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EMERGENCE ECOLOGY AND BODY SIZE DIMORPHISM IN *SYMPETRUM FONSCOLOMBII* AND *S. MERIDIONALE* (ODONATA: LIBELLULIDAE)

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Abstract. The study of dragonfly emergence provides insights into the understanding of their life history, ecology, and adaptation to abiotic and biotic factors. Here we investigate the emergence ecology and body size of two congeneric dragonflies (*Sympetrum fonscolombii* Selys, and *S. meridionale* Selys) in Northeast Algeria, highlighting the seasonal pattern, sex ratio at emergence, sexual size dimorphism (SSD), and vertical stratification. We found that both species, *S. fonscolombii* in particular, showed quite asynchronous emergence. In both species, and especially in the larger *S. meridionale*, sex ratio was found to be female-biased, which is in line with the hypothesis of a negative relationship between SSD and sex ratio. There was no seasonal pattern of body size observed in both species. In *S. meridionale*, SSD with regard to both body and wing sheath length was male-biased, while in *S. fonscolombii*, it was male-biased with regard to body length and female-biased with regard to wing length. Vertical stratification depended on support height (the higher the support, the higher the height of exuvia fixation) but had a complex relationship with the body size. The biological significance and implications of the vertical stratification-body size relationship are discussed.

INTRODUCTION

Emergence is an important event in the life cycle of odonates, during which major transitions in habitat, morphology, lifestyle, and behavior take place (Corbet 1980). It is a relatively lengthy process, in the course of which individuals stay motionless at the mercy of aquatic, terrestrial and aerial predators (Farkas, Móra, and Dévai 2012; Purse and Thompson 2003). Thus, odonates have developed antipredatory strategies as to where and when to emerge in order to reduce the likelihood of predation, and intraspecific competition for the best microhabitat might happen. In addition, the left-over material of emergence, exuvia, is used as a conservation tool to indirectly assess the distribution of species, taxonomy, ecology, and behavioral plasticity (Raebel et al. 2010; Khelifa, Zebsa, Kahalerras et al. 2013; Foster and Soluk 2004; Khelifa 2012; Khelifa et al. 2018).

There is both intra- and interspecific variation in the vertical stratification of ecdysis in odonates (Corbet 1999; Cordero 1995). It has been suggested that larger species occupy higher strata than smaller species (Cordero 1995). However, there are many intrinsic and extrinsic factors that may predict the individual-based vertical stratification. For example, physiological sex- or body size-related differences might affect microhabitat selection (Zebsa, Khelifa, and Kahalerras 2014; Zebsa et al. 2014). In addition, environmental factors such as wind can also affect the vertical distribution of individuals in the following way: the higher the wind speed, the lower larvae climb to avoid perturbation which could lead to potential permanent injury (Khelifa, Zebsa, Amari et al. 2013). Besides, flooding can also induce larvae to climb higher (Worthen 2010). Therefore, to gain a better knowledge of species requirements and explain demographic events such as colonization and predation, it is essential to understand the environmental factors that influence habitat choice during emergence.

Sexual size dimorphism (SSD) in odonates has been studied relatively well (Johansson, Crowley, and Brodin 2005; Serrano-Meneses et al. 2008; Crowley and Johansson 2002). Most species exhibit SSD, but dragonflies and damselflies often show different patterns. Using body length as a surrogate of body size, Serrano-Meneses et al. (2008) showed that damselflies display male-biased SSD, but dragonflies do not show significant SSD. However, selection may act differently on other traits such as wing length, which may result in the reversal of SSD with regard to this particular trait (Bouiedda et al. 2018). It is essential to investigate whether this occurs in other odonata species.

Body size of odonates is known to vary across the season (Corbet 1999). The generally observed pattern is seasonal body size decline (Corbet 1999; Falck and Johansson 2000; Purse and Thompson 2003; Wong-Muñoz et al. 2011), which means that individuals who emerge early in the season are often larger than those that emerge late in the season. It has been suggested that this pattern could be ecologically explained by the higher temperature later in the season, which increases development rate and results in body size decline (Vannote and Sweeney 1980). However, more recently, a seasonal increase of body size has been recorded in Northeast Algeria in different species (Bouiedda et al. 2018; Hadjoudj et al. 2014; Zebsa, Khelifa, and Kahalerras 2014), demonstrating that the seasonal body size pattern of odonates may change geographically.

Although the emergence of different dragonfly and damselfly species was investigated in North Africa, where the climate is among the driest in the Palearctic (Zebsa et al. 2014; Zebsa, Khelifa, and Kahalerras 2014; Mahdjoub et al. 2015; Khelifa, Zebsa, Kahalerras et al. 2013; Khelifa, Zebsa, Amari et al. 2013; Khelifa 2017; Hadjoudj et al. 2014), the emergence ecology of many other species such as *Sympetrum fonscolombii* (Selys, 1840) and *S. meridionale* (Selys, 1841) is still unknown, which in turn represents a gap in our knowledge of the biology, ecology and adaptation of odonates in the region. In this study, we investigate the seasonal pattern of emergence, sexual size dimorphism, seasonal pattern of body size, and microhabitat selection in two congeneric species, *S. fonscolombii* and *S. meridionale*, in Northeast Algeria, where the climate is particularly warm. These species have different life histories; *S. fonscolombii* does not have a diapause at the egg stage and starts reproducing in early spring, while *S. meridionale* shows an obligatory diapause and starts reproducing in autumn.

MATERIALS AND METHODS

Study site

Each species was studied at a separate site. *Sympetrum fonscolombii* was investigated in Beddoud pond, an artificial ovoid pond with an area of ca 0.4 ha and the circumference of 0.3 km, located 3 km northwest of El Fedjoudj province, Guelma, Algeria (36°31'54"N, 7°22'48"E). The site, which is at an elevation of about 300 m is characterized by the riparian vegetation dominated by *Typha angustifolia*, *Scirpus lacustris*, *Cyperus longus*, and *Paspallum distichum*. The species coexists with large populations of *Orthetrum cancellatum*, *Anax imperator*, *A. parthenope*, *Crocothemis erythraea*, *Orthetrum cancellatum*, *Trithemis annulata* and *T. arteriosa*. The second site, Messmassa pond (36°22'0"N, 7°24'48"E), where *S. meridionale* was studied, is a 0.1 ha-marshy pond at an elevation of about 1010 m with abundant vegetation consisting of *Sparganum* sp., *Ranunculus aquatilis*, *Phragmites australis*, *Juncus* sp. and *P. distichum*. The odonatofauna of the pond was dominated by *Anax imperator*, *A. parthenope*, *Aeshna mixta*, *C. erythraea*, *S. striolatum* and *S. sanguineum*.

Exuviae sampling

We did not compare the emergence ecology of the two species since they were sampled on two different sites and in different seasons. This study is a parallel analysis of the emergence of two widespread dragonfly species. *Sympetrum fonscolombii* was studied in 2013, while *S. meridionale* in 2016. Daily visits to the study sites of both species started on the 20th of May and continued until the end of the emergence season. We recognized the end of the emergence season when no exuviae or tenerals were detected after 10 consecutive visits. Exuviae were collected in the late afternoon (at 04:00 pm) along a 60 m transect. Vegetation and other potential supports were checked carefully for the presence of exuviae. We made sure that no exuviae were left within the study transect after each visit in order to obtain a good estimation of the temporal pattern of emergence. When we collected exuviae, we recorded the height of the chosen support (Hs), and the height (He) of the exuvia fixation (with respect to the water surface) with a 10 m decameter to the nearest 1 cm. To gain a better understanding of vertical stratification it is important to take into account both Hs and He, because we acquire the information on the potential height with Hs and the realized height with He. Exuviae were brought to the laboratory, where they were sexed and measured. We measured the lengths of the body and wing sheath using a digital caliper to the nearest 0.01 mm. We calculated EM50, which is the number of days when half (50%) of the population emerged.

Statistical analyses

All statistical analyses were conducted with R 3.3.2 (R Development Core Team 2018). Sex ratio was tested for departure from unity with Chi-square tests. Two-way ANOVAs were conducted to reveal potential SSD with regard to both body and wing sheath length using species and sex as factors. The seasonal pattern of body size was assessed in both species with multiple linear regressions using the Julian date, species and sex as explanatory variables and body and wing sheath lengths as response variables. To investigate factors that affect vertical stratification of exuviae, we assessed the relationship of He (response variable) with Hs, body size and sex (explanatory variables), testing for potential interactions between variables with multiple linear regressions. Values below are mean ± SD.

RESULTS

Temporal pattern of emergence

A total of 447 exuviae of *S. fonscolombii* were collected during 55 days, starting from 23 May to 20 July 2013. Figure 1 presents the cumulative percentage of emerged individuals. The peak of exuviae was recorded in the third week of June, while EM50 was 24 days. Due to the fragmentation of exuviae, the total number of the exuviae sexed was 430 with 240 females and 190 males. Sex ratio was slightly female-biased (55.8%; $\chi^2 = 183.8$, $p < 0.0001$).

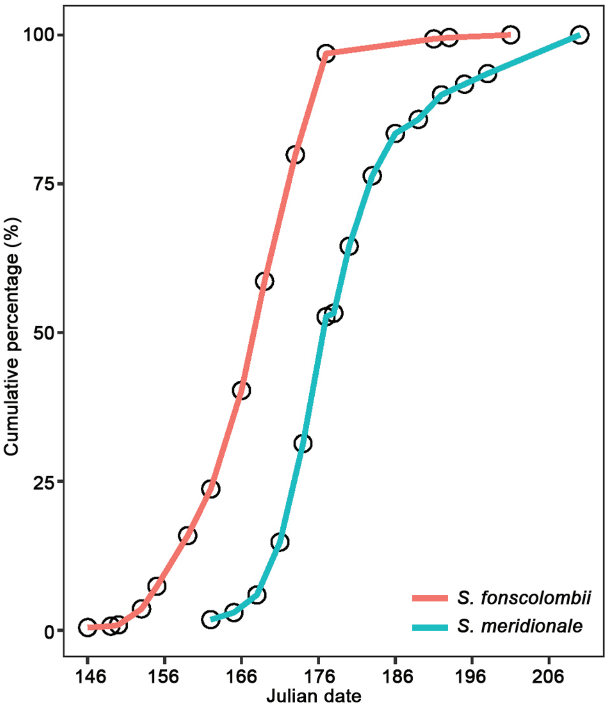

Figure 1. Cumulative percentage of the emergent population of *Sympetrum fonscolombii* and *S. meridionale*.

We collected 169 exuviae of *S. meridionale* between 11 June and 29 July 2016, showing that the emergence season lasted 48 days. The cumulative percentage of emerged individuals is presented in Figure 1. The maximum number of exuviae was recorded in the last week of June. EM50 was 16 days. We could not sex five individuals because the parts essential for sex determination were damaged. We recorded almost twice as many females as males with a total of 110 females and 54 males, showing a significantly female-biased sex ratio at emergence (67.1%; $\chi^2 = 98$, $p < 0.0001$).

Body size

Table 1 shows the mean ± SD of both sexes of the two dragonfly species. *S. meridionale* was larger than *S. fonscolombii* (ANOVA: $F_{1,566} = 29.5$, $p < 0.0001$ for body length; ANOVA: $F_{1,567} = 14.03$; $p < 0.0001$ for wing sheath length). Males were found to be larger than females in both species (ANOVA: $F_{1,566} = 2.95$, $p = 0.04$ for body length; ANOVA: $F_{1,567} = 2.32$; $p = 0.001$ for wing sheath length). There was a significant interaction between species and sex (ANOVA: $F_{1,566} = 3.03$, $p = 0.04$ for body length; ANOVA: $F_{1,567} = 2.99$; $p = 0.0002$ for wing sheath length), revealing that the difference in body length between males and females was greater in *S. meridionale* than in *S. fonscolombii*, however, the difference in wing sheath length was inverted, i.e. *S. meridionale* males had larger wing sheaths than females, but *S. fonscolombii* females had larger wings than males (Figure 2). Furthermore, there was no significant seasonal pattern of body length and wing sheath length recorded in both species (Table 2), showing that individuals were as large in the early season as in the late season ($R^2 = 0.14$, $p = 0.26$, for body length; and $R^2 = 0.08$, $p = 0.10$ for wing sheath length).

Microhabitat choice

The mean height of exuvia fixation (He) was 28.16 ± 22.45 cm and 22.35 ± 8.00 cm for *S. fonscolombii* and *S. meridionale*, respectively. In both species, there was no significant difference determined in He between

Table 1. Mean ± SD of body and wing sheath length of both sexes of *Sympetrum fonscolombii* and *S. meridionale*.

Trait	Species	Sex	Mean	SD	n
Body length (mm)	*S. fonscolombii*	Female	16.10	0.95	240
	S. fonscolombii	Male	16.16	0.85	190
	S. meridionale	Female	16.51	0.71	110
	S. meridionale	Male	16.92	0.75	54
Wing sheath length (mm)	*S. fonscolombii*	Female	5.98	0.41	240
	S. fonscolombii	Male	5.77	0.49	190
	S. meridionale	Female	6.20	0.45	110
	S. meridionale	Male	6.32	0.61	54

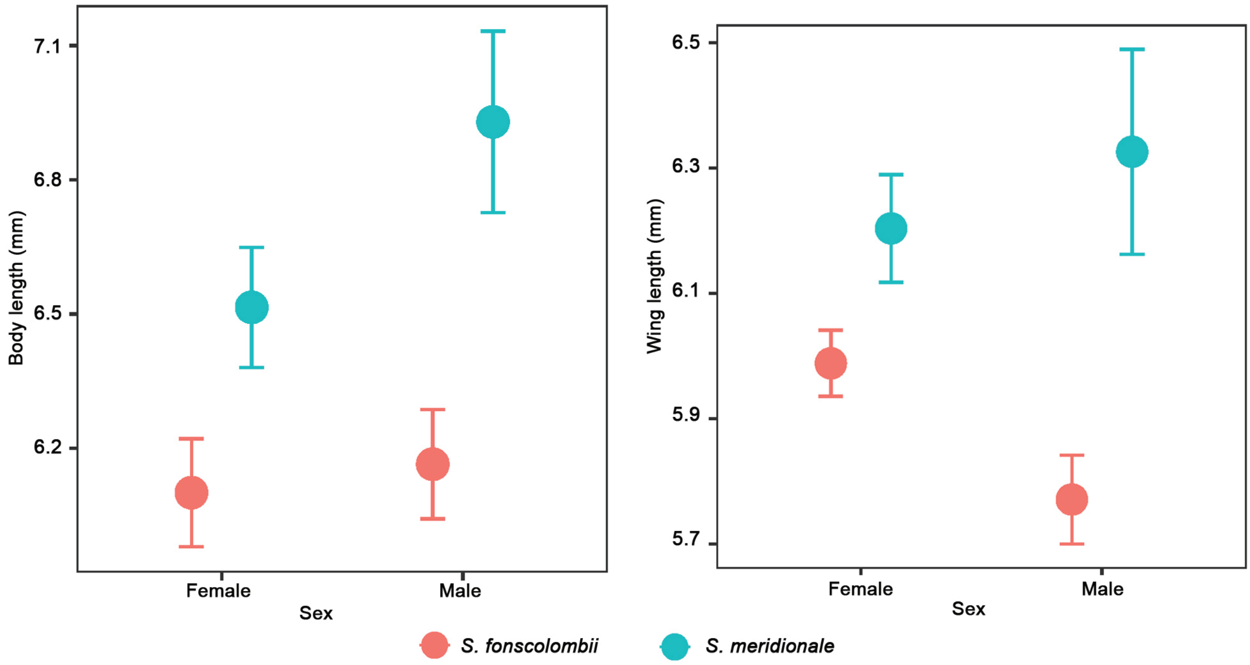

Figure 2. Body and wing sheath length of exuviae of *Sympetrum fonscolombii* and *S. meridionale* for both sexes. Error bars are 95% confidence intervals.

Table 2. Summary results of the seasonal pattern of body and wing sheath length of exuviae of *Sympetrum fonscolombii* and *S. meridionale*.

Body length		Estimate	Std. Error	*t* value	*p* value
S. meridionale	Intercept	15.519	1.264	12.280	<0.0001
	Season	0.006	0.007	0.790	0.431
	Sex [Male]	4.553	2.326	1.958	0.052
	Season: Sex [Male]	–0.023	0.013	–1.782	0.076
S. fonscolombii	Intercept	18.786	1.261	14.902	<0.0001
	Season	–0.016	0.007	–2.132	0.033
	Sex [Male]	–2.190	2.016	–1.087	0.277
	Season: Sex [Male]	0.013	0.012	1.101	0.271
Wing sheath length		**Estimate**	**Std. Error**	***t* value**	***p* value**
S. meridionale	Intercept	7.061	0.872	8.094	<0.0001
	Season	–0.005	0.005	–0.984	0.326
	Sex [Male]	–3.095	1.538	–2.012	0.046
	Season: Sex [Male]	0.018	0.008	2.094	0.037
S. fonscolombii	Intercept	6.354	0.651	9.767	<0.0001
	Season	–0.002	0.004	–0.562	0.574
	Sex [Male]	–0.651	1.017	–0.640	0.523
	Season: Sex [Male]	0.003	0.006	0.423	0.673

sexes (Table 3). However, He was positively related to the height of the support (Hs) in both species (Table 3), showing that the higher the support, the higher the larvae climbed to perform ecdysis. Furthermore, He showed a complex relationship with body length, with a positive effect of the main effect and a negative interaction with Hs. This means that when Hs is short, larger individuals choose higher He, but when Hs is longer, larger individuals choose lower He (Figure 3). The ratio He/Hs was 0.51 and 0.54 in *S. fonscolombii* and *S. meridionale*, respectively, which means that larvae selected the height that was about 50% of the total support height. In addition, the ratio He/Hs did not show a significant seasonal pattern in both species (Table 4).

Table 3. Summary results of the relationship between He, Hs and body size of exuviae of *Sympetrum fonscolombii* and *S. meridionale*.

		Estimate	Std. Error	*t* value	Pr (>|t|)
S. meridionale	Intercept	8.828	9.078	0.973	0.332
	Hs	0.443	0.028	15.807	<0.0001
	Sex [Male]	–0.938	0.890	–1.054	0.293
	Body	–0.273	0.546	–0.499	0.618
S. fonscolombii	Intercept	–101.007	54.279	–1.861	0.065
	Hs	2.934	0.698	4.203	<0.0001
	Sex [Male]	–1.062	2.991	–0.355	0.723
	Body	6.496	3.344	1.943	0.054
	Hs: Body	–0.155	0.043	–3.577	0.000

He: exuvia height fixation; Hs: support height.

Table 4. Summary results of the linear model regressing the ratio He/Hs against season and body size of *Sympetrum fonscolombii* and *S. meridionale*.

		Estimate	Std. Error	*t* value	*p* value
S. meridionale	Intercept	0.794	0.342	2.320	0.022
	Season	0.000	0.001	0.002	0.998
	Sex [Male]	–0.010	0.026	–0.396	0.692
	Body	–0.014	0.016	–0.866	0.388
S. fonscolombii	Intercept	0.432	0.686	0.630	0.530
	Season	0.001	0.002	0.247	0.805
	Sex [Male]	–0.012	0.048	–0.257	0.798
	Body	0.001	0.032	0.043	0.966

He: exuvia height fixation; Hs: support height.

DISCUSSION

Our study presents new information on the biology, morphology and habitat preferences of two dragonfly species widespread in the Palearctic at their southern range limit. Both species had a female-biased sex ratio at emergence. Male-biased SSD with regard to both body and wing sheath length was observed in *S. meridionale*, but reversed SSD was noticed in *S. fonscolombii*, that is, males had longer bodies than females, but females had larger wings than males. There was no seasonal pattern of body size. The choice of vertical position for ecdysis depended on the height of the support and the body size.

S. fonscolombii started emerging much earlier than *S. meridionale*, probably due to the colder climate at the location where the latter species was studied (300 m vs 1010 m of elevation) (Samways and Niba 2010). Elevational cline in emergence and reproductive seasons has been observed in odonates (Amari et al. 2019) and other insects (McCoy 1990). Both *S. fonscolombii* and *S. meridionale* had a relatively long emergence season, which is typical of life histories of the ‘summer species’ type (Corbet 1954). A northern population (southern Sweden) of *S. sanguinum* showed a more synchronized emergence (Falck and Johansson 2000), probably due to the shorter warm season (seasonal constraints) (Nilsson-Örtman et al. 2013). *Sympetrum meridionale* showed a more synchronous emergence. The interspecific difference in emergence pattern is likely due to the different life histories. *Sympetrum meridionale* diapause at the egg stage, which suggests that hatching is likely more synchronized than in other species with direct embryonic development on which the hatching season depends, mostly, on the duration of the reproductive season (Verberk, Siepel, and Esselink 2008). Sex ratio at emergence was significantly female-biased in both species, especially in *S. meridionale*. This is probably due to the difference in mortality rates during the larval stage. The higher mortality in males might be due to its

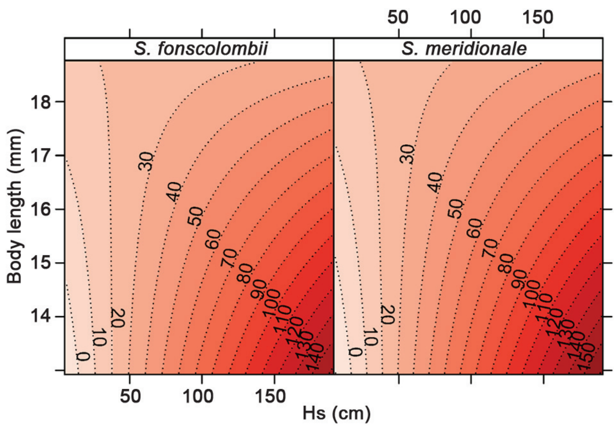

Figure 3. The relationship between vertical stratification of exuviae (He). Support height (Hs) and body length of *Sympetrum fonscolombii* and *S. meridionale*. Contours refer to the predicted He.

larger size (more conspicuous) or less vigilant (more active) foraging behavior (Baker, Elkin, and Brennan 1999). This finding is in line with the negative relationship between sex ratio and SSD (Johansson, Crowley, and Brodin 2005).

Body and wing sheath lengths showed male-biased SSD in *S. meridionale*, but reversed SSD patterns in *S. fonscolombii*, that is, males had a longer body but shorter wings. A positive relationship between larval and adult size was found in odonates (Serrano-Meneses, Azpilicueta-Amorín et al. 2007), which means that our findings are likely to be applicable to the adult stage. SSD was greater in the larger species *S. meridionale* than in the smaller species *S. fonscolombii* which is concordant with the Rench's rule (Johansson, Crowley, and Brodin 2005); however, to confirm this hypothesis, it would be necessary to increase the sample size in terms of the species number. The different patterns of SSD with regard to body and wing lengths suggest that selection acted differently on body and wing traits in the two species. Longer bodies may confer stronger ability to defend territories, acquire a mate and reproduce (Serrano-Meneses, Córdoba-Aguilar et al. 2007), whereas larger wings may give flight advantage, which could also translate into greater dispersal ability and greater foraging success (Rundle et al. 2007). The larger wings of *S. fonscolombii* females could be the result of their more dispersive behavior than that of males, as is the case with many dragonflies (Angelibert and Giani 2003). This study showed the first case of absence of a seasonal pattern of body size in North Africa, where other odonates exhibited either an increase (Hadjoudj et al. 2014; Zebsa, Khelifa, and Kahalerras 2014) or a decrease (Mahdjoub et al. 2015). The selection of the height at which ecdysis is conducted by both *S. fonscolombii* and *S. meridionale* was found to be similar, although they live in different environments (open vs. marshy habitat). Larvae selected heights that mainly depended on the height of the chosen support, fixing themselves in positions that were on average half of the support height. Surprisingly, this pattern did not change over the season, meaning that even when the vegetation structure changes with the season, microhabitat choice does not change. The vertical stratification in sexes of both species was similar, which suggests that predation during emergence in terrestrial habitat acts on both males and females similarly. Like in riverine dragonflies (Zebsa et al. 2014; Zebsa, Khelifa, and Kahalerras 2014), body size (body length) played a significant role in determining the vertical stratification of individuals in both species, although the relationship was quite complex. When the support was short (<50 cm), body size was positively correlated to He, but when the support was larger (>50cm), body size was negatively correlated to He. This complex body size-dependent microhabitat choice might be due to abiotic and/or biotic factors. Firstly, it could be partly caused by wind (Khelifa, Zebsa, Amari et al. 2013). It is likely that the stability of the plant support against the wind is higher when it is short, thus climbing higher does not jeopardize the emerging individuals, but rather keeps them farther from terrestrial predators. However, when the plant support is tall, the stability becomes mass-dependent, i.e. larger individuals tend to occupy lower strata because it is more stable for them, whereas smaller individuals can occupy higher strata. Secondly, microhabitat choice might be partly governed by intra- and interspecific competition for favorable ecdysis space; a hypothesis that has been raised by Corbet (1957). Larger larvae may exclude smaller larvae from the best microhabitats (places with more stability and less predation risk) that increase their probability of emerging successfully. Thus when the support is long, it is risky to be at higher strata because of the potential detection by predators and being blown away by wind, so larger larvae occupy relatively low heights. However, when support is short and thus stable, it is better to stay in higher positions to avoid terrestrial predators (Mellal, Zebsa et al. 2018). These hypotheses should be tested with experiments, which manipulate abiotic and biotic characteristics of the microhabitat to pinpoint the main factors that influence vertical stratification of odonates.

The present study presents new data on the life history, SSD and microhabitat choice at emergence of two *Sympetrum* species in North Africa. This study opens a debate about: (1) the implication of the biased sex ratio at emergence on the evolution of territoriality and mating system (Suhonen, Rantala, and Honkavaara 2008), (2) the frequency of trait-based reversal of SSD in odonates and the understanding of the mechanisms underlying these patterns (Blanckenhorn 2005), (3) the role of body size in determining the microhabitat choice and the implication of the latter on adult survival and reproductive success (Serrano-Meneses, Córdoba-Aguilar et al. 2007). There are also aspects related to the abiotic and biotic factors which could influence spatial and temporal niche axes of emergence that require future investigations. Even though the species studied are listed as "least concern" in the IUCN Red list, the data presented in this paper broaden our current knowledge of the emergence ecology of local odonates and potential niche similarities among species (Khelifa, Zebsa, Moussaoui et al. 2013), which might be of interest for better management and conservation of other threatened odonates (Khelifa et al. 2018, 2016; Mellal, Bensouilah et al. 2018).

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