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Reproductive behaviour of *Erythromma lindenii* in Northeast Algeria (Odonata: Coenagrionidae)

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Abstract. The reproductive behaviour of the Atlanto-Mediterranean *Erythromma lindenii* Selys has been studied before in Europe, but not in North Africa where the climate is warmer. We investigated the reproductive behaviour in a natural population in Northeast Algeria. We found that the species is non-territorial with quasi-exclusive underwater oviposition. The duration of underwater oviposition was positively correlated to the maximum water depth. We suggest that females predominantly lay eggs underwater to avoid water evaporation, which is common in North Africa. We discuss the differences in the reproductive behaviour between European populations and one in North Africa.

Further key words. Damselfly, Zygoptera, copulation, underwater oviposition, drought, North Africa

Introduction

Populations across geographic gradients encounter different environmental conditions, which may affect their biology and behaviour (Stoks & McPeek 2006; Johansson 2003; Śniegula et al. 2012; Nilsson-Örtman et al. 2012). In warm climates, odonates face the problem of rapid evaporation of reproductive sites. To cope with this ecological constraint, species have developed various biological and behavioural strategies (Rebora et al. 2007; Strachan et al. 2015). For instance, at the egg stage, species oviposit underwater so that hatching can occur before drought and desiccation (Fincke 1986). Although the latter has been observed in many species of damselflies (Johnson 1961, 1962; Bick & Bick 1963; Cordero 1995; Mahdjoub et al. 2014), there is still little knowledge on whether populations living in warmer climates are more likely to express underwater oviposition than those living in colder environments.

Erythromma lindenii (Selys, 1840) is a widespread zygopteran in Western Europe and in the Western Mediterranean basin. Its geographic distribution has expanded northwards since the 1990s (Boudot & Kalkman 2015). Studies on the reproductive behaviour of the species in Central and Southern Europe showed that underwater oviposition was quite occasional (Heymer 1973; Utzeri et al. 1983; Hunger 1998). In this study, we carried out a survey of the reproductive behaviour of the species in a population in Northeast Algeria, where the climate is probably the hottest of the entire range. The study included recording of diel reproductive activity, copulation, the frequency of underwater oviposition, and clutch size.

Material and methods

Study site

This study was conducted in spring 2013 at an artificial oval pond with a water surface area of *ca* 0.4 ha and circumference of 0.3 km situated 3 km northwest of El Fedjoudj province, Guelma, Algeria (36°31'54"N, 07°22'48"E). The water was clear, allowing us to observe submerged oviposition. The pond had emergent vegetation only in the littoral zone. Bank vegetation was dominated by *Typha angustifolia*, *Scirpus lacustris*, *Cyperus longus*, and *Paspalum distichum*. The most abundant submerged plant species was *Myriophyllum spicatum*, which was used by *Erythromma lindenii* for oviposition. During

the study period, *E. lindenii* coexisted with a zygopteran community consisting of a large population of *Sympecma fusca* (Vander Linden, 1820) and smaller populations of *Ischnura graellsii* (Rambur, 1842), *Coenagrion scitulum* (Vander Linden, 1820), and *C. puella* (Linnaeus, 1758) and an anisopteran community dominated by *Anax imperator* Leach, 1815, *A. parthenope* (Selys, 1839), *Crocothemis erythraea* (Brullé, 1832), *Orthetrum cancellatum* (Linnaeus, 1758), *Sympetrum fonscolombii* (Selys, 1840), *Trithemis annulata* (Palisot de Beauvois, 1807), and *T. arteriosa* (Burmeister, 1839). The pond was stocked with common carp *Cyprinus carpio* Linnaeus, 1758.

Reproductive behaviour

To determine the hourly pattern of abundance of individuals, we carried out hourly counts of males and pairs daily from 09:00 to 16:00 h CET (UTC+1) across the entire length of the pond banks. We recorded the time (to the nearest minute) of the appearance of the first individual at the pond. To test whether temperature influences the onset of reproductive activity in *E. lindenii*, we carried out circular-linear correlations between the time of the appearance of the first individual at the study site and mean and maximum air temperature obtained from a meteorological station 9 km away. Circular-linear correlations were conducted with ORIANA 4.02 (Kovach Computing Services, Pentraeth, Wales, UK). Mature individuals were marked daily with alphanumeric codes on the left hind wing with permanent markers from 29-iii- to 29-v-2013 along the banks of the pond, from 09:00 to 17:00 h. The entire reproductive episode – tandem formation, copulation, post-copulatory resting, and oviposition – was surveyed and timed to the nearest second. We placed some graded sticks into the water at potential oviposition sites to make depth estimations easier and visually estimated the depth of oviposition site selection to the nearest 5 cm. To reveal potential relationships between male harassment and oviposition site selection, we tested the correlation between water depth and male density within 50×50 cm of the oviposition site. To determine the clutch sizes before and after underwater oviposition, we collected a sample of females during copulation in the morning (n = 51) and after emerging from the water in the afternoon (n = 35), then we dissected them in the laboratory and counted the eggs with a dissecting microscope. Values are mean ± SD.

Results

The activity of *Erythromma lindenii* was limited to the period from 09:00 to 16:00 h CET (UTC+1; solar time ~ -30 min). The number of males began to increase from 09:00 h, peaked between 11:00 and 14:00 h, and declined gradually until 16:00 h (Fig. 1a). The number of reproductive pairs began to increase from 10:00 h, peaked at 12:00 h, and decreased until 16:00 h (Fig. 1b). The starting time of activity was negatively correlated to diurnal mean and maximum temperature (Circular-linear correlation: $r = -0.647$, $p < 0.0001$, Fig. 2a; $r = -0.742$, $p < 0.0001$, Fig. 2b; respectively). The sex ratio across the bank of the pond was highly male-biased during the entire period when the species was active (09:00–16:00) with a daily average of 70.7% (95% CI: 64.4–76.9; $\chi^2 = 90.42$, $p = 0.0004$).

Males arrived first at the water. They did not show any territorial behaviour. Females were seized as soon as they arrived at reproductive sites. Copulations lasted on average 5.95 ± 4.56 min (range: 1–28 min, n = 119). After copulation, the reproductive pair flew to floating leaves of *T. angustifolia*. Endophytic oviposition took place quasi-exclusively underwater. Based on 161 ovipositions, we recognized three main modes of egg laying: (1) exclusively underwater (88%) from the first to the last egg laid, (2) partially underwater (8%), *i.e.*, females started ovipositing on floating leaves then went under the water surface, (3) exclusive oviposition on the water surface (4%). Males did not immerse with the females. Females descended gradually under water by climbing backward and inserting eggs along the plant stem continually as they lowered themselves into deeper strata. The average maximum depth was 33 ± 23 cm (range: 0–105 cm, n = 143), and underwater oviposition lasted $1\,960 \pm 1\,193$ sec (range: 300–6 300 sec, n = 143). Maximum water depth of the submerged female was positively correlated with oviposition duration (Spearman's rank correlation: $r = 0.32$, $p = 0.0001$; Fig. 3) but was not correlated to the number of surrounding males (Spearman's rank correlation: $r = 0.01$, $p = 0.88$). Clutch size was significantly higher before oviposition (369.52 ± 342.22 eggs, range: 1–1 120 eggs, n = 51) than afterwards (108.00 ± 146.91 eggs, range: 0–636 eggs, n = 35) (Wilcoxon rank sum test: W = 441, $p < 0.0001$). After egg-laying, females emerged from the water and floated on the surface until they reached a substrate on which they climbed and rested.
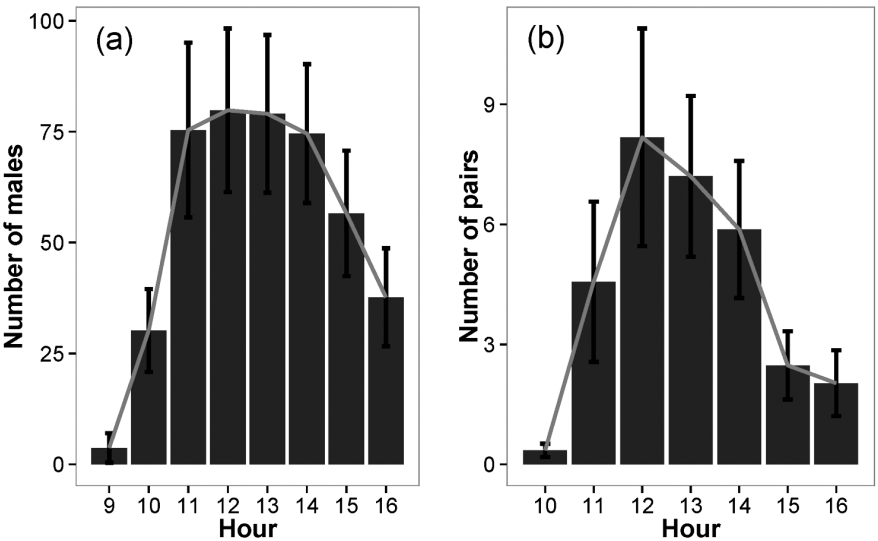
Figure 1. Abundance of (a) males and (b) reproductive pairs during day hours of reproductive activity of *Erythromma lindenii*, recorded in spring 2013 at a pond in El Fedjoudj province, Guelma, Algeria. Bars are means. Error bars are 95 % confidence intervals. Red lines link the mean values of each hour.
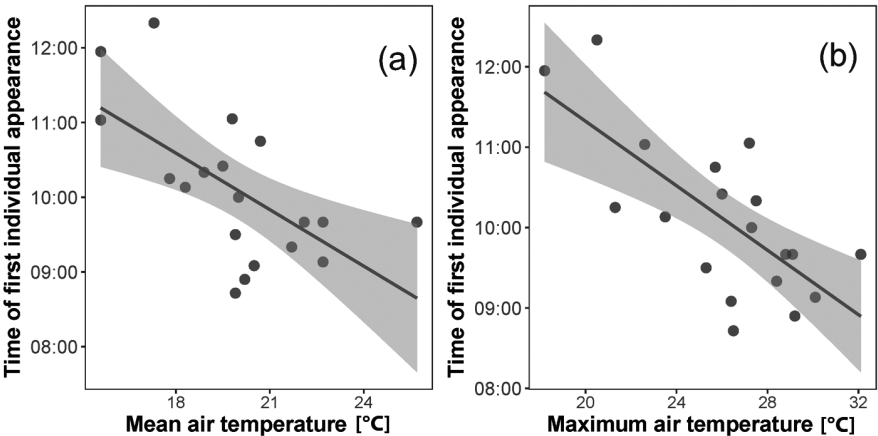

Figure 2. Relationship of the timing of arrival of the first individual of *Erythromma lindenii* to the pond and (a) mean and (b) maximum air temperature, recorded in spring 2013 at a pond in El Fedjoudj province, Guelma, Algeria. The blue line is a regression line, and the grey ribbon is the standard error.

Discussion

In our study we describe the sequential primary aspects of the reproductive behaviour of *Erythromma lindenii* at its southern distribution limit. The species' reproductive behaviour was mainly distinguished by a quasi-exclusive underwater oviposition, which is different from previous studies on European populations.

The high male-biased sex ratio at reproductive sites is a common pattern in odonates and has been explained by the cryptic behaviour of females (STOKS 2001). Indeed, females spend more time in terrestrial habitats than at reproductive sites. However, the extreme sex ratio obtained in our study was partly the result of non-detectability of females performing underwater oviposition. Furthermore, males arrived earlier at the water than females as observed in other odonates as well (STOKS et al. 1997). This sexual difference in dial activity probably results from intraspecific competition among
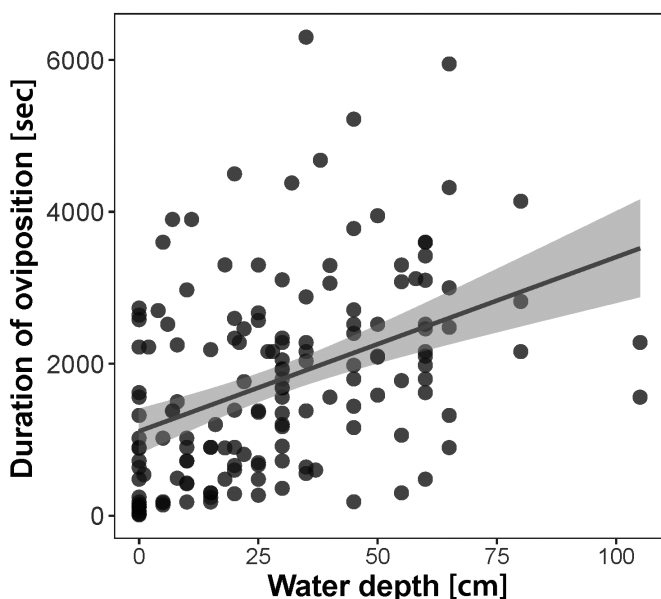

Figure 3. Relationship of the duration of underwater oviposition to maximum water depth in *Erythromma lindenii* recorded in spring 2013 at a pond in El Fedjoudj province, Guelma, Algeria. The blue line is a regression line, and the grey ribbon is the standard error.

males for mating, since occupying reproductive sites earlier might increase the likelihood of finding mates (Takeuchi & Honda 2009). The time of the first appearance at the reproductive site was negatively correlated to temperature. This is consistent with the physiological response of odonates to temperature (May 1979). In fact, individuals expose themselves to the sun in the morning to warm up their bodies and then start feeding and reproductive activities. Thus, the warmer the day, the faster the body warming, and the earlier the appearance at reproductive sites.

Males in our study population were not territorial, which is different from the studied European populations, where males are both territorial and non-territorial (Utzeri et al. 1983). It is difficult to disentangle the cause of geographic differences in mating tactics due to the implication of intra- and interspecific cues (Suhonen et al. 2008). However, a smaller population living in lotic habitat of Northeast Algeria also showed territoriality in *E. lindenii* males (RK pers. obs.), which suggests that population density might play an important role in determining mating tactics. The duration of copulation of *E. lindenii* recorded in this study was shorter than that reported for an Italian population (average: 17 and 18 min; range: 8–30 min in 1972; average: 6.59; range: 2–13.49 min in 1979; Utzeri et al. 1983). A similar difference between southern and northern populations was recorded in copulation duration for *Coenagrion mercuriale* (Purse & Thompson 2003; Mahdjoub et al. 2014). This variation could be due to the warmer climate in North Africa, which may accelerate sperm production and transfer (Katsuki & Miyatake 2009).

The high frequency of underwater oviposition in the study population of *E. lindenii* was an interesting finding. Utzeri et al. (1983), in their study in Italy, did not report underwater oviposition being as common as it was in the present study in Algeria. The warmer environmental conditions are most likely the main factors responsible for increasing the frequency of underwater oviposition. In a hot climate like that in North Africa, water evaporation is fast and thus eggs are exposed to the risk of drought resulting in the death of embryos (Fincke 1986). The positive relationship between oviposition duration and water depth reveals that the latter can be used as a surrogate for oviposition duration, but it also suggests that females distribute eggs vertically along the plant stem probably to reduce predation

(ANHOLT 1994). Further studies should investigate the relationship between clutch size, oviposition duration, and water depth. The absence of a correlation between oviposition depth and male density around oviposition sites shows that, since males cannot harass females underwater, their density has no effect on the vertical stratification of oviposition. We suggest that males have not evolved such harassment behaviour because of the high predation costs that involve going underwater to seize ovipositing females. However, other ecological factors affecting the tendency to oviposit underwater, such as water transparency and vegetation type, have been suggested for other damselflies (DOLNÝ et al. 2014).

This study presents new information on the reproductive behaviour of *E. lindenii* from the margin of its southernmost range. Future studies should focus on the fitness costs of underwater oviposition and whether this behaviour may vary in lotic habitats where water flow might be a problematic limiting factor. The interaction of abiotic and biotic cues in determining behavioral decisions during oviposition will help to understand behavioral plasticity and the resolution of conflicting cues.

Acknowledgements

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