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Life cycle and seasonal regulation of Onychogomphus forcipatus unguiculatus in the Seybouse River, Algeria (Insecta: Odonata)

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Abstract. Understanding the seasonal regulation and life cycle patterns of Odonata is critical to identifying the factors that influence their voltinism. While the life history and seasonal regulation of Odonata, particularly gomphids, has been studied extensively, few studies have focused on North African gomphids. This study aims to contribute to the understanding of the life cycle of Onychogomphus forcipatus unguiculatus (Vander Linden, 1823), a western Mediterranean gomphid, on the Seybouse River in northeastern Algeria and discuss its seasonal regulation. Our results imply that a generation of O. f. unquiculatus requires two years to develop. The appearance of small (F-6) larvae in early spring can be attributed to the hatching of eggs in the previous year, followed by their overwintering in interstitial habitats. This abrupt appearance of small larvae is the result of their unique life history strategy of developing and surviving in specialized habitats during winter, then continuously growing and developing. The senior cohort overlaps with its junior counterpart, overwintering primarily in instars F-1, F-2, and, to a lesser extent, F-3, before beginning to emerge in late spring and early summer. By examining the voltinism and life cycle patterns of O. f. unguiculatus, this study contributes to our understanding of the reproductive strategies and population dynamics of this western Mediterranean gomphid, as well as of factors affecting the phenology and ecology of Odonata, particularly in North Africa, and in this manner contributes to overall efforts to protect and manage freshwater ecosystems in this region.

Key words. Dragonfly, Anisoptera, freshwater ecosystems, phenology, voltinism, Western Mediterranean

Introduction

Aquatic insects exhibit diverse life cycles, with larval stages often playing a key role in regulating their development (Bauernfeind & Soldán, 2012; Corbet, 1999; Wiggins, 1996). The interplay of environmental factors such as temperature and photoperiod influences the growth and timing of the life cycle of these insects (Koch, 2015; Norling, 1984). The study of voltinism, the number of generations completed in a year, allows the identification of factors that determine seasonal regulation in Odonata (Corbet et al., 2006).

Research Article

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> > within the paper.

Odonata larval growth is subject to the influence of environmental conditions, resulting in considerable variability in voltinism both within and among taxa (Farkas et al., 2012; Suhling, 1995). The interaction between growth and predation risk is determined by several factors, including behavioural adaptations along a habitatpermanence gradient, larval density, and food availability (Anderson & Cummins, 1979; Banks & Thompson, 1987; Wellborn et al., 1996). Originally, life cycles of temperate Odonata used to be divided into three distinct types: first, spring species exhibit a diapause during their last larval stage, resulting in their synchronized emergence in early spring. Second, summer species do not have a diapause during their last larval stage, resulting in a later and less synchronized emergence as most larvae overwinter in earlier stages. Finally, obligate univoltine species complete their growth and development in spring and/or summer due to their exposure to higher thermal coefficients (Corbet, 1962).

However, later research has questioned the clear distinction between "spring species" and "summer species," leading Corbet (1999) to propose a reclassification into "unregulated" and "regulated" life cycles. The latter category was further subdivided into "regulated: voltinism obligate" and "regulated: voltinism facultative", which include both spring and summer species and their intermediate forms (Norling, 2021). Despite its limitations, the classification of Odonata into spring and summer species, especially in northern regions, remains a useful concept for describing the life cycles and phenologies of Odonata populations.

While the literature is replete with studies on life cycle patterns and seasonal regulation of temperate Odonata (e.g., Benke & Benke, 1975; Corbet, 1999; Norling, 1971, 1984), with many of these focusing on gomphids (e.g., Ferreras-Romero et al., 1999; Schütte et al., 1998; Suhling, 1995; Suhling & Müller, 1996; Velasco-Villanueva et al., 2018), our understanding of the life histories of many species, especially those living in arid North Africa, has remained rather limited. For example, very few studies have addressed the life histories of North African gomphids (Samraoui et al., 2019, 2023; Zebsa et al., 2014).

The western Mediterranean gomphid Onychogomphus forcipatus unquiculatus (Vander Linden, 1823) is distributed in southern Europe (from Italy to the west) and in the coastal areas of the Maghreb, from Tunisia to Morocco (Boudot et al., 1990; 2009). Throughout its range, this subspecies lives at larger streams or rivers with fast currents and a coarse bottom substrate and is more abundant at mid-altitudes (Ferreras-Romero & García-Rojas, 1995; Hamzaoui et al., 2015; Suhling, 2001). This taxon has received relatively little attention in odonatological studies, and its life cycle has remained uncertain due to conflicting study results: some researchers have described it as semivoltine in southern Europe (Ferreras-Romero & García-Rojas, 1995; Ferreras-Romero & Márquez-Rodríguez, 2014; Suhling, 2001), whereas others suggest it to be partivoltine, taking up to three years to complete a generation in southern France (Suhling, 2001). However, a recent study by Martín & Maynou (2023) has shown that *O. f. forcipatus* may have a univoltine life cycle in northeastern Spain.

In this study, our primary objective was to investigate the distribution of O. f. unguiculatus on the Seybouse River in northeastern Algeria, with particular attention to its larval growth and development patterns. Our overall objectives included assessing the status of this subspecies, elucidating its temporal dynamics, exploring its generation time, and discussing the mechanisms that control its seasonality. We were particularly interested in clarifying the timing of key life cycle events and this subspecies' adaptations to environmental factors. Our efforts to map the life cycle of O. f. unguiculatus and compare it to those of other Mediterranean gomphids are intended to contribute to our broader understanding of aquatic insect life cycles and to provide insights into the adaptations and survival strategies of Odonata.

Methods

Between 2013 and 2019, we conducted extensive sampling at 30 sites along the Seybouse River as part of a study on the ecology of gomphids (Bouhala et al., 2019; Hamzaoui et al., 2015; Samraoui et al., 2019, 2023; B.S., unpubl. data). Detailed descriptions of the sampling sites are provided in Bouhala et al. (2019) and Samraoui et al. (2021). Based on this knowledge, we selected an ephemeral stream, Wadi Aar, a tributary of the Seybouse River in northeastern Algeria (36°13'34" N, 7°19'11" E, 617 m a.s.l.), characterized by a bottom substrate of gravel and stones (see Fig. 1). Fish, in the shape of the Algerian barbel (*Luciobarbus callensis*), were present in the stream.

The regular presence of adults and exuviae at this particular site indicated its suitability as a habitat for *O. f. unguiculatus* (Figs 2a, 2b) (Hardersen, 2008). Due to the considerable amounts of water abstracted for irrigation purposes, the sampled site often dries out during the summer months. Therefore, and due to the limited number of larvae present, our quarterly sampling period spanned four years, from 31 October 2015 to 18 September 2019 (Table 1). Further visits were made to monitor the hydrology of the wadi and assess the presence of exuviae. In response to the threat of drought, we brought forward our sampling schedule to summer in 2016 and undertook additional sampling in late summer of 2019.

During each visit, we recorded the presence of adult individuals during a 20-minute search and collected exuviae along a 60 m transect. Larvae were collected by kick sampling, using a hand net with a mesh size of 1 mm and a diameter of 35 cm, in different microhabitats within an area of 100 m². Similar sampling methods were applied throughout the study period. Collected samples were immediately placed in a plastic container filled with water. After rinsing and removing coarse debris, the contents were filtered through a fine mesh (100 μ m) and larvae were carefully picked out with forceps. Larval identification was based on the morphological descriptions provided by Suhling & Müller (1996). The terminology of seasons follows their astronomical definition as follows: Spring (21 March–20 June), Summer (21 June–20 September), and Winter (21 December–20 March). Subsequent measurements of larval characteristics, such as head width and body length, were taken in the laboratory, using a steel ruler, ensuring an accuracy of 0.1 mm. The collected specimens were preserved in 70% ethanol and are now in the collection of the Laboratoire de Conservation des Zones Humides at the University of Guelma, Algeria. It is worth noting that the term "wadi" is used for Oued (stream/river) here.



Figure 1. Map of Algeria with the Seybouse River sampling locations. Black circles indicate records of *Onychogomphus forcipatus unguiculatus* at WadiAar (S14) and Wadi Zimba (S26).

Data analysis

The recorded morphometrics were used to create scatter plots that allowed us to visualize the relationship between head width and body length. Based on the terminology introduced by Corbet (2002), we classified the larval stages as F-0 (final instar), F-1 (penultimate instar), etc. To identify the last five stages (F-0, F-1, F-2, F-3, F-4) and distinguish them from others, we performed a fast density-based clustering analysis for body length data and head width. This data analysis technique groups objects into clusters based on their similarity and facilitates the discovery of arbitrarily shaped clusters (Hahsler et al., 2019), and we used the density-based spatial clustering of applications with a noise algorithm incorporated in the R package (dbscan) (Hahsler et al., 2019). This algorithm requires two primary parameters: Eps, or epsilon, is the minimum distance required for two objects to be considered neighbours, and MinPts, the minimum number of objects required to define a cluster (Ester et al., 1996).



Figure 2. View of Wadi Aar, a tributary of the Seybouse River, northeastern Algeria (a); close-up view of *Onychogomphus forcipatus unguiculatus* (b).

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Table 1. Seasonal sampling of *Onychogomphus forcipatus unguiculatus* at Wadi Aar: dates and sample counts. Drought and water abstraction for agriculture disrupted sampling between summer 2016 and spring 2018.

Date	Season	Sample (N)
31/10/2015	Autumn	41 larvae
07/01/2016	Winter	58 larvae
25/03/2016	Spring	26 larvae
05/06/2016	Spring	29 exuviae
22/06/2016	Summer	1 larva
Drought + water abstraction		N/A
24/05/2018	Spring	0
30/06/2018	Summer	0
29/09/2018	Autumn	0
17/06/2019	Spring	0
02/07/2019	Summer	0
18/09/2019	Summer	7 larvae

To comprehensively represent the size-frequency distribution of larval growth and development, we used violin plots. These plots illustrate the density of data points at different measured values and provide intuitive insights into seasonal larval size variation. Data visualization was carried out using the software package ggplot2 v. 3.4.4 (Wickham, 2016). All statistical analyses, including clustering, were performed with R v. 4.3.1 (R Development Core Team, 2023).

Results Phenology

Our surveys at the Seybouse River indicate that *O. f. unguiculatus* is a subspecies of relatively low local abundance. Adult specimens were noted at two specific sites, i.e., at Wadi Zimba (36°27'49" N, 7°29'15" E, 205 m a.s.l.) and Wadi Aar, both of which are tributar-

Table 2. Mean head widths and body lengths (with sd) for recorded last instars of *Onychogomphus forcipatus unguiculatus* at the Seybouse River.

Stadium	Head width (mm)	Body length (mm)	Ν
F-0	5.0	23.2	1
F-1	3.9 ± 0.2	17.8 ± 1.3	40
F-2	3.1 ± 0.1	12.6 ± 0.6	62
F-3	2.4 ± 0.1	9.8 ± 0.4	21
F-4	1.9 ± 0.2	7.0 ± 0.5	6
F-5	1.4 ± 0.0	5.5 ± 0.0	2
F-6	1.0	5.0	1

ies to the Seybouse River. Observations of adult *O. f. unguiculatus* in flight began as early as on 5 June, with the recorded flight period extending throughout June and July. The flow of the Wadi Aar was significantly disrupted between the summer of 2016 and the spring of 2018, primarily due to drought conditions and significant water withdrawals for agricultural purposes. During our study period, we collected 29 exuviae (5 June 2016) and a combined total of 133 larvae (Table 1). Other gomphid species encountered next to *O. f. unguiculatus* in Wadi Aarwere relatively rare, but included *O. costae*, with one female observed laying eggs, and a single larva of *Gomphus lucasii*.

Larval stages and size differentiation

Analysis of larval stages revealed no significant overlaps in size, indicating a clear distinction between developmental stages. Figure 3a plots the scattering of head width against total body length and provides a visual representation of the distinctiveness of each larval stage. In particular, the last seven stages are easily distinguished based on head width and total body length (Table 2). The collected larvae had body lengths of 5.0– 23.2 mm, with head widths varying between 1.0 and 5.0 mm. The dbscan clustering method confirmed the



Figure 3. Relationship between body length and head width in *Onychogomphus forcipatus unguiculatus,* (a) distinct larval stadia delineated by ellipses and circles (F-0–F-6), (b) dbscan clustering results confirming the differentiation of the last five stadia (F-0–F-4). Identified clusters have distinct colours with colourless dots denoting "outliers".

lack of overlap between larval stadia and separated all groups corresponding to the last five instars (F-O–F-4), further enhancing the discrimination observed in the scatter plot. Figure 3b depicts the results of this analysis, with each point representing a single larva. The ability of the dbscan algorithm to accurately distinguish larval groups based on their proximity in the feature space of head width and total body length highlights the robustness of our results.

Growth and development

Larval size distribution showed a bimodal pattern in both spring and summer. The smallest larva, with a total length of 5 mm, first appeared on 25 March, and the last F-0 larva, with a total length of 23.2 mm, was found on 22 June (Fig. 4). The absence of F-1 and F-2 instars during summer is noteworthy. After overwintering in instars F-1, F-2, and, to a lesser extent, F-3, the senior cohort continued its growth and development to the final instar in spring and early summer (Fig. 4). This larval pattern coincides with the presence of exuviae and adults in late spring/summer (early June–July). Similarly, the junior cohort, which had overwintered as F-6 and smaller instars, continued its growth throughout spring, summer, and autumn until it reached the stages F-1, F-2, and F-3 (Fig. 4).

Discussion

In this study, we collected several indicators, including the timing of F-O, exuviae, and flight period, that suggest a prolonged emergence period of O. f. unquiculatus in the Seybouse River region. The presence of overwintering larvae, particularly in developmental stages F-1 and F-2, indicates that these would not be able to emerge in synchrony with the F-O larvae. Our infrequent sampling of exuviae, combined with the small size of the investigated population, has surely limited the quality of our emergence data, however. Therefore, we can only assume that emergence probably begins in late spring (late May or early June) and may continue until early July. Our observations of O. f. unquiculatus in the Seybouse River nevertheless contribute significantly to our understanding of the timing of its emergence, a crucial phase in the life cycle of Odonata. These results are consistent with findings from southern Europe, where O. f. unguiculatus typically emerges from May to mid-July and the flight period extends from May to early September (Ferreras-Romero & García-Rojas, 1995; Ferreras-Romero & Márquez-Rodríguez, 2014; Wendler & Nüss, 1991 in Fide Suhling & Müller, 1996). Similar patterns, albeit with a delayed emergence, were observed at two lotic sites in Lombardy, Italy. In these cases, the emergence period extended from 16 June



Figure 4. Size–frequency distribution plot of *Onychogomphus forcipatus unguiculatus*. White dots within boxplots indicate median values: (a) body length, (b) head width. Dotted lines indicate the development of the F-1 and F-2 stadia into F-0, whereas dashed lines suggest arrested or minimal development of F-3 larvae.

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to 22 September, with adult flight observed from mid-June to early October (Hardersen, 2004, 2008).

Our study reveals that head width and body length serve as effective measurements to distinguish the last seven larval instars of *O. f. unguiculatus*. This realization is consistent with the results of previous research on *O. uncatus* (Schütte et al., 1998) and *O. costae* (Samraoui et al., 2023), suggesting that these morphological characters provide reliable means for classifying larval stages. Accurate identification of the last instars (F-O–F-3) is of utmost importance for understanding the complex life cycles of Odonata. Nevertheless, it is equally important to sample smaller larvae (i.e., F-6 and below) to derive accurate voltinism patterns (Aoki, 1999; Folsom & Manuel, 1983).

Interestingly, our results seem to diverge from those of Martín & Maynou (2023), who observed a considerable overlap in larval sizes and could only distinguish stages up to F-2. This discrepancy may be attributed to differences in the ecological context of the respective studies. Further investigation and comparative analyses are needed to elucidate the factors contributing to these differences. In any case, our current study underscores the importance of measuring head width and body length as effective tools for accurately characterizing larval stages in Odonata.

The presence of F-6 instars in spring suggests that egg development occurs in a direct manner (without diapause) and that these larvae hatch in the previous year (Folsom & Manuel, 1983). However, this is a hypothesis that will require confirmation. In addition, the presence of small larvae in the spring prior to emergence raises the possibility that the mesh size of the hand net we used was too wide to capture these smaller larvae, allowing them to escape our sampling. Another plausible explanation would be that these earlyinstar larvae sought refuge in the hyporheic zone and underwent gradual development during the preceding summer, autumn, and winter seasons (Reygrobellet & Castella, 1987; Seyed-Reihani et al., 1982; Stubbington, 2012). The hyporheic zone has previously been suggested as a summer refuge for semivoltine gomphids such as G. pulchellus and O. forcipatus (Ferreras-Romero & García-Rojas 1995). In any case, it is likely that two cohorts coexist for several months, with the smaller larvae evading detection and possibly finding shelter in interstitial spaces.

During summer and beyond, the newly hatched cohort spends its first winter as 'small larvae', i.e., smaller than the F-6 instar, coexisting with the senior cohort that has hatched in the previous year. This younger cohort may not yet have reached a 'winter critical size' (WCS) and, according to the model proposed by Norling (1984), enters a long-day diapause with arrested or minimal growth and overwinters as F-6 and smaller instars. Growth and development resumes in the following spring, with these larvae reaching F-1, F-2, and F-3 instars by early autumn and overwintering primarily as F-1 and F-2 instars. In late spring and early summer, the senior cohort gradually reaches the final instar stage, resulting in asynchronous emergence.

Growth and development of *O. f. unguiculatus* may be controlled by a biphasic photoperiodic and thermal response, as has been proposed by Norling (1984). However, empirical data are needed to validate this seasonal regulation. Temperature is a critical factor that significantly influences several facets of insect development, including larval growth rates, emergence patterns, and flight periods (Corbet, 1999; Leggott & Pritchard, 1985; Suhling & Müller, 1996) and applies to Odonata that live in aquatic environments during their larval stages.

In the Seybouse River region, the mean annual water temperature for Wadi Aar was reported to be 18.6 ± 8.1°C (Bouhala et al., 2019), and water temperatures during the winter months (December-March) in the Haut Seybouse region vary between 7.1 and 12.0°C (Bouhala et al., 2021). Our data derived from the relative abundance of F-2 and F-1 between winter and spring suggest that some growth and development indeed occurred. A recent study of the life cycle of O. f. unguiculatus in the Tordera River in northeastern Spain revealed a univoltine pattern (Martín & Maynou, 2023). It is noteworthy that winter water temperatures of 8.3–11°C in this region are similar to those observed in the natural habitat of O. f. unguiculatus in the Seybouse River. However, despite this similarity in water temperatures, the voltinism of the species varies geographically (see below), and temperature conditions alone may not be the primary cause of this unexpected result. These results not only highlight the remarkable plasticity of the life cycle of O. f. unquiculatus, but also suggest the presence of other important factors affecting its life cycle (Corbet et al., 2006).

In contrast to the results for O. uncatus at Canal Centre Crau, southern France (Suhling, 1995) or Gomphus lucasii (Samraoui et al., 2019), our data do not support the notion of an early emergence or a high degree of synchrony in the senior cohort of O. f. unguiculatus. This cohort overwintered primarily as F-1, F-2, and possibly F-3 instars. Thus, the available information from southern Europe (Suhling & Müller, 1996) and Algeria consistently indicates that this species exhibits the generation succession typical of a summer species (Corbet, 1962; Corbet & Corbet, 1958). No final instar larvae of O. forcipatus were collected in either Spain or Algeria during autumn and winter; most belonged to the F-1, F-2, or smaller instars (Ferreras-Romeros & García-Rojas, 1995). Final-instar larvae typically emerge in late spring and early summer, reflecting the characteristic protracted emergence pattern of a summer species (Corbet, 1954, 1964). Interestingly, the emergence pattern of the closely related O. f. forcipatus in the Tisza River system, Hungary, follows that of spring species (Farkas et al., 2012). Nevertheless, remarkable intraspecific variation in emergence periodicity and synchrony has been documented for numerous gomphids, including O. uncatus and G. flavipes (Farkas et al., 2012; Suhling, 1995).

In contrast, the larval development and emergence pattern of *G. lucasii* (Samraoui et al., 2019), *G. pulchellus* (Ferreras-Romero & García-Rojas, 1995; Müller & Suhling, 1990), and some populations of *O. uncatus* (Suhling, 1995) correspond to the typical characteristics of spring species. In these species, the final instar larvae are present in autumn and overwinter in this stage, followed by an 'explosive' mass emergence in spring. In spring species such as *Anax imperator* Leach, 1815, or *Gomphus lucasii*, almost half of the population emerges within three days (Corbet, 1957; Samraoui et al., 2019).

Onychogomphus f. unguiculatus, O. uncatus, and G. lucasii may differ in Winter Critical Size (WCS), resulting in different larval growth and development patterns. Alternatively, WCS, which is typically responsible for cohort splitting, may be most effective at higher latitudes (Norling, 1971, 1984). The observed differences in growth and development between the two species could simply be proportional to the number of degreedays experienced by the respective larvae, or could be due to different growth rates (Corbet, 1999; Lutz, 1974).

The presence of at least two distinct cohorts in spring and summer rules out the possibility of a univoltine life cycle for O. f. unquiculatus in the Seybouse River region and strongly suggests a semivoltine life cycle. Thus, our results are consistent with the hypothesis that a generation of O. f. unguiculatus requires two years to develop. The life cycles of O. f. unguiculatus and G. lucasii in the Seybouse River area are similar to those reported by Ferreras-Romero & García-Rojas (1995) for O. f. unguiculatus and G. pulchellus on the Yeguas River in southern Spain. At both rivers, O. forcipatus is more abundant upstream, and all three gomphids exhibit semivoltine life cycles (Ferreras-Romeros & García-Rojas, 1995; Samraoui et al., 2019; this study). However, the life cycle of O. f. unquiculatus on the Seybouse River appears to be less flexible and prolonged than those of O. uncatus and G. vulgatissimus, which exhibit semivoltine and partivoltine (3-year) life cycles in southern (Ferreras-Romero et al., 1999; Schütte et al., 1998) and central Europe (Müller et al., 2000), respectively. This lower degree of flexibility in the life cycle could of course also be due to the very small sample size of our study population. Therefore, further studies on different populations are needed to confirm this hypothesis.

Coexistence of *O. f. unguiculatus* and *G. lucasii* has been documented from numerous lotic sites in Tunisia, ranging from 250 metres to sea level (Korbaa et al., 2018). The observed temporal separation between these two gomphids may reduce potential competitive pressure (Benke, 1970). *Onychogomphus f. unguiculatus*, like the large-bodied burrower *G. lucasii*, exhibits a 'slow' lifestyle as has been highlighted by Samraoui et al. (2019), placing it at one end of the predatorpermanence gradient (Johansson, 2000; Johansson & Suhling, 2004; McCauley, 2008; Wellborn et al., 1996). Nevertheless, the "slow" lifestyle of *O. f. unguiculatus* is much less pronounced compared to its congeneric species *O. uncatus*, as was pointed out by Suhling (2001). This observation is consistent with the characteristics of all other Palaearctic gomphids studied so far, as they all require at least two years to produce a generation (Corbet et al., 2006), with a single exception: *Paragomphus genei* (Selys, 1841), which has either a univoltine (Testard, 1975) or even a bivoltine life cycle (Jödicke, 2001; Suhling & Martens, 2007; Weihrauch & Weihrauch, 2003), enabling it to make use of temporary habitats.

In arid North Africa, the Mediterranean summer does not provide many permanent lotic habitats, with the lower Seybouse River being a notable exception. Freshwater species with long life cycles, such as semivoltine and partivoltine species, face major challenges to survive during the extended dry and hot summer months, especially in the context of ongoing climate change. While residual pools in drying rivers (Bonada et al., 2020; Bourke et al., 2020) and hyporheic habitats can serve as refugia for some species (Stanford & Ward, 1988; Williams, 1977, 1984), continuous water withdrawal for irrigation purposes and impoundment of water by means of dams and reservoirs have been leading to rapid declines in freshwater biodiversity throughout North Africa (Riservato et al., 2009; Samraoui et al., 2010) by turning suitable habitats into ecological traps (Hardersen, 2008). Human encroachment (Benslimane et al., 2019; Morghad et al., 2019) and the impact of these two anthropogenic stressors on the natural flow regime of rivers and streams require remedial measures, including the implementation of environmental flows (Bergkamp et al., 2003; Matthews et al., 2014) as part of integrated river basin management.

While *O. f. unguiculatus* is classified as 'Least Concern' (LC) in the IUCN Red List of Mediterranean Odonata (Riservato et al., 2009), the present study confirms previous findings by Hamzaoui et al. (2015), Samraoui & Corbet (2000) and Samraoui & Menaï (1999), and that indicated that this subspecies is sparsely distributed along the Seybouse River, absent from the El Kala region, and possibly altogether rare in Algeria (B.S. unpubl.). In contrast, *O. f. unguiculatus* has been reported to be abundant on streams crossing both forested and agricultural landscapes in neighbouring Tunisia (Korbaa et al., 2018). Further investigations are needed to clarify the local and regional status of this and other North African gomphids.

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