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Aspects of the emergence ecology of the regionally endangered *Coenagrion mercuriale* (Odonata: Coenagrionidae) in Northeast Algeria

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ABSTRACT

Emergence is a critical phase in the life cycle of odonates because then they are highly susceptible to predation and damage. Thus the ecological understanding of this phenomenon is crucial, particularly for the conservation and management of threatened species. We studied the emergence ecology of the regionally endangered damselfly (*Coenagrion mercuriale*) in Northeast Algeria where the species produces two generations per year (spring and autumnal), focusing on the temporal emergence pattern, body size and vertical stratification of exuviae of the autumnal population. Emergence was synchronous with 50% of the population emerging within eight days. Sex ratio at emergence was slightly female biased. A seasonal decline was observed in the body size of the autumnal population like in that of the spring population. Vertical stratification of exuviae at ecdysis depended on the height of the support and vegetation density. These data are expected to be important for the management and conservation of this threatened species in Northeast Algeria and elsewhere within the distribution range.

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Exuviae; body size; conservation; threatened species; Odonata; Damselfly; North Africa

Introduction

The understanding of habitat utilization is a key to effective conservation of threatened species (Morris 2003; Stamps and Swaisgood 2007). Species live within complex habitats where they select specific microclimates maximizing their survival and reproductive success. The knowledge of intrinsic and extrinsic mechanisms underlying microhabitat selection in the wild should be integrated in order to ensure efficient management of threatened populations (Samways, McGeoch, and New 2010).

Freshwater ecosystems harbor very diverse fauna, particularly macroinvertebrates (Clarke et al. 2008). Yet, they are continually threatened with pollution and habitat degradation (Dudgeon et al. 2006). Odonates is a widespread group of insects, occurring in all continents except the Antarctic (Corbet 1999). In the Mediterranean region, 20% of species are threatened with extinction and about 2.5% are currently regionally extinct (Riservato et al. 2009). *Coenagrion mercuriale* Charpentier, 1840 is a damselfly that shows population decline in the region (Ferreira et al. 2015). However, several populations were reported in Northeast Algeria, of which some were relatively large (Khelifa et al. 2016). In this region, *C. mercuriale* produces two generations per year (Mahdjoub et al. 2015).The first generation emerges in spring and the second one in late summer and early autumn. The temporal pattern of emergence of the first generation has been studied already, and that of the second generation has not been investigated yet.

The emergence, when larvae choose a support (plant, rock, etc.) and remain static at a certain height, is a risky phase in the lifetime of odonates. The choice of the ecdysis height is variable within and among species (Cordero 1995). It can be hypothesized that selection of a particular stratum is not random, but is rather controlled by micro-abiotic (local temperature, exposure to sunlight, or humidity) and biotic factors (predation or competition) (Corbet 1957). Thus, the height of exuviae could be used as a surrogate for the microhabitat choice, and the understanding of microhabitat selection during ecdysis, especially for the species of conservation concern, is crucial for better management. Such data are not available for many dragonflies and damselflies, and particularly for the threatened populations of *C. mercuriale* in North Africa.

At the northern limit of its distribution range, this Atlanto-Mediterranean species has been studied thoroughly with investigations covering the species life history (Corbet 1955; Purse and Thompson 2002, 2003), its reproductive behavior (Purse and Thompson 2009), genetics (Watts et al. 2005; Watts and Thompson 2012), ecology (Rouquette and Thompson 2005; Watts et al. 2005) and conservation issues (Purse 2002; Thompson et al. 2015). The species is known to be

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semivoltine at the Northern range limit (Purse and Thompson 2003), but partially bivoltine at the southern range limit (Mahdjoub et al. 2015) with remarkable geographic variation in life history (Corbet, Suhling, and Soendgerath 2006). In the present paper, the temporal pattern of emergence, body size, and vertical stratification of the autumnal generation of *C. mercuriale* in Northeast Algeria is discussed for the first time. We hypothesize that (1) the emergence season of the second generation is shorter than that of the first generation given the short flight season in late summer/early autumn (Mahdjoub et al. 2015), (2) the body size of the second generation individuals like that of the first generation and many other odonates shows a seasonal decline (Corbet 1999; Mahdjoub et al. 2015), and (3) the height of exuviae depends mainly on the height of the support (Zebsa, Khelifa, and Kahalerras 2014).

Materials and methods

Study sites

Coenagrion mercuriale was studied upstream of the Seybouse River in the old Bridge canal, Northeast Algeria (36°28′24″N, 7°22′24″E) (Figure 1). It is a shallow watercourse with an average depth of 7 cm and width of 120 cm. The aquatic vegetation therein was mainly represented by shrubs of *Nerium oleander* L., tufts of *Typha angustifolia* L., *Juncus maritimus* Lam, and *Paspalum distichum* L. The site was rich in amphipods, which might be the primary food source for odonate larvae. The population of *C. mercuriale* cohabited with other odonates, namely *Ischnura graellsii* Rambur, 1842, *Calopteryx haemorrhoidalis* Vander Linden, 1825, *Orthetrum nitidinerve* Selys, 1841, and *O. coerulescens* Fabricius, 1798.

Exuviae sampling

Exuviae of *C. mercuriale* were daily collected in the late afternoon (at 04:00 pm) along three 10 m- long transects in two habitat types – dense high vegetation (mainly *Typha angustifolia*) and short sparse vegetation (mainly *Paspalum distichum*). These sections were chosen based on the occurrence of larvae, and they were demarcated and labelled with small flags. Knowing when the flight season of the second generation begins (Mahdjoub et al. 2015), we started sampling from the third week of August 2016 and continued until the end of the emergence season. We determined the end of the emergence season when after multiple consecutive visits (at least 10), we found no exuviae or tenerals (Figure 2). The vegetation in sampling sections of the watercourse was searched thoroughly so that no exuvia was left after each sampling. The height of the exuvia fixation (HE) (distance between the water surface and the tip of exuvia abdomen) and the height of the chosen support (HS) were measured for each exuvia to the nearest 1 cm. Vegetation density within 1 m^2 of the exuvia was estimated visually to the nearest 5%. To investigate the potential effects of body size and sex, the exuviae were sexed and the length of the body, the width of the head and the length of the wing sheath were measured to the nearest 0.01 mm using a digital caliper in the laboratory. We also calculated EM50 as the number of days when 50% of the population had emerged. The fragmented exuviae, in which the body

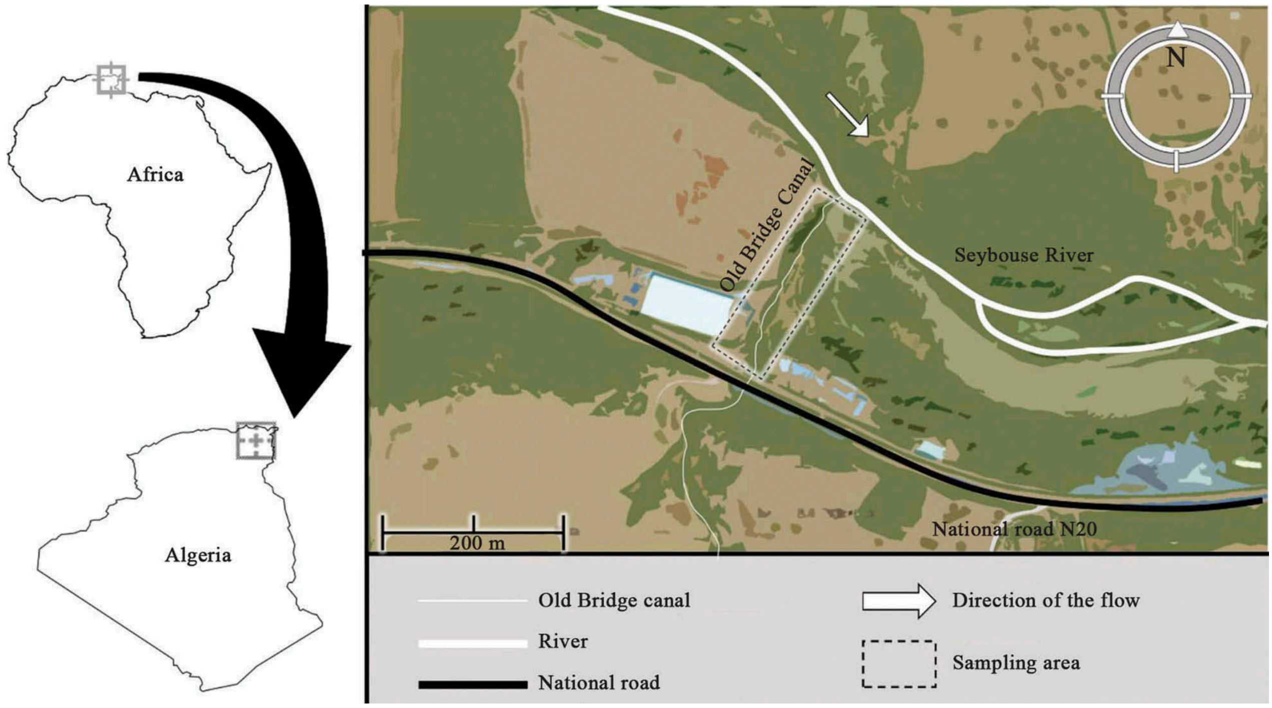

Figure 1. The map showing location of the study area in Northeast Algeria.

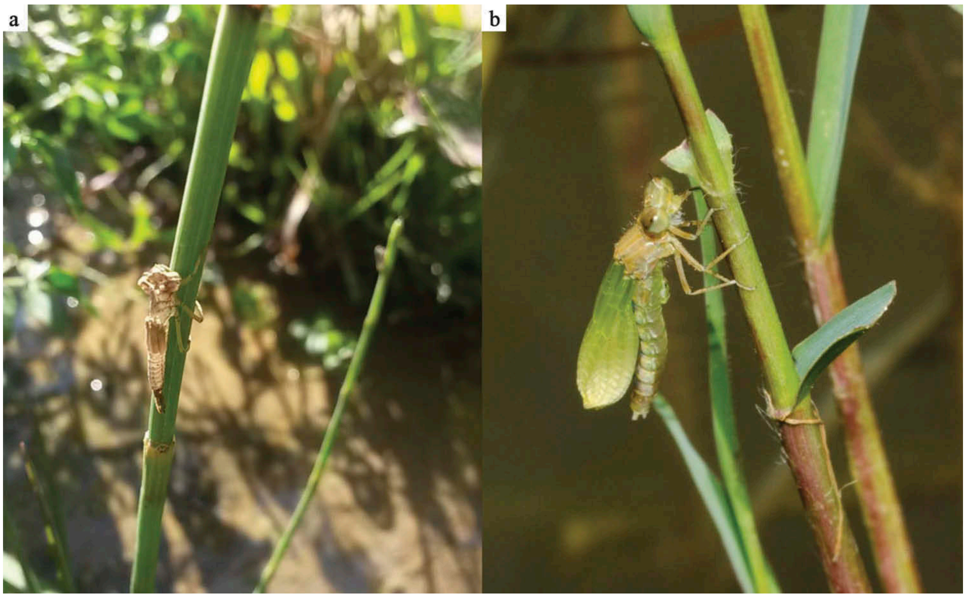

Figure 2. (a) Exuvia and (b) teneral of *Coenagrion mercuriale* in the field.

size and sex were not measured or identified, were excluded from statistical analyses. As the body size might change during the emergence season (Falck and Johansson 2000; Purse and Thompson 2003), we investigated the temporal pattern of body size using the wing sheath length as a surrogate for body size.

Statistical analysis

We conducted all statistical analyses using R 3.4.0 (R Development Core Team 2018). Chi-square tests were used to see whether sex ratio at emergence deviates from unity (1:1). Multiple linear regressions were used to look for the seasonal pattern of body size using days of the year (Julian date) and sex as explanatory variables and the wing sheath length as a response variable. Mann Whitney U-tests were used to test for differences in body measurements between males and females and in vertical stratification between habitat types. Spearman correlation tests were used to look for potential relationships between the three body size measurements, HE and HS, and HS and vegetation density surrounding the exuvia. To investigate the effect of HS and sex (explanatory variables) on HE (response variable), we conducted multiple linear regressions. HS was log-transformed to linearize the data when analyzing the vertical stratification in dense high vegetation. Unless indicated, values are mean ± SD.

Results

Temporal pattern of emergence

We collected 110 exuviae during the entire season of the second generation. The autumnal emergence season of *C. mercuriale* lasted for 16 days, starting on 29 August and finishing on 13 September 2016. Half of the exuviae were collected within eight days. Of the 110 exuviae collected, 11 were found degraded with the abdomen partially fragmented and thus sex was not identified. Sex ratio was slightly, but not significantly female biased (58.8%, $\chi^2 = 2.9$, $p = 0.08$).

Body size

Females had a longer body ($W = 1650.5$, $p = 0.001$) and longer wing sheaths ($W = 1714$, $p = 0.0002$) than males, but no sexual difference was recorded for the head width ($W = 1356$, $p = 0.23$) (Table 1). A positive correlation was found to exist between the body length and the head width (Spearman correlation: $r = 0.33$, $p < 0.001$), the body length and the wing sheath length ($r = 0.40$, $p < 0.0001$) and the head width and the wing sheath length ($r = 0.26$, $p = 0.007$). As correlations between the three morphological traits were significant, the seasonal pattern of body size was investigated only based on the wing sheath length because of its lower susceptibility to measurement errors due to exuvia deformation. We found a seasonal decline in the wing sheath length ($R^2 = 0.33$, Table 2, Figure 3) revealing that the individuals emerging early in the season had longer wings than those emerging later.

Table 1. Mean, SD, SE and 95% confidence intervals of three morphological variables of *Coenagrion mercuriale*.

Variable	Sex	Mean	N	SD	SE	LCI	UCI
Body length (mm)	Female	16.00	58	1.22	0.16	15.69	16.31
	Male	15.17	41	0.65	0.10	14.97	15.37
Head width (mm)	Female	3.24	58	0.26	0.03	3.17	3.30
	Male	3.18	41	0.27	0.04	3.10	3.26
Wing sheath length (mm)	Female	3.70	58	0.28	0.04	3.63	3.77
	Male	3.47	41	0.26	0.04	3.39	3.55

Table 2. Summary statistics of the linear model assessing the seasonal pattern of wing sheath length in *Coenagrion mercuriale*.

	Estimate	Std. Error	*t* value	*p* value
Intercept	11.065	1.574	7.032	< 0.0001
Season	−0.030	0.006	−4.667	< 0.0001
Sex[Male]	−0.202	0.048	−4.211	0.0001

Vertical stratification

Of the total number of exuviae, 65 (58.5%) were found in sparse vegetation areas whereas 46 (41.5%) were found in densely vegetated ones. There was a positive correlation revealed between HS and vegetation density ($r = 0.34$, $p = 0.0005$), showing that shorter substrates occurred in open areas whereas longer substrates occurred in dense areas. Overall, the average height at which ecdysis occurred (HE) was 5.90 ± 3.11 cm, and there was no difference revealed between habitat types (W = 1286, $p = 0.49$). To determine the relationship between HE and HS, we analyzed the two habitat types separately. The vertical stratification of exuviae showed a positive logarithmic pattern in dense high vegetation ($R^2 = 0.25$, Figure 4(a)) and a non-significant linear pattern in sparse short vegetation ($R^2 = 0.11$, Figure 4(b)). In both habitat types, there was no difference observed in the vertical stratification between males and females (Table 3).

Discussion

Our study focuses on some aspects of the emergence ecology of a locally endangered odonate in a North African population and presents the information that might be useful for this species conservation and management. In summary, the emergence season of the second generation of *C. mercuriale* was found to be short; the seasonal pattern of body size during the emergence season was declining; and as expected,

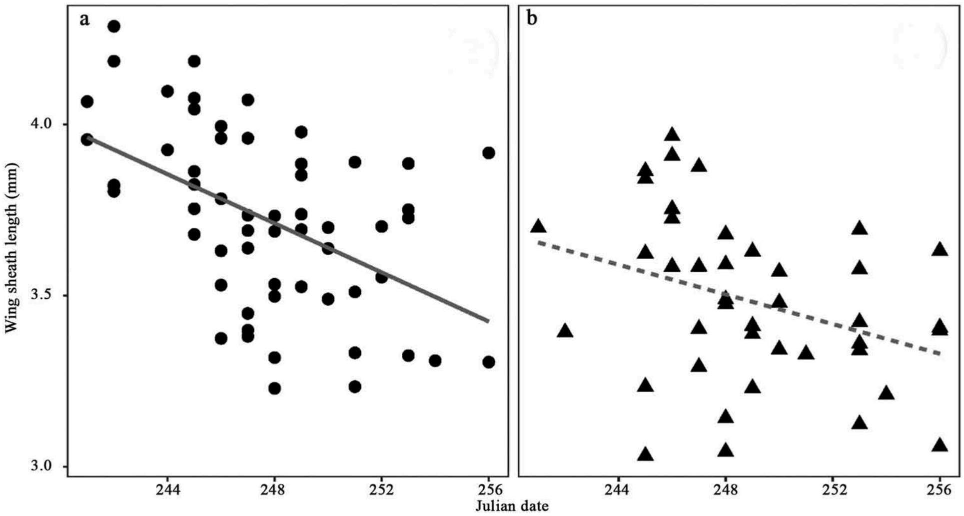

Figure 3. A seasonal pattern of the wing sheath pad of *Coenagrion mercuriale* female (a) and male (b) exuviae. Dashed and solid lines indicate males and females, respectively.

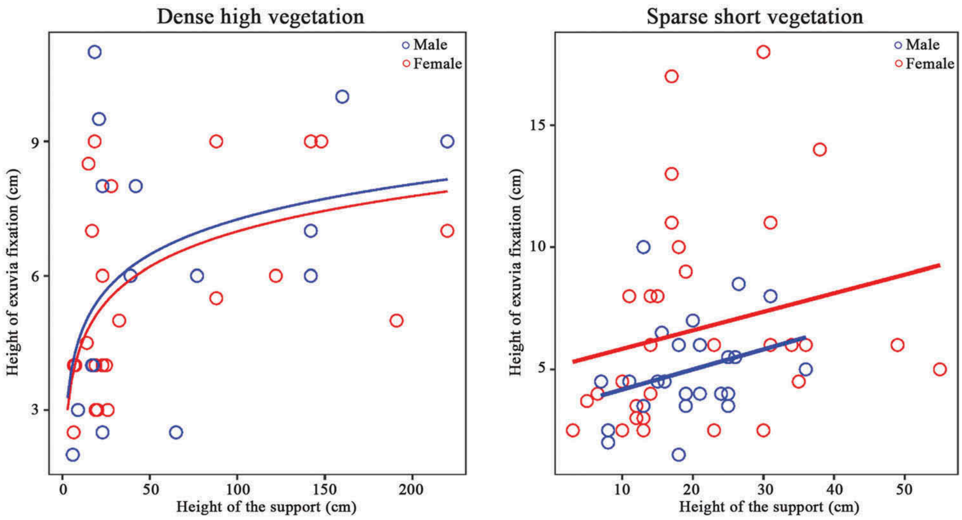

Figure 4. The relationship between the height of exuvia fixation and the support height in *Coenagrion mercuriale*. Red stands for females and blue for males.

Table 3. Summary statistics of the linear model assessing the vertical stratification of *Coenagrion mercuriale* exuviae. In dense high vegetation, HS was log-transformed to fit a linear model.

Habitat type	Explanatory variable	Estimate	Std. Error	*t* value	*p* value
Dense high vegetation	Intercept	1.753	1.220	1.437	0.159
	log(HS)	1.136	0.323	3.510	0.001
	Sex[Male]	0.268	0.714	0.375	0.710
Short sparse vegetation	Intercept	5.052	1.062	4.754	< 0.0001
	HS	0.077	0.042	1.809	0.076
	Sex[Male]	−1.607	0.894	−1.797	0.078

the height at which ecdysis occurred was positively correlated to the support height and also depended on vegetation density.

The number of exuviae collected during the emergence season of the second *C. mercuriale* generation is consistent with the partial bivoltinism suggested for the population (Mahdjoub et al. 2015). In fact, the first generation of the population under study was investigated employing the same methodology as the one used in the current study, i.e. a similar surface was sampled, yielding 317 exuviae (Mahdjoub et al. 2015). The size of the emerged second generation in late summer and early autumn accounts for about one third of that of the first generation. Nevertheless, the mark-capture-recapture (CMR) of adults of the first generation conducted during the same year yielded a total of 1008 marked individuals (772 males and 236 females) and an estimated population size of 1800 individuals (Khelifa et al. 2016). Based on CMR of the second generation of the year, a total of 252 individuals were marked (Khelifa R., unpublished data), which corresponds to a quarter of the abundance of the first generation. Our results also suggest that the population size of adults produced during a year is larger than expected (Khelifa et al. 2016), and might approximate 2500 imagoes emerged per year. This unprotected site, which also harbors a large population of the Mediterranean endemic *Orthetrum nitidinerve*, is under constant habitat degradation and disturbance (fire, wild stock pasturing, and pollution), and thus needs an urgent conservation plan.

The emergence of the second generation of *C. mercuriale* was quite synchronous. Compared to the first generation of the same population, the EM50 of the second generation was three times shorter (Mahdjoub et al. 2015). Similar partial bivoltinism was recorded in the endemic endangered damselfly *Calopteryx exul* in Northeast Algeria (Khelifa 2017). The shorter EM50 is probably partly due to the smaller population size of the second generation of the year and partly due to different climatic conditions (warmer temperatures) that promote synchronous development and emergence. It is still unclear whether the partially bivoltine life history pattern is due to plasticity, i.e. response to warm conditions – warmer temperatures allow some individuals to develop faster and emerge before winter, or to adaptive mechanisms – emerging in late summer offers an advantage in fitness. Indeed, the recently revealed genetic differentiation between North African and European populations of the congeneric species *C. puella* (Ferreira et al. 2015) suggests that partial bivoltinism is likely to be the outcome of *C. mercuriale* life history adaptation to North African climatic conditions. However, further experimental investigations are needed to reveal the origin of partial bivoltinism.

The body size of both sexes declined during the emergence season. The seasonal decline of body size during emergence is considered as the norm because it has been observed in many dragonflies and damselflies (Banks and Thompson 1985; Corbet 1999; Inden-Lohmar 1997; Purse and Thompson 2003). Similar seasonal decline was observed in the first generation of C. *mercuriale* (Mahdjoub et al. 2015). The body size is often related to the development rate, i.e. the faster development leads to a smaller body size (Blanckenhorn 2000). If the seasonal pattern is purely a result of thermal plasticity, the seasonal decline of the body size can be explained by the fact that the eggs that were laid in late spring and early summer develop slower than those that were laid in midsummer due to the seasonal increase of temperature (Vannote and Sweeney 1980), which leads to differential size at emergence. There is another mutually non-exclusive hypothesis that may explain the seasonal decline of body size. Johansson & Rowe (1999) illustrated that the decrease of body size at emergence may result from mechanisms that are not related to thermal response, which suggests an evolutionary explanation. As hypothesized by Rowe and Ludwig (1991), there could be a conflict between age and size at emergence, that is, the cost of emerging late increases with the emergence season due to the shorter reproductive season, thus individuals could 'decide' to emerge smaller rather than spending longer time growing at the aquatic stage.

As expected, the height at which ecdysis took place was mainly dependent on the height of the chosen support. The relationship between HE and HS was positive, which is similar to several other species (Zebsa, Khelifa, and Kahalerras 2014; Zebsa et al. 2014; Hadjoudj et al. 2014). However, the peculiarity of *C. mercuriale* is that this relationship had a logarithmic shape even when the support height was not a limiting factor. This means that there are other factors besides the height of the support that limit larvae to a particular stratum height. Further experimental studies should reveal the implication of predation and other sources of mortality on the height of exuvia fixation in particular and emergence site selection in general (Jakob and Suhling 1999). Our present investigation has provided new data on the emergence ecology of *C. mercuriale*; a species that requires an urgent management plan. In order to manage potential habitats for reintroduction or translocation (Thompson et al. 2015), it is important to have information on the habitat selection during emergence. The availability of preferred emergence sites is a key to predator and disturbance avoidance that could be fatal during ecdysis. Information presented in this article is essential for developing the conservation plan for *C. mercuriale* not only on the regional scale but also on a larger scale. Freshwater communities in Northeast Algeria are threatened with habitat degradation and pollution (Khedidja and Boudoukha 2013; Reggam et al. 2017). This has led to the extinction of several subpopulations of the endemic damselfly *Calopteryx exul* (Khelifa and Mellal 2017). Although a dozen of *C. mercuriale* subpopulations are currently existing in the Seybouse watershed (Khelifa et al. 2016), rapid extinction of some of them could be expected in years to come. In addition, we still have little data on the distribution of the species in other Algerian watersheds and thus further investigations are needed. A better knowledge of the factors that facilitate colonization of new habitats and the application of conservation measures to maintain the currently existing populations are required.

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Disclosure statement

No potential conflict of interest was reported by the authors.

References

Banks, M. J., and D. J. Thompson. 1985. "Emergence, Longevity and Breeding Area Fidelity in *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae)." *Odonatologica* 14 (4): 279–286.

Blanckenhorn, W. U. 2000. "The Evolution of Body Size: What Keeps Organisms Small?" *The Quarterly Review of Biology* 75 (4): 385–407. doi:10.1086/393620.

Clarke, A., R. M. Nally, N. Bond, and P. S. Lake. 2008. "Macroinvertebrate Diversity in Headwater Streams: A Review." *Freshwater Biology* 53 (9): 1707–1721. doi:10.1111/j.1365-2427.2008.02041.x.

Corbet, P. S. 1955. "The Larval Stages of Coenagrion Mercuriale (Charp.) (Odonata: Coenagrionidae)." *Proceedings of the Royal Entomological Society, London (A)* 30: 115–126.

Corbet, P. S. 1957. "The Life-History of the Emperor Dragonfly *Anax imperator* Leach (Odonata: Aeshnidae)." *The Journal of Animal Ecology* 1–69. doi:10.2307/1781.

Corbet, P. S. 1999. *Dragonflies: Behaviour and Ecology of Odonata*. Colchester: Harley Books.

Corbet, P. S., F. Suhling, and D. Soendgerath. 2006. "Voltinism of Odonata: A Review." *International Journal of Odonatology* 9 (1): 1–44. doi:10.1080/13887890.2006.9748261.

Cordero, A. 1995. "Vertical Stratification during Emergence in Odonates." *Notulae Odonatologicae* 4 (6): 103–105.

Dudgeon, D., A. H. Arthington, M. O. Gessner, D. J. Zen-Ichiro Kawabata, C. L. Knowler, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, and M. L. J. Stiassny. 2006. "Freshwater Biodiversity: Importance, Threats, Status and Conservation Challenges." *Biological Reviews* 81 (2): 163–182. doi:10.1017/S1464793105006950.

Falck, J., and F. Johansson. 2000. "Patterns in Size, Sex Ratio and Time at Emergence in a South Swedish Population of *Sympetrum sanguineum* (Odonata)." *Aquatic Insects* 22 (4): 311–317. doi:10.1076/0165-0424(200010)22:4;1-Y;FT311.

Ferreira, S., F. Martínez-Freiría, J.-P. Boudot, M. E. Haissoufi, N. Bennas, P. C. Alves, P. C. Watts, D. J. Thompson, and J. C. Brito. 2015. "Local Extinctions and Range Contraction of the Endangered *Coenagrion mercuriale* in North Africa." *International Journal of Odonatology* 18 (2): 137–152. doi:10.1080/13887890.2015.1017846.

Hadjoudj, S., R. Khelifa, A. Guebailia, H. Amari, S. Hadjadji, R. Zebsa, M. Houhamdi, and M. Riadh. 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. doi:10.1080/00379271.2014.938941.

Inden-Lohmar, C. 1997. Sukzession, struktur und dynamic vonLibellenpopulationen an Kleingewassern unter besonderer BerucksichtiKleingung von Aeshna cyanea Odonata: Aeshnidae. Ph.D. dissertation, University of Bonn, Germany.

Jakob, C., and F. Suhling. 1999. "Risky Times? Mortality during Emergence in Two Species of Dragonflies (Odonata: Gomphidae, Libellulidae)." *Aquatic Insects* 21 (1): 1–10. doi:10.1076/aqin.21.1.1.4537.

Johansson, F. and Rowe, L. 1999. "Life history and behavioral responses to time constraints in a damselfly." *Ecology* 80: 1242–1252. doi: 10.2307/177071

Khedidja, A., and A. Boudoukha. 2013. "Risk Assessment of Agricultural Pollution on Groundwater Quality in the High Valley of Tadjenanet: Chelghoum Laid (Eastern Algeria)." *Desalination and Water Treatment* 51 (1–3): 292–301. doi:10.1080/19443994.2012.714521.

Khelifa, R. 2017. "Partial Bivoltinism and Emergence Patterns in the North African Endemic Damselfly *Calopteryx exul*: Conservation Implications." *African Journal of Ecology* 55 (2): 145–151. doi:10.1111/aje.2017.55.issue-2.

Khelifa, R., and M. K. Mellal. 2017. "Host-Plant-Based Restoration as a Potential Tool to Improve Conservation Status of Odonate Specialists." *Insect Conservation and Diversity* 10 (2): 151–160. doi:10.1111/icad.12212.

Khelifa, R., R. Zebsa, H. Amari, M. K. Mellal, H. Mahdjoub, and A. Kahalerras. 2016. "A Hotspot for Threatened Mediterranean Odonates in the Seybouse River (Northeast Algeria): Are IUCN Population Sizes Drastically Underestimated?" *International Journal of Odonatology* 19 (1–2): 1–11. doi:10.1080/13887890.2015.1133331.

Mahdjoub, H., R. Khelifa, R. Zebsa, Z. Bouslama, and M. Houhamdi. 2015. "Bivoltinism in *Coenagrion mercuriale* (Zygoptera: Odonata) in the Southern Margin of Its

Distribution Range: Emergence Pattern and Larval Growth." *African Entomology* 23 (1): 59–67. doi:10.4001/003.023.0120.

Morris, D. W. 2003. "How Can We Apply Theories of Habitat Selection to Wildlife Conservation and Management?" *Wildlife Research* 30 (4): 303–319. doi:10.1071/WR02028.

Purse, B. 2002. "The Ecology and Conservation of the Southern Damselfly (*Coenagrion mercuriale* – Charpentier) in Britain." In *R&D Technical Report W1-021/TR*, edited by Environment Agency, Bristol, BS32 4UD: University of Liverpool.

Purse, B. V., and D. J. Thompson. 2002. "Voltinism and Larval Growth Pattern in *Coenagrion mercuriale* (Odonata: Coenagrionidae) at Its Northern Range Margin." *European Journal of Entomology* 99 (1): 11–18. doi:10.14411/eje.2002.004.

Purse, B. V., and D. J. Thompson. 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): 93–100. doi:10.14411/eje.2003.018.

Purse, B. V., and D. J. Thompson. 2009. "Oviposition Site Selection by *Coenagrion mercuriale* (Odonata: Coenagrionidae)." *International Journal of Odonatology* 12 (2): 257–273. doi:10.1080/13887890.2009.9748344.

R Development Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reggam, A., E.-H. Bouchelaghem, S. Hanane, and M. Houhamdi. 2017. "Effects of Anthropogenic Activities on the Quality of Surface Water of Seybouse River (Northeast of the Algeria)." *Arabian Journal of Geosciences* 10 (10): 219. doi:10.1007/s12517-017-3010-4.

Riservato, E., J.-P. Boudot, S. Ferreira, M. Jovíc, V. J. Kalkman, W. Schneider, B. Samraoui, and A. Cuttelod. 2009. "The Status and Distribution of Dragonflies of the Mediterranean Basin." Gland, Switzerland and Malaga, Spain: IUCN. vii + 33 pp

Rouquette, J. R., and D. J. Thompson. 2005. "Habitat Associations of the Endangered Damselfly, *Coenagrion mercuriale*, in a Water Meadow Ditch System in Southern England." *Biological Conservation* 123 (2): 225–235. doi:10.1016/j.biocon.2004.11.011.

Rowe, L., and D. Ludwig. 1991. "Size and Timing of Metamorphosis in Complex Life Cycles: Time Constraints and Variation." *Ecology* 72 (2): 413–427. doi:10.2307/2937184.

Samways, M. J., M. A. McGeoch, and T. R. New. 2010. *Insect Conservation: A Handbook of Approaches and Methods*. Oxford: Oxford University Press.

Stamps, J. A., and R. R. Swaisgood. 2007. "Someplace like Home: Experience, Habitat Selection and Conservation Biology." *Applied Animal Behaviour Science* 102 (3): 392–409. doi:10.1016/j.applanim.2006.05.038.

Thompson, D. J., A. L. Thompson, L. Kerry, and P. Gotham. 2015. "Reintroduction and Establishment of *Coenagrion mercuriale* (Charpentier) (The Southern Damselfly) on Venn Ottery Common, Devon." *Journal of the British Dragonfly Society* 31: 14–23.

Vannote, R. L., and B. W. Sweeney. 1980. "Geographic Analysis of Thermal Equilibria: A Conceptual Model for Evaluating the Effect of Natural and Modified Thermal Regimes on Aquatic Insect Communities." *The American Naturalist* 115 (5): 667–695. doi:10.1086/283591.

Watts, P. C., and D. J. Thompson. 2012. "Developmental Plasticity as a Cohesive Evolutionary Process between Sympatric Alternate-Year Insect Cohorts." *Heredity* 108 (3): 236. doi:10.1038/hdy.2011.63.

Watts, P. C., S. J. Kemp, I. J. Saccheri, and D. J. Thompson. 2005. "Conservation Implications of Genetic Variation between Spatially and Temporally Distinct Colonies of the Endangered Damselfly *Coenagrion mercuriale*." *Ecological Entomology* 30 (5): 541–547. doi:10.1111/j.0307-6946.2005.00721.x.

Zebsa, R., R. Khelifa, and A. Kahalerras. 2014. "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. doi:10.1080/01650424.2015.1083587.

Zebsa, R., R. Khelifa, A. Kahalerras, H. Djalal, and M. Houhamdi. 2014. "Emergence Pattern, Site Selection, and Seasonal Regulation of *Onychogomphus costae* Selys, 1885 (Odonata: Gomphidae) in Northeastern Algeria." *Aquatic Insects* 36 (3–4): 257–265. doi:10.1080/01650424.2015.1087574.