviposition tactic and especially egg mortality during overwintering.

Key words. Dragonfly, damselfly, Zygoptera, submerged oviposition, oviposition site selection, anti-predation strategy

Introduction

Two main types or modes of oviposition are usually distinguished in the Odonata. These primarily correspond to phylogenetic relationships between individual taxa and their morphological adaptations (Corbet 1999: 21 ff.). Exophytic oviposition is a strategy whereby a female with a reduced and non-functioning ovipositor lays eggs on the surface of the water or on

the exposed bottom or bank substrate. The second type is endophytic oviposition in dragonflies with complete and functioning ovipositors, which lay eggs in plant tissue. Several authors, such as Mathavan & Pandian (1977), have distinguished an additional, third category of epiphytic oviposition: laying eggs on the surface of a plant. Underwater oviposition is a special subtype of endophytic oviposition whereby a single female or pair in tandem lay eggs in tissue of plants under the water and at least the female thorax inclusive of wings is submerged beneath the water's surface. This constitutes the predominant or exclusive mode of oviposition for certain species of Calopterygidae and Coenagrionidae. It is very rare in the Lestidae and the Anisoptera (Wesenberg-Lund 1913; Münchberg 1937; Robert 1958: 98 ff.; Itô & Eda 1977; Jödicke 1997: 236 ff.; Corbet 1999: 30 ff.; Hawking et al. 2004; Tsubaki et al. 2006).

Staying underwater is associated with many risks and a high mortality rate, especially because the adults are not adapted to this environment (Fincke 1986). Tsubaki et al. (2006) provided experimental evidence, however, that females are able to stay underwater for a relatively long time, and especially when ovipositing in tandem. According to several studies, submerged oviposition is an adaptation which may be advantageous in certain circumstances. Fincke (1986) provided some evidence that by ovipositing underwater females of *Enallagma hageni* (Walsh, 1863) decrease the risk that their eggs will be exposed to desiccation. More precisely, protection of eggs against abiotic stressors and incidental predators are considered to be the main benefits of an endophytic and, consequently, also of an underwater oviposition strategy (Spence 1986; Miller 1994). Sometimes (when male density is high) the strategy is also used by females as a means of escape and protection against male harassment (Hilfert-Rüppell 2004). In addition, the eggs of *Lestes sponsa* (Hansemann, 1823) oviposited underwater had significantly fewer egg parasitoids than did eggs oviposited above the water (FH unpubl. data). During this research also a stronger tendency to lay eggs underwater at sites with a high risk of predation was recorded. An additional advantage may be that dragonflies are able to find underwater sites without other, competing eggs.

Although underwater oviposition has been observed repeatedly in the widespread species *L. sponsa* in various parts of the Palaearctic (e.g.,

Wesenberg-Lund 1913; Andoh 1969; Jödicke 1997: 236 ff.), only little attention has been devoted to this phenomenon. It is not known whether underwater oviposition in this species is only an accidental event. Likewise, the circumstances leading to submerged oviposition and its other relevant characteristics are not known. We were therefore interested to learn how common this phenomenon is at regional and local levels. The aims of the study were to 1) identify key factors and/or environmental attributes that influence the decision to oviposit underwater, and 2) characterize in detail several ecological parameters of underwater oviposition in the regionally common damselfly species *L. sponsa*.

Methods

Target species

Lestes sponsa is widely distributed in the Palaearctic apart from its southern and northern range. Females are endowed with a well-developed ovipositor, and they can lay hundreds of eggs throughout their lives. Oviposition proceeds immediately after copulation and usually while males remain together with females in tandem. Exceptionally, females will lay eggs alone (Loibl 1958; Stoks 1995; Stoks et al. 1997). *Lestes sponsa* usually places its eggs into the stalks of emergent plants (e.g., *Juncus*, *Equisetum*, *Schoenoplectus*, or *Eleocharis* spp.), but also into the leaf tissues of halophytes, e.g., *Iris* or *Stratiotes* spp. The female first penetrates the plant tissue with her ovipositor and then lays two to four eggs in the groove (Wesenberg-Lund 1913; Robert 1958). The females from the genus *Lestes* lay egg sets along a line ('ideal line') oriented along the fibres of the plant tissue (Jödicke 1997; Matushkina & Gorb 2002).

Study sites

The study area (about 1,260 km^2) was situated in the foothills of the Beskydy Mountains in the north-eastern part of the Czech Republic. It lay within a radius of 20 km around the city of Štramberk, where in July 2009 we had observed oviposition in a population of *Lestes sponsa* (Fig. 1). Sixteen sites in the area were surveyed, comprising all known locations with recent or historical (cf. Dolný et al. 2008) records of *L. sponsa* around Štramberk (Loc. 13 in Tab. 1). Each site was visited four times during the flight period

of *L. sponsa* from June to September in 2010 and 2011. The study sites consisted of extensive ponds (n = 8), flooded quarries (n = 3), natural wetlands (n = 2) and small flooded depressions (n = 3). All sites were habitats with lush littoral and submerged vegetation, which is crucial for the occurrence of the species and thus also for underwater oviposition. The climate of the study area is characterized by long, warm, and moderately dry summers, warm springs and slightly warm autumns. Winter is short, warm, and very dry, with a short duration of snow cover. The average annual temperature is in the range of 6–7°C and annual rainfall is 650–750 mm. The most common rock subsoil is coarse to fine-grained limestone. There are therefore several limestone quarries in the area.
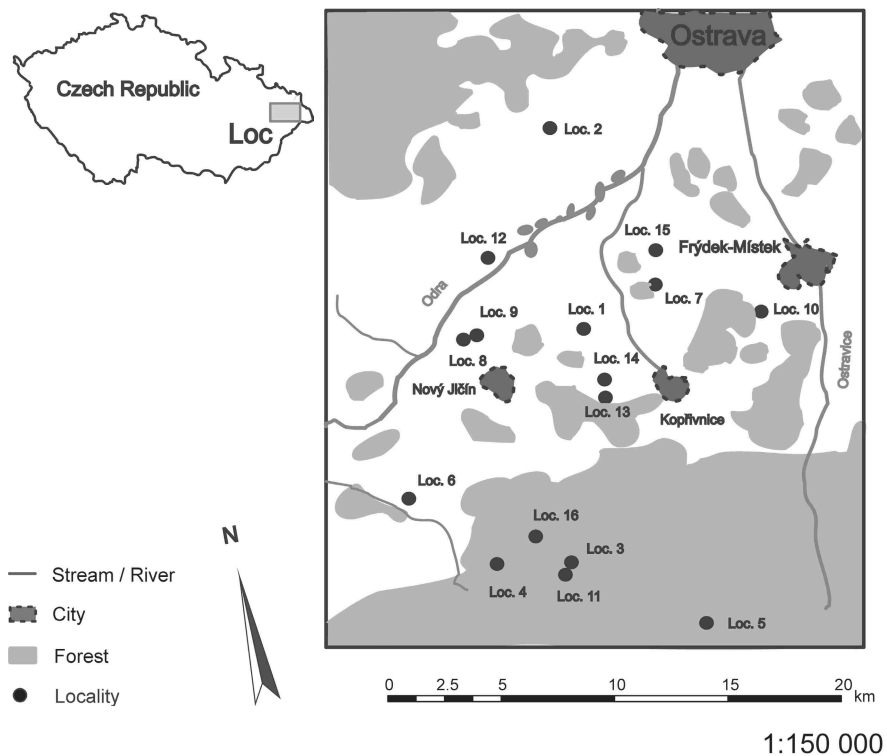

Figure 1. Location of study sites to survey underwater oviposition of *Lestes sponsa* south of Ostrava, Moravia, Czech Republic.

Table 1. Individual characteristics of study sites.

Locality	Latitude	Longitude	Habitat type	Dominant plant genera
Loc. 1	49°37′57.149′′N	18°06′09.616′′E	Fish pond	*Persicaria, Chara, Carex*
Loc. 2	49°46′16.138′′N	18°04′34.249′′E	Fish pond	*Phragmites, Lemna*
Loc. 3	49°27′49.517′′N	18°04′33.519′′E	Fish pond	*Eleocharis, Typha, Phragmites*
Loc. 4	49°28′05.346′′N	17°59′56.604′′E	Fish pond	*Typha, Phragmites, Juncus*
Loc. 5	49°25′18.331′′N	18°13′11.548′′E	Flooded depression	*Eleocharis, Phragmites, Alisma*
Loc. 6	49°31′81′′N	17°54′18′′E	Wetlands	*Typha, Carex, Phragmites, Juncus*
Loc. 7	49°39′39.520′′N	18°11′04.321′′E	Fish pond	*Typha, Carex*
Loc. 8	49°37′44.474′′N	17°58′35.275′′E	Quarry	*Alisma, Persicaria, Phragmites*
Loc. 9	49°37′46.250′′N	17°59′06.895′′E	Fish pond	*Typha, Lemna*
Loc. 10	49°38′36.645′′N	18°17′02.525′′E	Flooded depression	*Typha, Phragmites, Juncus*
Loc. 11	49°27′22.154′′N	18°04′00.403′′E	Wetlands	*Phragmites, Typha, Hydrocharis*
Loc. 12	49°41′04.194′′N	17°59′57.358′′E	Fish pond	*Persicaria, Verbascum*
Loc. 13	49°35′19′′N	18°07′28′′E	Quarry	*Schoenoplectus, Eleocharis, Equisetum*
Loc. 14	49°34′35′′N	18°07′01′′E	Quarry	*Juncus*
Loc. 15	49°40′59.489′′N	18°10′58.368′′E	Fish pond	*Typha*
Loc. 16	49°29′20.581′′N	18°02′41.495′′E	Flooded depression	*Typha, Carex*

Data collection

Ovipositing pairs of *Lestes sponsa* were observed in the main flight period of this species during July and August 2010 and 2011. We actively sought out ovipositing pairs of *L. sponsa* in vegetation at each site for a period of 30 minutes. The counting of adult individuals took place between 10:00 and 16:00 h CEST during windless days with cloud cover less than 20 %.

The following parameters were measured in the field: percentage of shading (%), relative water transparency (measured using a Secchi disc), fish presence (present/absent), character of the surrounding vegetation cover around the habitat (open, fragmented, forest), and percentage of aquatic vegetation cover (0 %, 1–25 %, 26–50 %, 51–100 %). The percentage cover-

age of the dominant plants was measured in a 5 m-strip along each habitat. Plants were generally identified to genus level, and for certain readily determined species to species level.

The proportions of eggs laid under and above the water's surface were evaluated at those locations where we recorded underwater oviposition (localities 6, 13, 14). Approximately ten days after the last recorded oviposition event, a random sample of plants was made for each location whereby every fifth plant (ca 20 %) with oviposition marks was removed.

In addition to these data, we also observed maximum depth of underwater oviposition, duration of stay underwater, and presence of males during underwater oviposition. These observations were made only at locality 13. The duration of underwater oviposition was determined as the time from complete submergence of the pair (i.e. when the head and thorax of the male passed below the water's surface) and subsequent emergence of the pair (i.e. when the head and thorax of the female appeared above the water's surface). The maximum oviposition depth was determined as the distance to the lowest oviposition scar beneath the water's surface.

Statistical methods

The relationships between the occurrence of underwater oviposition and environmental variables were analysed using generalized linear models (GLM). A binomial model with logit function was used to analyse the effect of a given environmental (explanatory) variable on the occurrence of underwater oviposition (response variable). For final model selection, R package glmulti, Version 1.0.7 (Calcagno & Mazancourt 2010) was applied. This package enables selection of the best-fit model using the corrected Akaike information criterion (AICc) by means of the glmulti function. Models having $\Delta AICc \pm 2$ in comparison to the best model were regarded as equivalent (Burnham & Anderson 2002). The final model was verified using standard statistical diagnostics (Crawley 2007). Differences in environmental variables at individual sites were analysed (essentially summarized) via principal component analysis (PCA, Fig. 2). All analyses were performed using the R software package version 2.13. (R Development Core Team 2011).

Table 2. Proportion of eggs laid above and beneath the water's surface in individual localities by year and plant species.

Locality	Year	Plant taxon	Number of plants	Number of eggs	Above water n	Above water %	Under water n	Under water %
Loc. 6	2011	*Juncus effusus*	58	1,034	460	44.5	574	55.5
		Equisetum variegatum	30	158	93	58.9	65	41.1
Loc. 13	2010	*Juncus effusus*	160	1,151	159	13.8	992	86.2
		Eleocharis auricularis	12	94	0	0.0	94	100.0
Loc. 14	2011	*Juncus effusus*	86	3,564	1,872	52.5	1,692	47.5
		Equisetum variegatum	4	548	127	23.2	421	76.8
	2010	*Schoenoplectus lacustris*	6	581	173	29.8	408	70.2
		Eleocharis auricularis	5	43	43	100	0	0.0
	2011	*Eleocharis palustris*	7	526	13	2.5	513	97.5
Total			368	7,699	2,940		4,759	

Results

Frequency of underwater oviposition at regional and local levels

While the frequency of underwater oviposition at the various sites within the study region was relatively low ($< 20\%$), the proportional use of this strategy at individual locations could be high. Underwater oviposition was observed at only three of 16 sites (locations 6, 13 and 14). At all three locations where underwater oviposition was clearly visible, we recorded a higher number of eggs underwater than above. A total of 7,699 eggs were counted, of which 4,759 eggs (62 %) were laid underwater (Tab. 2).

Factors influencing underwater oviposition

Common attributes among those habitats in which the pairs oviposited underwater were low water turbidity and a relatively low degree of shading. Transparency – i.e. clear water – was the only significant factor affecting the decisions of females to oviposit underwater (Tabs 3, 4). The other habitat attributes were less important. Two of these sites were flooded quarries having clear water. The sites were markedly less overgrown and had less heterogeneous vegetation than did the third location (natural wetlands) where underwater oviposition was observed. The most important habitat conditions influencing underwater oviposition are water transparency, vegetation

Table 3. Model specification and AICc values for the best five GLM of underwater oviposition (Underwater). Shading – shading of water surface (%); transparency – relative water transparency; fish occurrence (present/absent); surrounding – character of vegetation cover around the habitat (open, fragmented, forest); vegetation – aquatic vegetation cover

Model	AICc	Weights
Underwater ~ 1 + Transparency + Vegetation:Transparency + Fish:Transparency + Surrounding:Transparency	-6.28	0.132
Underwater ~ 1 + Shading:Transparency + Macrophyte:Transparency + Vegetation:Transparency + Fish:Transparency	-5.61	0.095
Underwater ~ 1 + Transparency + Vegetation:Transparency + Vegetation:Macrophyte + Fish:Transparency + Surrounding:Transparency	-5.53	0.091
Underwater ~ 1 + Surrounding + Transparency + Vegetation:Transparency + Fish:Transparency	-5.06	0.072
Underwater ~ 1 + Shading:Transparency + Vegetation:Transparency + Fish:Transparency	-4.98	0.069
Underwater ~ 1 + Transparency + Vegetation:Transparency + Fish:Transparency + Surrounding:Transparency	-6.28	0.132
Underwater ~ 1 + Shading:Transparency + Macrophyte:Transparency + Vegetation:Transparency + Fish:Transparency	-5.61	0.095

Table 4. Significance of individual habitat variables for the occurrence of underwater oviposition derived from GLM with binomial errors. Transparency – relative water transparency; surrounding – character of vegetation cover around the habitat (open, fragmented, forest); vegetation – aquatic vegetation cover

Variable	df	Deviance	Residual deviance	P
NULL			15.44	
Transparency	1	7.43	8.01	0.006
Surrounding	2	1.07	6.94	0.586
Transparency:Vegetation	1	6.94	0	0.008

heterogeneity, and perhaps their interaction (Tabs 3, 4). The decision to oviposit is nevertheless likely to be affected by other factors, such as the availability of suitable submerged plants. Because of the small number of sites where underwater oviposition was observed and the very different characteristics of their vegetation, however, it was not possible to analyse this effect. Based on our observations, it appears that while no particular plant species was significantly conducive to underwater oviposition, the plant's overall morphological structure (especially the stem diameter and toughness) was important. Females clearly preferred thin and soft stems of *Eleocharis*, *Juncus*, and *Schoenoplectus* over those of *Equisetum* or *Typha* for underwater oviposition. Not all of these plants were common at all sites.

Descriptive characteristics of underwater oviposition

Underwater oviposition occurred mostly on clear, warm days at times when the air temperature exceeded 22°C. In all observations, females of *L. sponsa*
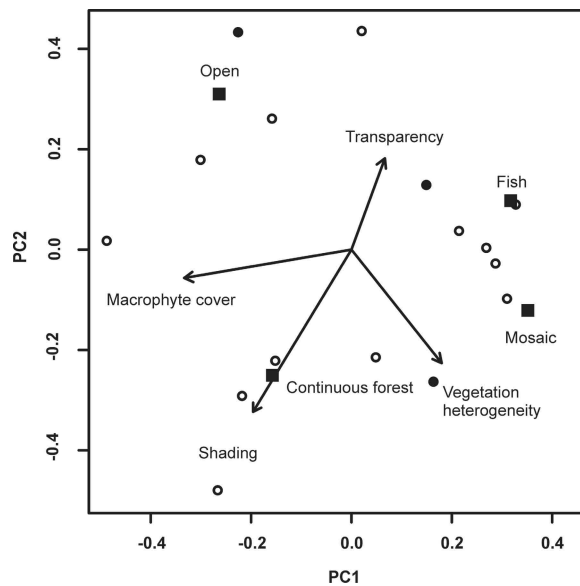

Figure 2. Principal component analysis (PCA) showing correlation among environmental variables at individual sites. A filled circle means a site with occurrence of underwater oviposition in *Lestes sponsa* (first axis: 34.4 %, second axis: 25.6 % of the explained variance).

oviposited in tandem (Fig. 3). Both partners landed at a part of an emerging plant. Shortly after landing the female curved the abdomen and started palpating the substrate with its ovipositor. In all cases, the female began above the water's surface, and oviposited continuously by moving backwards underwater. Oviposition was briefly interrupted only when both partners folded their wings and passed through the water's surface (Fig. 3a). If the tandem was disrupted, both individuals immediately tried to get out of the water. The males remained connected to the females throughout underwater oviposition in all cases (Fig. 3b). Ovipositing pairs of *L. sponsa* spent on average 338 seconds beneath the water's surface, the maximum duration of underwater stay was 1,268 seconds (Fig. 4). We also observed ovipositing pairs that probably did not lay an entire clutch during a single dive and oviposited underwater repeatedly, one tandem doing so seven times within a few minutes.

The maximum recorded oviposition depth was 55 cm beneath the water's surface. The maximum depth, however, often corresponded with the bottom of the water body. The majority of observed ovipositions were at maximum depths in the range of 10–20 cm (Fig. 5).
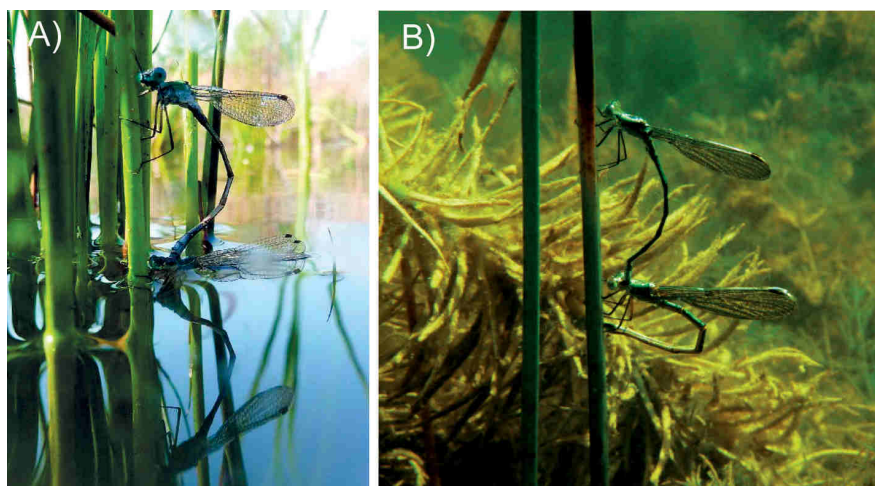

Figure 3. (a) Submerging tandem of *Lestes sponsa* (Loc. 13, Štramberk, Czech Republic, 20-viii-2010); (b) Tandem pair of *L. sponsa* ovipositing underwater (Loc. 13, 15-viii-2010). Photos: JH

Discussion

Our results are in accordance with our general assumption that underwater oviposition in Lestidae is only a facultative type of behaviour. On the other hand, it seems that on the micro- and meso-scale, under certain conditions, this phenomenon may constitute a very useful and common tactic. Thus,
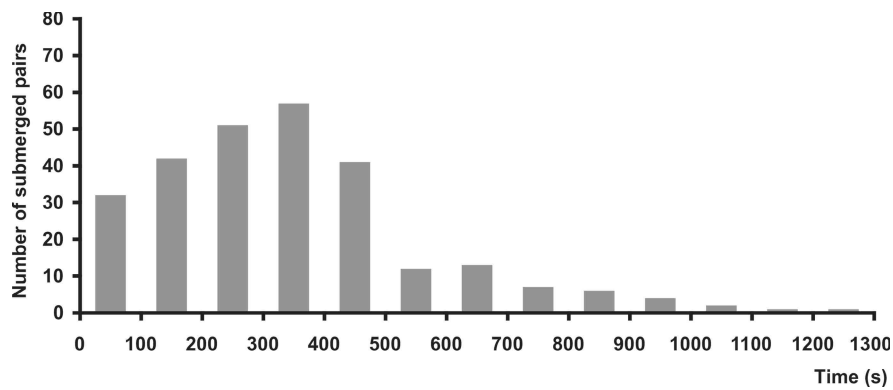

Figure 4. Duration of the underwater oviposition stay of *Lestes sponsa* recorded during this study in 2010 and 2011 in the Czech Republic (n = 267).
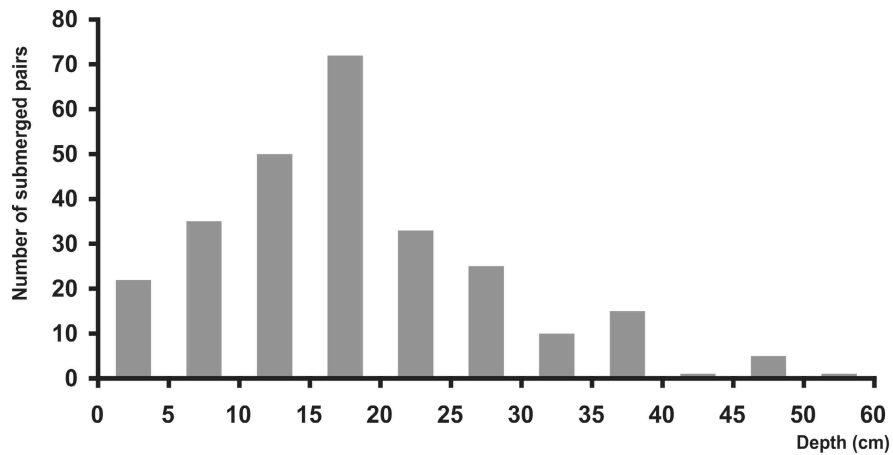

Figure 5. Maximum observed oviposition depths of *Lestes sponsa* recorded during this study in 2010 and 2011 in the Czech Republic (n = 267).

the frequency of this behaviour was very high at sites where underwater oviposition occurred. This implies that the largest numbers of eggs at these locations were laid underwater. It seems that underwater oviposition in Lestidae is a behavioural pattern constituting alternative tactics ('underwater oviposition' versus 'terrestrial oviposition') within the same overall genetic strategy. This is probably a conditional strategy within which individuals vary their behaviour (alternate tactics) depending on their environment. In this conditional strategy, the tactics involve a 'choice' or 'decision' by the individual. Individuals are genetically monomorphic for the decision, and the choice of tactic results in higher fitness for the individual (Gross 1996; Davies et al. 2012).

A key environmental factor affecting the decision to oviposit underwater is probably transparency of the water, but it can be also influenced by vegetation structures and density (Buchwald 1989; Wildermuth 1992). Although not much is known about oviposition site selection in dragonflies, it has been shown that they recognise the habitat mainly by visual cues (Wildermuth 1993) and the dragonflies' ability to perceive horizontally polarized light reflected from the water plays a significant role in this process (Wildermuth 1998). The degree of polarization can be influenced by the bottom substrate as well as the turbidity and transparency of the water (Horváth & Varjú 1997). The fact that dragonflies are able to evaluate transparency does not, however, explain why dragonflies submerged only at sites with transparent water. Turbidity can substantially reduce the orientation of adults underwater and may thus influence the risk of drowning and significantly limit the ability to detect predators (Lima & Dill 1990). Staying below the surface is always risky, because the adults are not adapted to movement underwater.

Damselflies oviposit their eggs into dead or fresh plant material. Based on the available evidence, we can conclude that the availability of a certain type of submerged vegetation (i.e. morphological character of stems and leaves) may also be significant. Not only may vegetation serve as a suitable substrate for oviposition, it may also be associated with movement underwater. Submerged pairs rarely oviposit into the stalks of larger plants like *Typha* but prefer emergent plants with thinner stalks for example *Juncus*, *Equisetum*, *Schoenoplectus*, or *Eleocharis*, which can serve as solid supports for climbing (Miller 1994).

Our field observations showed that the presence of a male may also be crucial for the female decision to oviposit underwater. Fincke (1986) had shown that females ovipositing underwater in tandem profited from the males' assistance during resurfacing, while the males may have benefited from the fact that females ovipositing underwater cannot be attacked by other males. Because the females of *Lestes sponsa* we observed ovipositing underwater always did so in tandem, it was not possible to assess the role of the male during resurfacing. In cases where the tandem broke apart, however, both individuals immediately tried to reach the surface.

The maximum recorded duration of underwater oviposition in our study corresponded to that from previously published data (summarized by Jödicke 1997: 236 ff.). However, the average duration of an individual staying underwater was significantly shorter. Based on a comparison of several species, Tsubaki et al. (2006) found that the submergence potential, i.e. the ability to remain underwater, is related both to the physical and chemical properties of the aquatic environment and to the morphological characteristics of wing surfaces. The association of submerged oviposition and presence of wing bristles is significant. Species which rarely perform submerged oviposition have few or no wing bristles (Tsubaki et al. 2006). In accordance with these findings, we can assume that the submergence potential of *L. sponsa* may be related to the presence or absence of bristles on the wings in this species, however, this was not investigated in this study. On the one hand, deep sites are safe from egg parasitism, but on the other hand, may be unsuitable for hatching due to environmental factors (Hirayama & Kasuya 2010). Further research should focus on the benefits of this specific oviposition strategy, and especially upon egg mortality during the overwintering period.

Acknowledgements

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198