Emergence ecology of Orthetrum cancellatum: temporal pattern and microhabitat selection (Odonata: Libellulidae)

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Published online: 15 Aug 2014.

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Summary. Knowledge of both phenology and habitat selection are important assets for conservation and management purposes. Generally, aquatic insect species have an optimal season and larval microhabitat in which their survival and reproductive success are high. In odonates, emergence is usually a seasonal-restricted process during which the insect has to find a good timing and a convenient microhabitat to carry out the final ecdysis out of the water. We investigated temporal emergence pattern and microhabitat choice in *Orthetrum cancellatum* in northeast Algeria, which represents the southern limit of its distribution range. The emergence season lasted 56 days starting from 30.IV and ended on 25.VI, showing a peak on 19.V. The time by which 50% of the annual population has emerged (EM_{50}) was 20 days and the sex ratio was slightly male-biased, with 51.53%. Final instar larvae chose areas with relatively dense vegetation, and this selection was positively dependent on the mean vegetation height and not on sex or body size. Height selection was positively dependent only on the support height that the larva chose. We suggest that larvae consider both predation risks and mainly local microclimate to select their emergence site.

Résumé. Ecologie de l'émergence d'*Orthetrum cancellatum*: configuration temporelle et sélection de microhabitat (Odonata : Libellulidae). Les connaissances à la fois de la phénologie et de la sélection d'habitat constituent une base importante pour la conservation des espèces et leur gestion. En général, les espèces d'insectes aquatiques ont une saison optimale et un microhabitat larvaire qui maximisent leur survie et leur succès reproducteur. Chez les odonates, l'émergence est d'habitude un processus restreint à une seule saison durant laquelle l'insecte doit trouver le bon moment et le microhabitat adéquat pour la sortie de l'eau et la mue imaginale. Nous avons étudié la configuration temporelle de l'émergence et la sélection de microhabitat chez *Orthetrum cancellatum* au nord-est de l'Algérie. L'espèce trouve là la limite sud de son aire de distribution. La saison d'émergence a duré 56 jours à partir du 30.IV pour finir le 25.VI, avec un pic le 19.V. Le délai médian d'émergence, qui correspond à l'émergence de 50% de la population annuelle (EM_{50}), a été de 20 jours, avec un sex-ratio de 51.53%, légèrement biaisé vers les mâles. Les larves de dernier instar ont choisi des endroits avec une végétation plutôt dense et cette sélection a été positivement dépendante de la hauteur de support disponible. Nous avons suggéré que les larves considèrent à la fois les risques de prédation et les microclimts locaux pour sélectionner leur site d'émergence.

Keywords: microhabitat; vegetation; emergence; Libellulidae; Odonata; *Orthetrum cancellatum*

Habitat selection is thought to be the result of ecological and evolutionary processes such as density dependence, interspecific interaction, resource distribution, spatial scale, and individual variations (reviewed in Morris 2003). It is common that different populations of the same species living in different areas may be adapted to different habitats as a result of differences in local environmental conditions (Grzybowski et al. 1994; Parody & Parker 2002; Väli et al. 2004; Johnson et al. 2006).

However, one population living in the same environment can display substantial individual variation in habitat use due to habitat heterogeneity (different microhabitats) (Williams 1983; Kronfeld-Schor et al. 2001) and intrinsic factors like body size, age, sex, or body condition (Hedrick 1993; Kroon et al. 2000; Szabo 2002; Davey et al. 2005; Heithaus et al. 2007). Optimal habitat use is usually followed by higher survival and reproductive success, which puts good patches of habitat under high

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intraspecific competition (Jaenike & Holt 1991). Determining which factors affect habitat choice in a population is crucial from ecological, evolutionary, and conservation perspectives.

Aquatic insects including odonates carry out several molts during the aquatic larval stage in order to reach the final instar and leave the water. Choosing the site where the final ecdysis takes place is crucial (Corbet 1999). The final ecdysis is usually a time consuming process that is achieved on a support out of the water. During this stage, the individual is mostly motionless, defenseless, and unable to escape potential predators. At the end of the process, the individual's body and wings are soft and vulnerable to any distortion that may last over the entire life and result in lower foraging and reproductive success (Corbet 1999). Therefore, the individual should have enough space to safely expand its wings and enough cover to hide itself from predators. In contrast to zygopterans, anisopterans expand their wings first then open them for the first time (horizontal to the body). Due to this and the larger body size, it is reasonable to assume that anisopterans require more space than zygopterans during emergence. In the same way, larger Anisoptera and larger individuals should also need more space than smaller ones. It has been shown that the microhabitat choice of individuals depends on both extrinsic factors such as wind and intrinsic factors such as body size and sex (Cordero 1995; Khelifa et al. 2013). Although the understanding of emergence site selection is crucial for species conservation, only a few studies have investigated this aspect.

Orthetrum cancellatum (L. 1758) is a large libellulid (Anisoptera) with a wide distribution throughout the Palearctic. Although the species' ecology and life cycle have well been studied in Europe (Schmidt 1982; Pickess 1987; Jödicke & Jödicke 1996; Katzur 1998), they have not been investigated in the southern limits of its distribution range. Because it is important to know when and where a species emerges to better conserve it, we investigated in the current study the temporal pattern of emergence and factors affecting emergence site selection in a population situated in the Seybouse watershed (Northeast Algeria), where the species is known to be rare (Khelifa et al. 2011).

Material and methods

The study was carried out in a 0.4 ha artificial pond 3 km northwest from El Fedjoudj province, Guelma, Algeria (36°31′ 54.30″N, 7°22′48.08″E). This fishless pond harbored *Anax imperator* and *A. parthenope* as top aquatic predators and *O. cancellatum* as the largest libellulid. Emergent plants were restricted to the banks and mainly consisted of *Typha angustifolia, Scirpus lacustris, Cyperus longus*, and *Paspallum distichum*. Bank vegetation was heterogeneous, i.e. dense in some parts and sparse in others. Terrestrial vegetation was mainly herbaceous and dominated by *Dittrichia viscosa* and *Lythrum junceum*.

Visits of the pond started on 20.IV.2013, i.e. before the flight period had begun, in order to record the exact onset of the emergence season. Daily exuvia collections were conducted along a transect of 100 m of bank vegetation (1 m wide) in late afternoon (at 4.00 pm local time). No exuviae were left in the sampling area after every visit. The end of the emergence season was noted when no exuviae were collected for seven consecutive visits. EM_{50}, the number of days after which 50% of the annual population has emerged, was calculated for both sexes to determine the degree of emergence synchrony and potential sexual differences.

The microhabitat at emergence was characterized using 'exuvia height' (He) (vertical distance from the water surface to the rear tip of exuvia) and 'vegetation density' (Dv) (vegetation cover around the exuvia). Both exuvia height (He) and total support height (Hs) were measured to the nearest centimeter using a 5 m decameter. By placing a 1×1 m^2 quadrat around the exuvia position vegetation density was estimated to the nearest 5%. Mean vegetation height (MHs) within the quadrat was estimated by randomly taking five supports and measuring the height to the nearest centimeter. When the exuvia was observed far from the water, the distance was estimated to the nearest centimeter. Exuviae that were found lying on the ground or on the water surface were not considered in the analyses of microhabitat choice. The sex was determined in the laboratory. Since the emergence season of the species is relatively long, day of the emergence season (ES), the number of days since the first recorded individual, was considered as a potential main effect in further analysis (e.g. all individuals that emerged in day 1 had an ES = 1). The total length of the exuviae was measured with a digital caliper to the nearest mm, as an indicator of body size.

All statistical analyses were carried out using the software R (R project 3.0.1), http://CRAN.R-project.org/. A chi-square test was conducted to determine if the sex ratio at emergence significantly deviated from 1:1. Kolmogorov–Smirnov 2-sample test was performed to test whether there was a significant difference in the emergence curve of males and females. An ANCOVA was carried out to compare the seasonal trend of body size between sexes. Wilcoxon rank sum test was conducted to test for sexual size dimorphism using body length. Residuals of the response variables (exuvia height) were checked for normality and homogeneous of variance. Model selection using the corrected Akaike information criterion (AICc) was carried out to identify which factors influence microhabitat choice at emergence. We used AICc instead of AIC because the number of included parameters was rather high in relation to sample size (Burnham & Anderson 2002). Collinearity between continuous explanatory variables (Hs, MHs, body length, ES, and Dv) was checked before setting the models. Significant correlations were recorded between body length and ES (Spearmann rank test: r = 0.4, $p = 0.002$) and Dv with MHs (Spearmann rank test: r = 0.44, $p < 0.0001$), therefore only one of them was taken as a main effect in the model. We set a global model for both Dv and He. Because Dv was proportional data, beta regression models were conducted using the betareg package (Gruen et al. 2012) using the following equation: Dv ~ sex + MHs + Hs + Si. The global model for He was fitted with a multiple linear regression: He ~ sex + MHs + Hs + Si. The dredge function of the MuMIn (multi-model inference) which generates all possible combinations between the main effects was used for model selection including two-way interactions between all variables (Barton 2013). The models were ranked according to their importance (lowest AICc and highest weight). We performed model averaging using the model.avg function on the top models showing a cumulative weight ≤ 2. Only the 10 top models are shown hereafter. Dv is presented as proportion varying from 0.05 to 1. Values are presented as mean ± SD.

Results

No congeneric species coexisted with *O. cancellatum* but exuviae of four other libellulids were rather common: *Crocothemis erythraea, Sympetrum fonscolombii, Trithemis annulata*, and *T. arteriosa*. A total of 130 exuviae were collected over 57 days of emergence. In 2013 the emergence season started on 30.IV and ended on 25.VI, showing a peak on 19.V. Only males were recorded on the first day of emergence. EM_{10}, EM_{50}, and EM_{90} were recorded after 5, 20 and 40 days of emergence and represented 8.77%, 35.09 % and 70.18% of the emergence period, respectively. There was no significant difference in the temporal pattern of emergence between sexes (Kolmogorov–Smirnov 2-sample test, $p = 0.47$). EM_{50} was 21 days for males and 19 days for females (Figure 1). The sex ratio was slightly male-biased with 51.53%, although the difference was not significant ($\chi^2 = 0.12$, $p = 0.72$). Figure 2 shows that the body length of both sexes increased throughout the season. ANCOVA showed that the effect of ES was significant on body length but both sex and interaction between sex and ES were not significant (Table 1, Figure 2).

Seven exuviae (7.4%) were detected out of the water at a mean distance of 101.42 ± 95.99 cm to the water line (86.66 ± 41.63 cm and 112.5 ± 129.96 cm for males and females, respectively). Table 2 presents model selection for Dv. Only two models showed a ΔAICc less than 2, and

the most parsimonious model (model 1 in Table 2) had only MHs as a main effect (Table 2). The relationship between Dv and MHs was positive with no differences between sexes (Figure 3). Mean exuvia height was 45.65 ± 21.82 cm, and it was not significantly different between sexes (Wilcoxon rank sum test: W = 1003, $p = 0.58$). Model selection for He showed that six models had a ΔAICc less than 2, and all of them had Hs effects. The most parsimonious model (model 4 in Table 3) included only the effect of Hs, showing that the higher the support the higher the exuviae (Figure 4).

Discussion

Orthetrum cancellatum showed an asynchronous emergence and could be considered as a "summer species" (Corbet 1954). In the study season, the species had an EM50 of 20 days, which is similar to that of *Aeshna cyanea* in the UK (EM50 = 25 days; Corbet 1962). However, EM50 may vary from one year to another (Maier & Wildermuth 1991; Cham 2012) depending on the environmental conditions. Using information on emergence and flight season, we infer that the species was univoltine in the study pond; however, it is possible that other populations living in habitats with high food productivity display partial or even total bivoltinism. In fact, a case of bivoltinism in *O. cancellatum* has already been

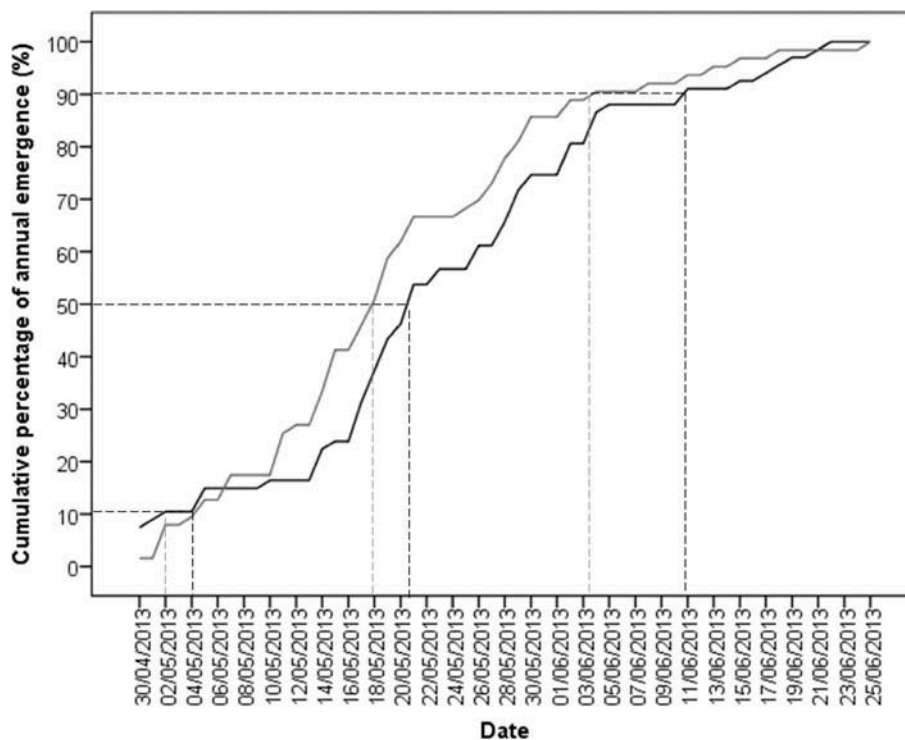**Figure 1.** Cumulative % emergence of *Orthetrum cancellatum* in 2013. Black and gray curves represent male and females respectively. EM_{10}, EM_{50}, and EM_{90} are represented with vertical lines for both sexes (black for males and gray for females).
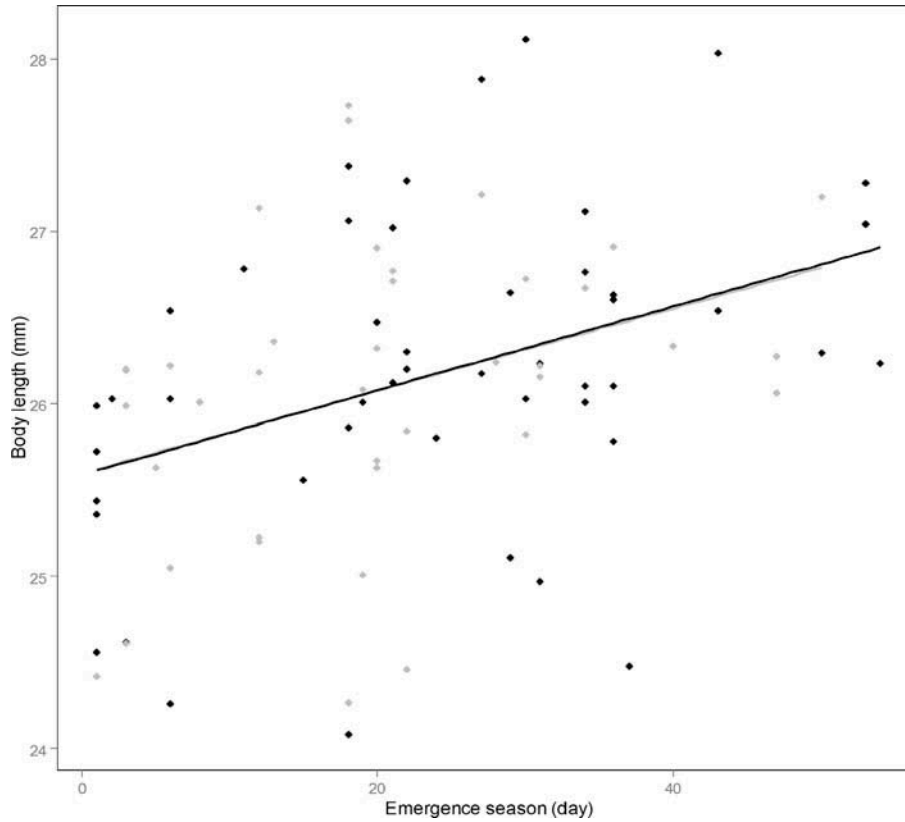
Figure 2.   Seasonal pattern of body size of exuviae of *Orthetrum cancellatum*. Black circles represent males while gray ones represent females. The regression lines of males and females are presented in black and gray, respectively.

Table 1.   Summary of ANCOVA for body length pattern during the emergence season in *Orthetrum cancellatum.*

	Sum of squares	Degree of freedom	F-value	P-value
Intercept	8486.5	1	11100	< 0.0001
ES	6.3	1	8.27	0.004
Sex	0.1	1	0.108	0.742
ES:sex	0.3	1	0.375	0.541
Residuals	80.8	106		

Notes: Multiple R^2 = 0.1178, adjusted R^2 = 0.09281, F-statistic = 4.717, *p*-value: 0.003. ES: emergence season.

Table 2.   Multimodel selection table showing the 10 top dredged models explaining vegetation density choice at emergence. The most parsimonious model is shown in bold.

N	Model	df	logLik	AICc	ΔAICc	Weight
1	**Dv ~ Int + MHs**	**3**	**20.911**	**−35.5**	**0**	**0.241**
2	Dv ~ Int + MHs + Hs	4	21.27	−34.1	1.48	0.115
3	Dv ~ Int + MHs + Sex	4	20.923	−33.4	2.17	0.081
4	Dv ~ Int + Size + MHs	4	20.917	−33.3	2.19	0.081
5	Dv ~ Int + MHs + MHs × Hs	5	21.614	−32.5	3.05	0.053
6	Dv ~ Int + Size + MHs+ Hs	5	21.277	−31.8	3.72	0.038
7	Dv ~ Int + Size + MHs + Size × MHs	5	21.27	−31.8	3.73	0.037
8	Dv ~ Int + MHs+ Sex + Hs	5	21.019	−31.3	4.24	0.029
9	Dv ~ Int + MHs + Sex + MHs × Sex	5	20.93	−31.1	4.41	0.027
10	Dv ~ Int + Size + MHs + Sex	5	20.928	−31.1	4.42	0.027

Note: He: exuvia height; Hs: support height; MHs: mean vegetation height; Int: intercept; df: degree of freedom; logLik: log Likelihood; AICc: corrected Akaike information criterion.
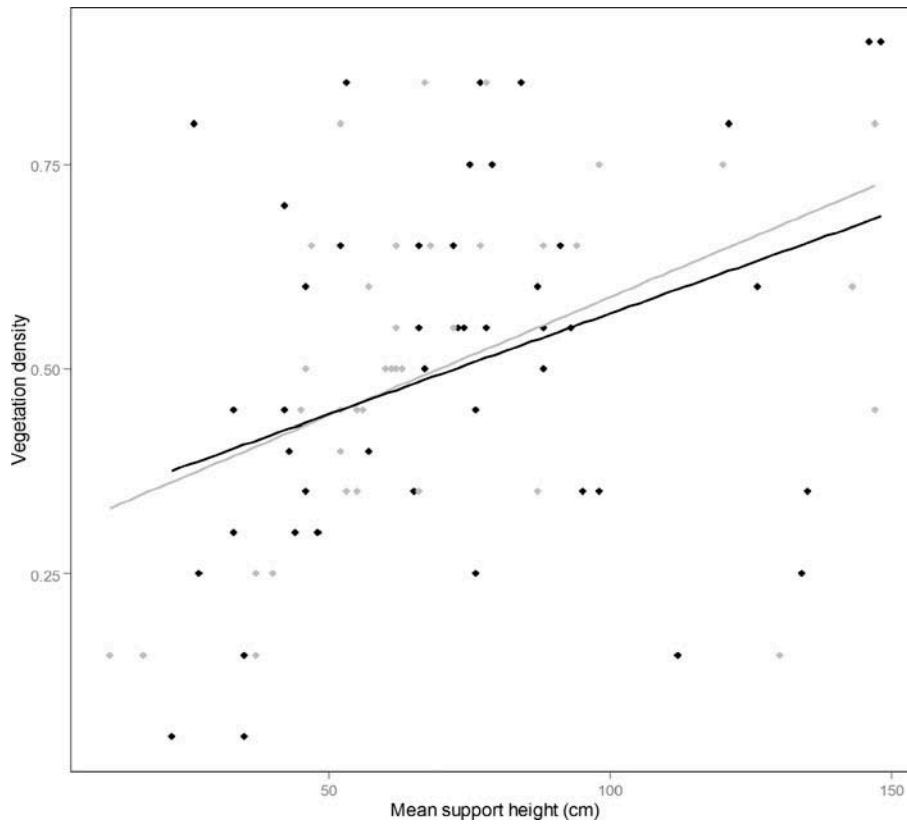
Figure 3. Relationship between vegetation density (Dv) and mean support height (MHs). Dv values were arcsin transformed. Black circles represent males while gray ones represent females. The regression lines of males and females are presented in black and gray, respectively. Multiple R^2 = 0.161.

Table 3. Multimodel selection table showing the 10 top dredged models explaining exuvia height choice at emergence. The most parsimonious model is shown in bold.

N	Model	df	logLik	AICc	ΔAICc	Weight
1	He ~ Int + MHs + Sex + Hs + Hs × Sex	6	−372.412	757.9	0	0.128
2	He ~ Int + Hs + Sex + Hs × Sex	5	−373.813	758.4	0.49	0.1
3	He ~ Int + MHs + Sex + Hs + Hs × Sex + MHs × Sex	7	−371.748	758.9	1.04	0.076
4	**He ~ Int + Hs**	**3**	**−376.61**	**759.5**	**1.63**	**0.057**
5	He ~ Int + MHs + Hs	4	−375.637	759.8	1.89	0.05
6	He ~ Int + MHs + Sex + Hs + MHs × Hs + Hs × Sex	7	−372.223	759.9	1.99	0.047
7	He ~ Int + Size + MHs + Sex + Hs + Hs × Sex	7	−372.262	759.9	2.07	0.046
8	He ~ Int + Size + Sex + Hs + Sex × Hs	6	−373.644	760.3	2.46	0.037
9	He ~ Int + Size + MHs + Sex + Hs + MHs × Sex + Hs × Sex	8	−371.582	761	3.14	0.027
10	He ~ Int + Size + Sex + Hs + Size × Hsx + Hs × Sex	7	−372.943	761.3	3.43	0.023

Note: He: exuvia height; Hs: support height; MHs: mean vegetation height; Int: intercept; df: degree of freedom; logLik: Log Likelihood; AICc: corrected Akaike information criterion.

noted in the Camargue, southern France (Katzur 1998). Although males emerged first, females reached EM_{50} two days earlier than males. Similar observations were made in the riverine *Onychogomphus costae* in the same region (Zebsa et al. submitted a). Both the small sample size and the slightly male-biased sex ratio could be the reason of this sexual variation. Further investigations should be carried out in large populations in order to determine whether

sexual difference in emergence pattern is the norm for the species. The male biased sex ratio, on the other hand, is probably the result of differential mortality during egg and/ or larval stages (Corbet & Hoess 1998; Cordero Rivera & Stoks 2008). Furthermore, sexual biased mortality during emergence due to differential microhabitat use is another possibility. The question of whether habitat selection at emergence differs between sexes has been raised in this
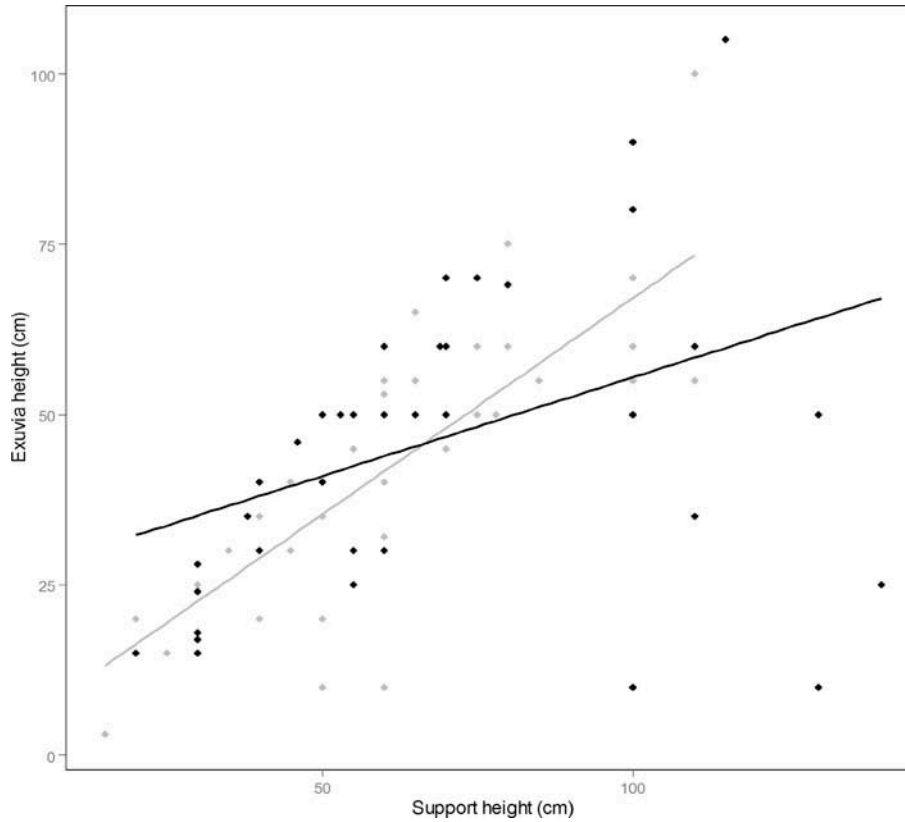
Figure 4. Relationship between exuvia height (He) and support height (Hs). Black circles represent males while gray ones represent females. The regression lines of males and females are presented in black and gray, respectively. Multiple $R^2 = 0.329$.

study. One unusual finding is that body size increased with the emergence season; a result that is rarely found in previous studies (Banks & Thompson 1985; Inden-Lohmar 1997; Purse & Thompson 2003). Sugimura (1983) showed an increasing trend in body size in *Deiela phaon* from Japan; however, the sample size was too small. Another study on the North African endemic *Gomphus lucasii* showed for the first time the same increasing pattern with a high sample size (Zebsa et al. submitted b). This was explained by the fact that late emerging larvae found a release from intra- and interspecific competition as the emerging season progressed, leading to more food availability and higher growth rate during their late aquatic life (Zebsa et al. submitted b).

The choice of vegetation density of *O. cancellatum* was influenced only by the mean support height around the exuvia, which means that emerging larvae chose patches with dense vegetation and long supports. Vegetated areas with long stands provide shelter against wind (Khelifa et al. 2013) and potential aerial predators (birds). Worthen (2010) suggested that the dragonfly *Epitheca spinosa* had an anti-flooding adaptation by using long supports and carrying out the ecdysis at higher strata. Exuviae vertical stratification estimated during this study (45.65 ± 21.82 cm) was similar to that recorded by Cordero (1995), 48.07 ± 3.47 cm for the

same species, and for two other large dragonflies, *Boyeria irene* (46.08 ± 7.38 cm) and *Anax imperator* (43.08 ± 3.87 cm). Similarly to studies on other odonates (*Erythromma lindenii*, Khelifa et al. 2013; *Gomphus lucasii*, Zebsa et al. submitted b), we found that larva selected higher strata when the support was high. Local microclimate (air temperature, relative humidity) is likely to change along the support and individuals might climb higher searching for warmer and less humid areas in order to receive the sun's first rays, dry faster and leave the water earlier. In addition, the species is known to delay emergence when the environmental conditions are not favorable (Jödicke & Jödicke 1996). The significant interaction between sex and support height means that males and females responded differently to the support height. Sexual difference in post-emergence behavior is a potential reason for such variation in microhabitat selection, but this requires further studies.

The current study showed for the first time the temporal pattern of emergence of *O. cancellatum* in the southern limit of its distribution range, and factors influencing larval microhabitat selection during emergence. Such exuvia-based studies should be promoted especially on threatened species because they have no effect on the population dynamics and provide reliable information on species ecology, seasonality, and status.

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