



## Niche partitioning at emergence of two sympatric top-predator dragonflies, *Anax imperator* and *A. parthenope* (Odonata: Aeshnidae)

Nedjwa Boucenna, Amin Kahalerras, Nabila Boukhemza-Zemmouri, Moussa Houhamdi & Rassim Khelifa

To cite this article: Nedjwa Boucenna, Amin Kahalerras, Nabila Boukhemza-Zemmouri, Moussa Houhamdi & Rassim Khelifa (2018): Niche partitioning at emergence of two sympatric top-predator dragonflies, *Anax imperator* and *A. parthenope* (Odonata: Aeshnidae), *Annales de la Société entomologique de France (N.S.)*, DOI: [10.1080/00379271.2018.1426492](https://doi.org/10.1080/00379271.2018.1426492)

To link to this article: <https://doi.org/10.1080/00379271.2018.1426492>



Published online: 01 Feb 2018.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)



## Niche partitioning at emergence of two sympatric top-predator dragonflies, *Anax imperator* and *A. parthenope* (Odonata: Aeshnidae)

Nedjwa Boucenna<sup>a</sup>, Amin Kahalerras<sup>a</sup>, Nabila Boukhemza-Zemmouri<sup>a</sup>, Moussa Houhamdi<sup>b</sup> & Rassim Khelifa<sup>\*c</sup>

<sup>a</sup>Department of Biology, Faculty of Biological and Agricultural Sciences, University of Tizi Ouzou, Tizi Ouzou 15000, Algeria;

<sup>b</sup>Department of Nature and Life Sciences, Faculty of Nature and Life Sciences and Earth and Universe Sciences, University of 8 May 1945, Guelma 24000, Algeria; <sup>c</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zurich CH-8057, Switzerland

(Accepted le 8 janvier 2018)

**Summary.** In natural communities, closely related species are phenotypically similar but usually spatially and/or temporally isolated. In odonates, interspecific competition occurs not only at the larval or adult stage but also during emergence. We investigated the emergence of two sympatric *Anax* species, focusing on the temporal pattern, vertical stratification, and body size trend over time. *Anax imperator* started to emerge two weeks earlier than *A. parthenope* but most of the emergence season overlapped. Both species showed an asynchronous emergence and the median emergence date was 10.3 days earlier in *A. imperator*. Sex ratio at emergence was not significantly different from 1:1. Body size of both species increased significantly over time, which contrasts many previous studies. The height of exuvia fixation was not significantly different between species but the larger species *A. parthenope* selected longer supports.

**Résumé.** Répartition des niches écologiques lors de l'émergence de deux Libellules sympatriques, *Anax imperator* et *A. parthenope* (Odonata : Aeschnidae). Dans les communautés naturelles, les espèces étroitement apparentées sont phénotypiquement similaires mais généralement isolées spatialement et/ou temporellement. Chez les Odonates, la compétition interspécifique se produit non seulement au stade larvaire ou adulte, mais aussi lors de l'émergence. Nous avons étudié l'émergence de deux espèces d'*Anax* sympatriques, en nous concentrant sur le modèle temporel, la stratification verticale et l'évolution de la taille du corps au fil du temps. *Anax imperator* a commencé à émerger deux semaines plus tôt qu'*A. parthenope*, mais la majeure partie de la saison d'émergence se chevauchait. Les deux espèces ont montré un décalage, la date d'émergence médiane se situant 10,3 jours plus tôt chez *A. imperator* que chez *A. parthenope*. Le sex-ratio à l'émergence n'était pas significativement différent de 1 : 1. La taille du corps des deux espèces augmente de façon significative avec le temps, ce qui semble contredire de nombreuses études antérieures. La hauteur de la fixation de l'exuvie n'est pas significativement différente entre les espèces, mais les individus de l'espèce la plus grande, *A. parthenope*, ont choisi des supports plus élevés.

**Keywords:** Competition; congenetics; exuvia; site selection; North Africa

Species coexistence has been a central topic in community ecology. Ecological theory predicts that species that are closely related and live in sympatry are expected to compete and eventually exclude one another (Chesson 2000). However, field studies have shown that such cases exist in nature (Harper et al. 1961; Broadhead & Wapshere 1966; Rydin & Barber 2001) and that niche partitioning through differential microhabitat use or seasonal and diurnal temporal pattern tends to reduce interspecific competition and allow coexistence (Schoener 1974). Understanding the key factors involved in niche partitioning is key for better management of biodiversity (Cornell & Lawton 1992).

Species of *Anax* are among the largest and most massive dragonflies in the world. They occur in the whole Palearctic, and dominate most freshwater systems. Larvae of *Anax* species represent the top predators of most fishless

ecosystems. They belong to the most widely used predators in experiments of community ecology and evolutionary biology (Blois-Heulin 1990; Werner & McPeck 1994; Werner & Anholt 1996). Although many studies have been devoted to their larval stage, little is known about the interspecific interaction during emergence between sympatric congeneric species of *Anax*.

In this study, we investigated two Palearctic widespread species of *Anax*, namely *A. imperator* Leach, 1815 and *A. parthenope* Sélys, 1839. The former species is widespread in Africa, Europe, and central and Southwest Asia (Mitra 2013a). The latter species is widespread in Europe, North Africa, and most Asia (Mitra 2013b). The geographic range of both species is shifting northward probably because of climate change, but the expansion is faster in *A. imperator* (Dijkstra & Lewington 2006). However, due to their high

\*Corresponding author. Email: [rassimkhelifa@gmail.com](mailto:rassimkhelifa@gmail.com)

flight ability, erratic individuals can be found further north in Scandinavia. In addition to the overlapping geographic range, those congeneric species of similar body size often exist together in the same system. Given that closely related species are less likely to coexist because of their ecological and phenotypic similarities (Colwell & Fuentes 1975), we hypothesize that two *Anax* species should be either temporally and/or spatially isolated (Schoener 1974; Khelifa et al. 2013b).

During emergence, individuals choose a suitable substrate to climb in order to conduct ecdysis (Corbet 1999). The latter process is time-consuming and thus puts the individuals in a vulnerable situation because the odonate is unable to move or escape predators. Ecdysis microhabitat is not only related to predation avoidance but probably also to microclimate (Bennett & Mill 1993) and intra- and interspecific competition for the best ecdysis location (Zesba et al. 2014a). In fact, during the peak of emergence the same substrate might be used by several individuals at the same time, and thus individuals might climb on each other and damage the larvae carrying out ecdysis (Corbet 1957), which would be deadly for trampled individuals. In addition, there is high intra- and interspecific variation in the vertical stratification of odonates, usually depending on body size (Cordero 1995; Khelifa et al. 2013a).

Although the life history of both species has been investigated mostly in Europe (Corbet 1957; Cayrou & Céréghino 2005), no study has been carried out in North Africa where the climate is typically Mediterranean. In this study, the emergence of both species was surveyed in two populations that live in sympatry in a natural habitat in Northeast Algeria, focusing particularly on the differences in temporal pattern, vertical stratification, and seasonal pattern of body size.

## Material and methods

### Study site

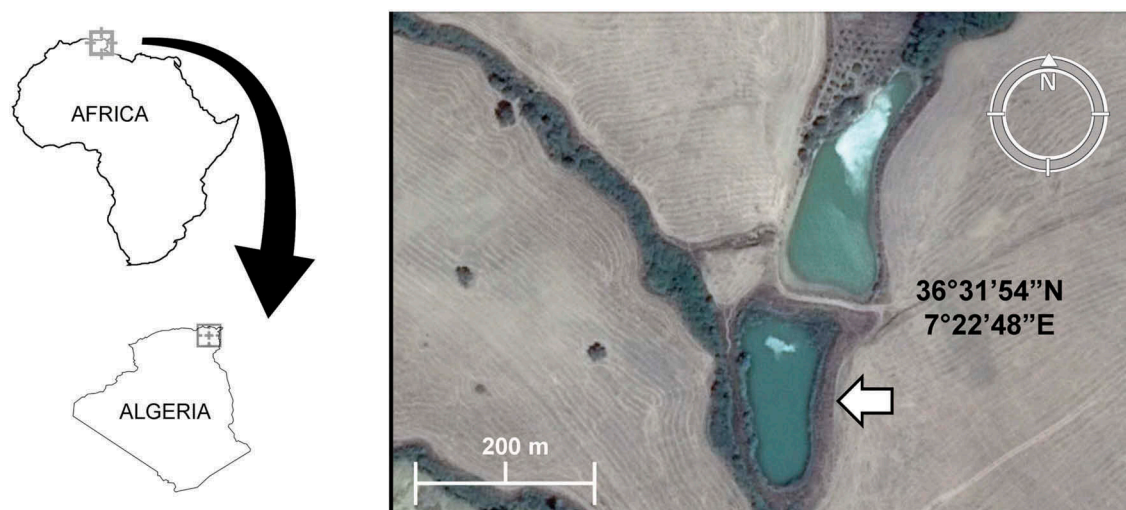
Beddoud pond is 0.4 ha artificial water body located 3 km northwest from El Fedjoudj province, Guelma, Northeast Algeria ( $36^{\circ}31'54''\text{N}$ ,  $7^{\circ}22'48''\text{E}$ ) (Figure 1). The pond was ovoidal with emergent plants only at the littoral zone. The dominant plants in the banks were *Typha angustifolia*, *Scirpus lacustris*, *Cyperus longus*, and *Paspalum distichum*. The study species coexisted with *Crocothemis erythraea* (Brullé, 1832), *Orthetrum cancellatum* (Linnaeus, 1758), *Sympetrum fonscolombii* (Sélys, 1840), *Trithemis annulata* (Palisot de Beauvois, 1807), *T. arteriosa* (Burmeister, 1839), *Sympecma fusca* (Vander Linden, 1820), *Ischnura graellsii* (Rambur, 1842), *Coenagrion scitulum* (Rambur, 1842) and *C. puella* (Linnaeus, 1758).

### Exuvia collection

Earlier visits were conducted in the pond to check the beginning of emergence, starting from early April 2013. When emergence started, exuviae were collected every other day within a transect of 120 m in the afternoon until the end of emergence, which was recorded after 10 visits of unsuccessful collections. No exuvia was left after each visit. Exuviae were sexed in the laboratory. EM50 was calculated as the number of days at which half of the annual population emerged.

### Vertical stratification

The position of the exuvia in the substrate is a good indicator of microhabitat choice because it usually stays fixed at the same place where the ecdysis took place. Two parameters were noted in the field to assess the vertical stratification of the two study species. First, the height of exuvia fixation (HE), which is the vertical distance from the water (or the ground) level to the top of the head of the individual. Second, the support height (HS), which is the height of the substrate chosen at emergence. Exuviae that were found on the water surface (9.7% and 12.1% for *A. imperator* and *A. parthenope*, respectively) were not considered in the analysis.



**Figure 1.** Geographic location of Beddoud pond in Northeast Algeria. The white arrow indicates the study site.

### Seasonal pattern of body size

To test how body size changes across the emergence season, linear regressions are often applied. However, the choice of the morphological trait that reflects body size is important. We measured three morphological traits with a digital caliper to the nearest 0.01 mm, including body length, head width, and hind wing sheath length. We performed pairwise correlations between the three morphological traits and found a positive correlation between body length and head width (Spearman correlation:  $r = 0.31, p < 0.0001$ ), body length and wing sheath length ( $r = 0.28, p < 0.0001$ ), and wing sheath length and head width ( $r = 0.14, p = 0.002$ ). Due to the collinearity between the morphological traits, we decided to drop body length and head width in further analysis of body size because the body and head are usually sensitive to distortion during emergence. In order to investigate the seasonal pattern of body size for each species, we used only wing sheath length and the day of the year (Julian date) as explanatory variables.

### Statistical analyses

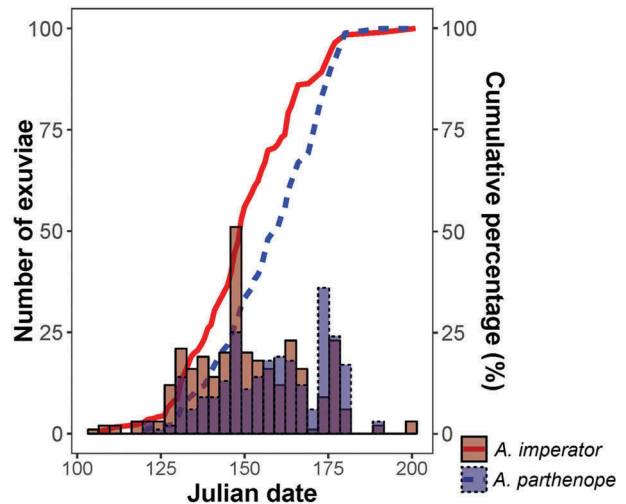
All analyses were conducted with the software R3.3.2 (R Development Core Team 2017). We tested for significant differences of the phenology of emergence between species by comparing the 10th, 50th, and 90th percentiles of the distribution using the function *qcomhd* in the WRS package for R (Wilcox & Schönbrodt 2014), which computes a bootstrap test using Harrell–Davis quantile estimator with 1000 simulations. We used the same analysis to test for potential differences between sexes for each species. Chi-square tests were conducted to test (1) if the proportion of males at emergence is equivalent to that of females and (2) if the two species used different types of plant supports for emergence. Wilcoxon rank tests were performed to test for differences in the height of exuvia fixation and support height between species and sexes. Simple linear regressions were computed to assess the seasonal trend of body size and vertical stratification. We carried out Spearman correlations between vertical stratification and morphological parameters.

## Results

### Temporal pattern of emergence

The temporal pattern of emergence of the two species overlapped but it showed some differences (Figure 2). *Anax imperator* emerged within 53 days starting from 16 April while *A. parthenope* emerged in 41 days starting from 30 April. The phenological distribution of the two species was compared using three quantiles which correspond to the early phase (quantile 10%), middle phase (quantile 50%), and late phase (quantile 90%) of the emergence phenology. We found that the phenology of *A. imperator* was earlier than that of *A. parthenope*, showing a difference of 4.90 days [95%CI: 1.17–10.0;  $p < 0.0001$ ] for the early phase, 10.37 days [6.12–14.24;  $p < 0.0001$ ] for the middle phase, and 1.72 days [0.13–6.79;  $p = 0.02$ ] for the late phase (Table 1).

The difference in the temporal pattern between sexes was not significant for the early, middle and late phenological phase in both species ( $p > 0.05$ ; Table 1). In *A. imperator*, males emerged two days earlier than females whereas males started to emerge three days later in *A.*



**Figure 2.** Temporal pattern of emergence of *Anax imperator* and *A. parthenope*. This figure shows the temporal distribution of the number of exuviae collected (left vertical axis) and the cumulative percentage of emergence (right vertical axis). Julian date 100, 125, 150, 175, and 200 are 10 April, 5 May, 30 May, 24 June, and 19 July.

*parthenope*. EM50 of *A. imperator* was 32 in both sexes, and it was 29 in females and 31 in males. Sex ratio at emergence of both species was not significantly different from the equilibrium (*A. imperator*:  $\chi^2 = 0.05, p = 0.82$ ; *A. parthenope*:  $\chi^2 = 3.01, p = 0.08$ ). The percentage of females was 50.6% in *A. imperator* and 55.4% in *A. parthenope*.

### Vertical stratification

Larvae of both species selected similar types of supports in the banks of the pond to carry out ecdysis (Table 2). Both species emerged exclusively on plant supports. Exuviae were mainly found on leaves and stems of *Typha angustifolia* and *Scirpus lacustris*, which together represented nearly 90% of supports used. Other supports that were rarely used were *Cyperus longus*, *Carex riparia*, *Paspalum distichum*, and branches of shrubs. Considering all plant support types for emergence, there was no interspecific significant difference in the distribution of larvae across supports ( $\chi^2 = 7.36, df = 5, p = 0.19$ ), which suggests that they used the same microhabitats for emergence.

Characteristics of the vertical stratification of both species are presented in Table 3. There was no significant interspecific and sexual difference in the height of exuvia fixation ( $p > 0.05$ ), but exuvia height was positively correlated to support height and season in both species ( $p < 0.0001$ ; Table 4; Figure 3). The significant negative interaction of HS-by-season shows that in late season the larva climbed lower with respect to the support height than in early season ( $p = 0.002$ ). The significant positive interaction between HS-by-sex shows that males climber

Table 1. Summary results of the bootstrap quantile estimator of the early (quantile 10%), middle (quantile 50%) and late phenological phase (quantile 90%).

Differences	q	n1	n2	ED1	ED2	ED1-ED2	CI.low	CI.up	P value
		( <i>A. imp</i> )	( <i>A. par</i> )	( <i>A. imp</i> )	( <i>A. par</i> )				
Interspecific	0.1	316	260	130.66	135.56	-4.90	-10.00	-1.17	<0.0001
	0.5	316	260	149.00	159.38	-10.37	-14.24	-6.12	<0.0001
	0.9	316	260	174.93	176.65	-1.73	-6.80	-0.13	0.02
Intersexual ( <i>A. imperator</i> )	q	n1	n2	ED1	ED2	ED1-ED2	CI.low	CI.up	P value
		( <i>Female</i> )	( <i>Male</i> )	( <i>Female</i> )	( <i>Male</i> )				
	0.1	156	160	130.54	130.42	0.12	-3.64	3.52	0.93
	0.5	156	160	148.95	149.17	-0.22	-4.32	3.76	0.93
	0.9	156	160	174.64	174.29	0.35	-7.10	7.51	0.91
Intersexual ( <i>A. parthenope</i> )	0.1	144	116	134.36	137.07	-2.71	-8.38	4.74	0.44
	0.5	144	116	158.90	159.92	-1.01	-5.75	5.07	0.80
	0.9	144	116	178.62	175.76	2.86	-0.68	5.61	0.06

Note: The variable is the emergence date (ED) and the unit is days. q, quantile; n, sample size; *A. imp*, *A. imperator* and *A. par*, *A. parthenope*; CI.low, lower 95% confidence interval for the interspecific difference between Julian dates; CI.up, upper 95% confidence interval of the difference.

Table 2. Percentage of plant support used by *Anax imperator* and *A. parthenope* for emergence in the study site.

Plant support	<i>A. imperator</i>	<i>A. parthenope</i>
<i>Typha angustifolia</i>	62.85% (N = 181)	72.41% (N = 168)
<i>Scirpus lacustris</i>	25.35% (N = 73)	17.24% (N = 40)
Shrubs (branches)	8.33% (N = 24)	7.76% (N = 18)
<i>Cyperus longus</i>	2.43% (N = 7)	2.16% (N = 5)
<i>Carex riparia</i>	0.69% (N = 2)	0% (N = 0)
<i>Paspalum distichum</i>	0.35% (N = 1)	0.43% (N = 1)
Total number of exuviae	288	232

Note: Exuviae that were found on the water surface were not considered here.

higher than females with respect to the support height ( $p = 0.01$ ). In addition, HS was significantly affected by species (two-way ANOVA:  $p = 0.005$ ), but not by sex ( $p = 0.35$ ) and species-by-sex interaction ( $p = 0.22$ ). HS was 14.6 cm [95%CI: 4.3–24.9] longer in *A. parthenope* than in *A. imperator*.

### Seasonal pattern of body size

A multiple linear regression assessing the temporal pattern of wing sheath length for each species and sex was carried

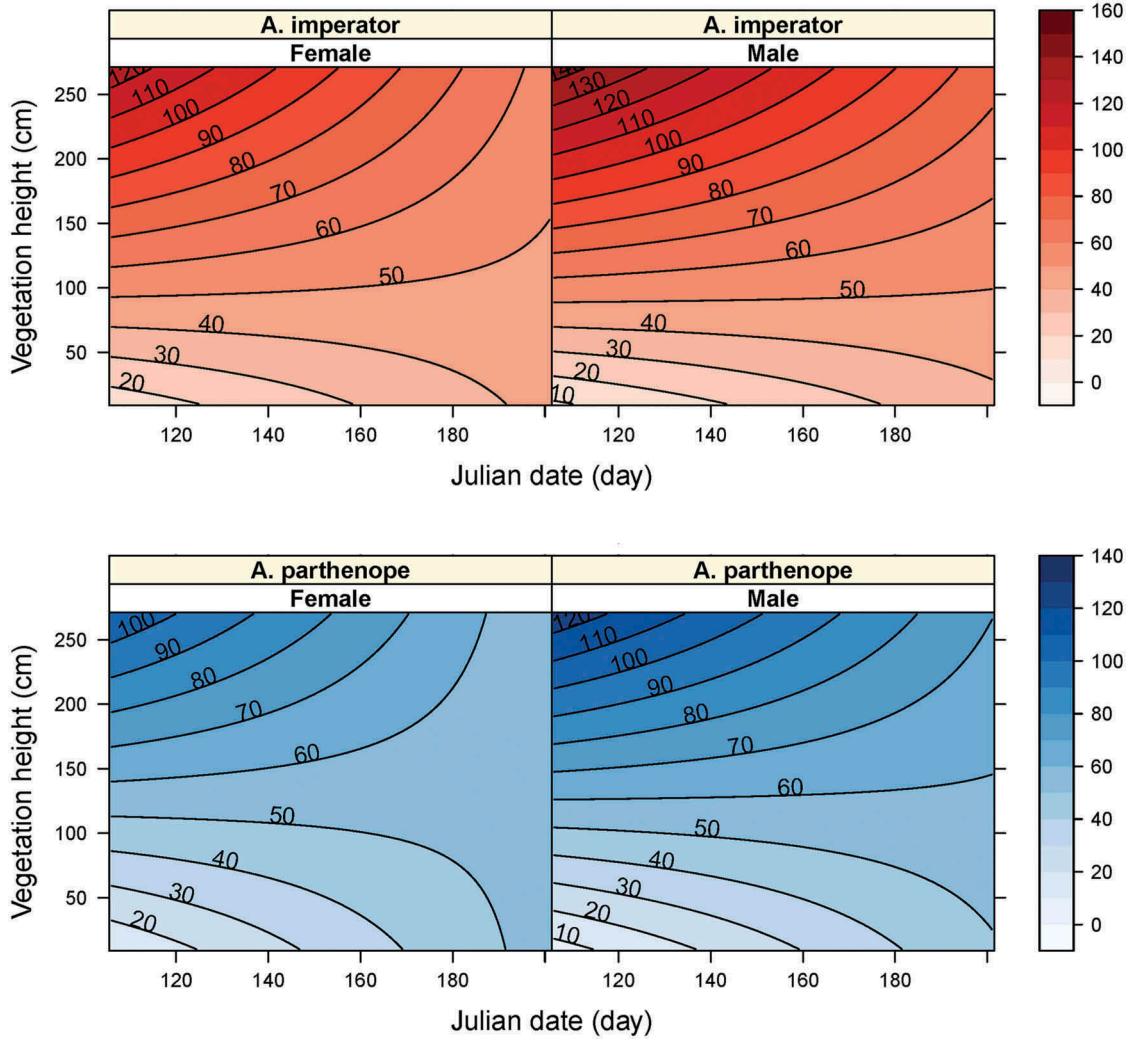
out (Table 5). We found that the wing sheath length was not significantly different between species ( $p = 0.55$ ), but it was marginally significantly different between sexes in *A. imperator* with females showing slightly longer wing sheaths ( $p = 0.059$ ). However, the significant season effect ( $p < 0.0001$ ) shows that wing sheath length increased across the season, and the non-significant effect of season-by-species ( $p = 0.79$ ) shows that the increasing pattern is applicable for the two species and the magnitude of the increase was not different among species (Figure 4). The non-significant season-by-sex term ( $p = 0.10$ ) shows that

Table 3. Exuvia vertical stratification of *Anax imperator* and *A. parthenope*.

Variable	<i>A. imperator</i>		<i>A. parthenope</i>	
	Female	Male	Female	Male
HE (cm)	47.64 ± 25.37 (132)	52.73 ± 28.66 (136)	49.21 ± 27.83 (108)	53.03 ± 29.21 (83)
HS (cm)	91.23 ± 48.50 (132)	101.62 ± 56.88 (136)	109.80 ± 60.96 (108)	110.77 ± 61.28 (83)
HE/HS	0.59 ± 0.25 (132)	0.57 ± 0.21 (136)	0.52 ± 0.26 (108)	0.55 ± 0.24 (83)

Note: HE: height of exuvia fixation, HS: support height. Values between brackets are sample size.





**Figure 3.** Relationship of vertical stratification of the two *Anax* species with emergence season and support height. Color gradient reflects the predicted height of the exuvia. Julian date 120, 140, 160, and 180 are 30 April, 20 May, 9 June, and 29 June.

the wing sheath length of both males and females increased similarly.

**Table 4.** Summary results of the multiple linear regression assessing the pattern of the height of exuvia fixation at emergence (HE) across support height length (HS), season (Julian date), species (*Anax imperator* and *A. parthenope*) and sex.

	Estimate	Standard error	t-value	p-value
Intercept	-26.045	23.641	-1.102	0.271
HS	0.855	0.201	4.253	<0.0001
Season	0.340	0.156	2.174	0.030
Species [ <i>A. parthenope</i> ]	-17.577	21.171	-0.830	0.407
Sex [Male]	-6.468	4.517	-1.432	0.153
Season:Species [ <i>A. parthenope</i> ]	0.147	0.141	1.042	0.298
HS:Season	-0.004	0.001	-3.110	0.002
HS:Sex [Male]	0.093	0.039	2.387	0.017
HS:Species [ <i>A. parthenope</i> ]	-0.060	0.041	-1.456	0.146

Note: *A. imperator* and female are used as the baseline levels for contrast calculations.  $R^2 = 0.27$ .

### Discussion

Studies on the ecology of closely related species that live in sympatry are important and informative about the ecological and behavioral mechanisms that allow their coexistence in natural habitat. In theory, such species are expected to show segregation at least at a niche axis which could be spatial (microhabitat) or temporal (season). Our study revealed similarities and differences in the emergence pattern and ecology of two large congeneric dragonflies that dominate most Palearctic freshwater systems.

Both species showed an asynchronous emergence, and so are typically summer species (Corbet 1954). Although the phenology of emergence of the two species presented a major overlap, the temporal distribution of *A. parthenope* was relatively later than that of *A. imperator*. For instance, the difference in the median date of emergence was about 10 days. It is likely that this small temporal shift plays a

Table 5. Summary results of the multiple linear regression assessing the seasonal pattern of wing sheath length at emergence in *Anax imperator* and *A. parthenope*.

	Estimate	Standard error	t-value	p-value
Intercept	8.838	0.337	26.262	<0.0001
Season	0.009	0.002	4.051	<0.0001
Species [ <i>A. parthenope</i> ]	0.257	0.435	0.590	0.556
Sex [Male]	-0.814	0.429	-1.896	0.059
Season:Species [ <i>A. parthenope</i> ]	-0.001	0.003	-0.263	0.793
Season:Sex [Male]	0.005	0.003	1.641	0.102
Species [ <i>A. parthenope</i> ]:Sex [Male]	-0.060	0.093	-0.645	0.519

Note: The model includes season, species and sex as main effects. *A. imperator* and female are used as the baseline levels for contrast calculations.  $R^2 = 0.20$ .

role in reducing the interspecific interaction between both species during emergence. Experimental studies raising the two species separately and together would reveal if development and emergence are manipulated as a result of interspecific competition.

Sex ratio was at about the equilibrium in *A. imperator*, similar to that presented by Corbet (1957) for the same species in the UK. The percentage of females of *A. parthenope* was slightly larger than that of males, which was similar to the observation of Taketo (1995) on *A. parthenope julius* with 54%. In fact, a female-biased sex ratio in dragonflies is typical (Corbet & Hoess 1998; Cordero-Rivera & Stoks 2008), and it probably results from differences in mortality rates at the larval stage due to sexual differences in activity or vigilance.

The two species chose similar types of supports and similar heights to carry out ecdysis. The mean height was similar to that noted by Cordero (1995) in *A. imperator* ( $43.0.8 \pm 3.87$  cm). However, the supports selected by *A. parthenope* were higher than those selected by *A. imperator*, which confirms spatial isolation between the species. It is difficult at this stage to know whether the observed sites occupied by exuviae of each species reflects the preferred microhabitat or is the result of competitive exclusion. This question can be answered

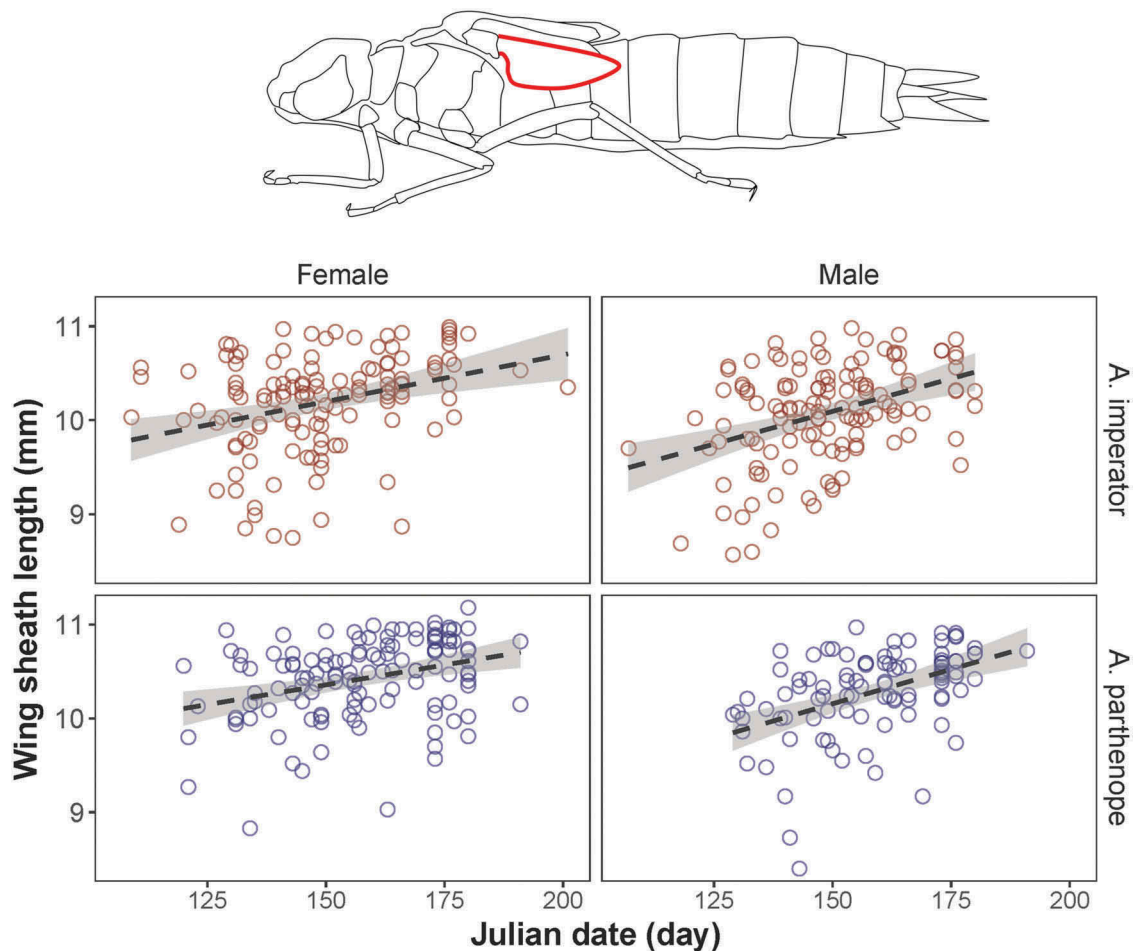


Figure 4. Seasonal pattern of body length in *Anax imperator* and *A. parthenope*, and in both sexes. Lines in black dashes correspond to regression lines and grey ribbons refer to standard error. Julian date 125, 150, 175, and 200 are 5 May, 30 May, 24 June, and 19 July. The sketch of the exuvia shows the hind wing sheath.

with experiments in the laboratory or in the field where final instar larvae are held under monospecific and bispecific conditions. In addition, by manipulating the densities of individuals, one would understand whether interspecific competition is stronger than intraspecific competition.

The height of exuvia fixation increased with the height of the support, a positive relationship that was documented in many species (Khelifa et al. 2013a; Hadjoudj et al. 2014; Zebba et al. 2014a, 2014b). The increase, however, was slightly steeper in males than in females. This sexual difference could be due to morphological (adult females are larger than males) or behavioral differences (e.g. differences in time of exposure to sun). The height of exuvia fixation increased with the season which is probably due to the growth of plant supports. Our results also point out that the relationship between exuvia height and support height declines with the season, that is, in late season, larvae climbed lower than expected with respect to the height of the support. Such a change in the exuvia–plant relationship could be explained by the interspecific competition for space among the odonatofauna. In fact, early in the season, many species of odonates begin to emerge, which increases the risks of mortality or morphological deformation due to trampling by larvae of other species. Thus, climbing higher may reduce this risk.

A question that may arise is how the dragonfly larva estimate the height of the substrate. We suggest that vision is the driver of habitat selection. In fact, it was reported that the larva prior to emergence remains near the water surface for hours (Corbet 1999), which could be considered, at least partly, as an assessment phase of the emergence site. However, determining the factors that control support height selection needs further experimental studies to control for plant structure and growth, and other confounding effects.

In odonates, body size usually shows seasonal decline at emergence (Michiels & Dhondt 1989; Anholt 1990). However, our study showed a seasonal increase in body size in both species, which has been so far observed only in a few species (Hadjoudj et al. 2014; Zebba et al. 2014a; Bouiedda et al. Forthcoming 2018). These findings are not explained by the adaptive tradeoff between age and size at emergence (Rowe & Ludwig 1991). To explain the seasonal decline of body size, it was suggested that there is a cost to grow longer, gain mass and emerge late because of the shorter reproductive season, and thus larvae should emerge smaller late in the season rather than spending more time to grow. The difference in the seasonal pattern of body size between North African and other northern populations of odonates (Michiels & Dhondt 1989; Purse & Thompson 2003) might reveal an interesting biological variation that may shed light on the relationship between environmental conditions and reproductive adaptation. In North Africa, drought is the major limiting factor for aquatic insects like

odonates. Thus, gaining mass is outweighed by the probability of drought and, therefore, the costs of emerging earlier but smaller (due to faster development) might not be considerably different from the costs of emerging late but larger. This could be an evolutionary explanation for the increasing pattern of body size across the season.

In conclusion, the temporal pattern of emergence and particularly site selection of the two *Anax* species were relatively different, which reduces interspecific competition and allows coexistence. The increasing pattern of body size found in both species has rarely been observed in previous studies outside North Africa and thus deserves further investigation. It is important to consider experimental studies in future work, to understand the ecological and behavioral mechanisms that control site selection during emergence and disentangle the implications of interspecific and intraspecific competition.

#### Acknowledgements

We thank three referees for their constructive comments. We are indebted to Mr. Benouikes Lakhdar for his field assistance and his help in transporting the authors to the study site.

#### References

- Anholt BR. 1990. Size-biased dispersal prior to breeding in a damselfly. *Oecologia*. 83(3):385–387.
- Bennett S, Mill P. 1993. Larval development and emergence in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica*. 22(2):133–145.
- Blois-Heulin C. 1990. Influence of prey densities on prey selection in *Anax imperator* larvae (Odonata: Aeshnidae). *Aquatic Insects*. 12(4):209–217.
- Bouiedda N, Amari H, Guebaila A, Zebba R, Boucenna N, Hadjadj S, Mayache B, Houhamdi M, Khelifa R. Forthcoming 2018. Reproductive behaviour and body size of *Erythromma lindenii* (Zygoptera: Coenagrionidae) in Northeast Algeria. *Odonatologica*.
- Broadhead E, Wapshere AJ. 1966. *Mesopsocus* populations on Larch in England—the distribution and dynamics of two closely-related coexisting species of Psocoptera sharing the same food resource. *Ecological Monographs*. 36(4):327–388.
- Cayrou J, Céréghino R. 2005. Life-cycle phenology of some aquatic insects: implications for pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 15 (6):559–571.
- Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*. 31(1):343–366.
- Colwell RK, Fuentes ER. 1975. Experimental studies of the niche. *Annual Review of Ecology and Systematics*. 6 (1):281–310.
- Corbet P. 1957. The life-history of the emperor dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). *The Journal of Animal Ecology*. 26(1):1–69.
- Corbet P. 1999. *Dragonflies: behaviour and ecology of Odonata*. Colchester: Harley books.
- Corbet P, Hoess R. 1998. Sex ratio of Odonata at emergence. *International Journal of Odonatology*. 1(2):99–118.
- Corbet PS. 1954. Seasonal regulation in British dragonflies. *Nature*. 174:655.



- Cordero A. 1995. Vertical stratification during emergence in odonates. *Notulae Odonatologicae*. 4(6):103–105.
- Cordero-Rivera A, Stoks R. 2008. Mark-recapture studies and demography. In: Córdoba-Aguilar A, editor. *Dragonflies and damselflies: model organisms for ecological and evolutionary research*. Oxford: Oxford University Press; p. 7–20.
- Cornell HV, Lawton JH. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *The Journal of Animal Ecology*. 61(1):1–12.
- Dijkstra K-DB, Lewington R. 2006. *Field guide to the dragonflies of Britain and Europe*. Dorset: British Wildlife Publishing.
- Hadjoudj S, Khelifa R, Guebailia A, Amari H, Hadjadj S, Zebba R, Houhamdi M, Moulaï R. 2014. Emergence ecology of *Orthetrum cancellatum*: temporal pattern and microhabitat selection (Odonata: Libellulidae). *Annales de la Société Entomologique de France (NS)*. 50(3–4):343–349.
- Harper JL, Clatworthy J, McNaughton I, Sagar G. 1961. The evolution and ecology of closely related species living in the same area. *Evolution*. 15(2):209–227.
- Khelifa R, Zebba R, Amari H, Mellal MK. 2013a. Does wind affect emergence site selection in Odonata? *African Entomology*. 21(2):383–387.
- Khelifa R, Zebba R, Moussaoui A, Kahalerras A, Bensouilah S, Mahdjoub H. 2013b. Niche partitioning in three sympatric congeneric species of Dragonfly, *Orthetrum chrysostigma*, *O. coerulea*, and *O. nitidulipes*: the importance of microhabitat. *Journal of Insect Science*. 13(71):1–17.
- Michiels NK, Dhondt AA. 1989. Effects of emergence characteristics on longevity and maturation in the dragonfly *Sympetrum danae* (Anisoptera: Libellulidae). *Hydrobiologia*. 171(2):149–158.
- Mitra A. 2013a. *Anax imperator*. The IUCN red list of threatened species; [accessed 2015 Jan 06]. [www.iucnredlist.org](http://www.iucnredlist.org).
- Mitra A. 2013b. *Anax parthenope*. The IUCN red list of threatened species; [accessed 2015 Jan 06]. [www.iucnredlist.org](http://www.iucnredlist.org).
- Purse BV, Thompson DJ. 2003. Emergence of the damselflies, *Coenagrion mercuriale* and *Ceriagrion tenellum* (Odonata: Coenagrionidae), at their northern range margins, in Britain. *European Journal of Entomology*. 100(1):93–99.
- R Development Core Team. 2017. *R: a language and environment for statistical computing* Vienna, Austria: R Foundation for Statistical Computing.
- Rowe L, Ludwig D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology*. 72(2):413–427.
- Rydin H, Barber KE. 2001. Long-term and fine-scale coexistence of closely related species. *Folia Geobotanica*. 36(1):53–61.
- Schoener TW. 1974. Resource partitioning in ecological communities. *Science*. 185(4145):27–39.
- Taketo A. 1995. Emergence pattern and sex ratio of four aeschnid dragonflies in newly formed ponds. *Tombo*. 38:48–50. Japanese.
- Werner EE, Anholt BR. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology*. 77(1):157–169.
- Werner EE, McPeck MA. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology*. 75(5):1368–1382.
- Wilcox R, Schönbrodt F. 2014. The WRS package for robust statistics in R (version 0.26). <https://github.com/nicebread/WRS>.
- Zebba R, Khelifa R, Kahalerras A. 2014a. Emergence pattern, microhabitat choice, and population structure of the Maghribian endemic *Gomphus lucasii* Selys, 1849 (Odonata: Gomphidae) in northeastern Algeria. *Aquatic Insects*. 36(3–4):245–255.
- Zebba R, Khelifa R, Kahalerras A, Djalal H, Houhamdi M. 2014b. Emergence pattern, site selection, and seasonal regulation of *Onychogomphus costae* Selys, 1885 (Odonata: Gomphidae) in northeastern Algeria. *Aquatic Insects*. 36(3–4):257–265.