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Potential fitness consequences of roosting spatiotemporal selection in an endangered endemic damselfly: conservation implications

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Understanding habitat requirements of species of conservation concern is central for their conservation and management. Although much of the research attention has been focused on reproductive sites, the understanding of roosting behavior and microhabitat selection, and their potential fitness consequences is also crucial. Here, we assess the roosting behavior of an endangered endemic damselfly *Calopteryx exul* Selys in a lotic habitat of Northeast Algeria. Based on marked individuals, we specifically investigated their vertical and horizontal distribution at roosting sites, as well as the timing of roosting and its correlation with lifespan (as a measure of fitness). We found that individuals were philopatric to roosting sites and less so to vertical stratification. Roosting sites were used for both foraging and roosting. Individuals that occupied lower strata in roosting sites had longer lifespans and ceased roosting earlier. Average temperature of the day affected the timing of roosting such that on warm days roosting started later and ended earlier. Individuals with longer lifespans roosted earlier, suggesting potential scramble competition for roosting sites. Our results suggest that *C. exul* individuals show variability in the vertical and horizontal location as well as the timing of roosting, and these choices potentially have fitness consequences. This study highlights the importance of bank vegetation as roosting sites for lotic insects, and emphasizes the benefits of protecting these sites and including them as integral parts of the conservation plans of species.

KEYWORDS

habitat preferences, resting, odonates, dragonflies, insects, *Calopteryx exul*

Introduction

Many threatened species of animals, including insects, are on the brink of extinction due to human activities (Maczulak, 2010; Wagner, 2020). Species of conservation concern need particular research attention because of their sensitivity to environmental disturbance (Maczulak, 2010; Samways et al., 2010; Samways, 2020). Conservationists have sounded the alarm about the rapid decline of insects in different regions worldwide due to various anthropogenic factors such as habitat destruction, pesticides, and climate change (Van Klink et al., 2020; Hallmann et al., 2021; Raven and Wagner, 2021; Uhler et al., 2021; Outhwaite et al., 2022). Thus, there is an increasing concern for threatened species because of their high sensitivity to habitat degradation and other anthropogenic stressors (New, 2009). Endemic species, in particular, are among the most threatened groups because their typical small range size limits their ability to cope with rapid changes in environmental conditions (Burlakova et al., 2011; Carmona et al., 2019). Because some anthropogenic factors are unavoidable in a human-dominated world, it is imperative to understand fundamental aspects of species' ecological requirements to increase their resilience and promote their persistence in their natural habitat.

There is a need to develop a holistic understanding of the habitat requirements of threatened species to better protect them and manage their habitat (Deacon et al., 2020; Samways et al., 2020; Kietzka et al., 2021). This involves a better comprehension of the spatial and temporal dimensions that species occupy to perform their ecological functions and fulfill their biological needs (Samways et al., 2020). While conservationists have paid particular attention to foraging and reproductive sites as vital habitat components for the conservation of species (Foster and Soluk, 2006; Majewska and Altizer, 2020; Shipley et al., 2023), other aspects of habitat preferences such as roosting sites have been understudied despite their crucial role in the species' life history (Grether and Switzer, 2000; Grether and Donaldson, 2007; Teng et al., 2012). Roosting sites may provide various services to individuals, including shelter, safety, and social information. Many species of animals, including mammals, birds, fish, and insects roost in communal aggregations of a dozen to millions of individuals (Krause and D., 2002). Compared to vertebrates (Laughlin et al., 2014; Deng et al., 2023), communal roosting behavior in insects has received far less research attention.

The evolution of communal aggregation behavior has been highly debated during the last centuries leading to various theories (Dwyer et al., 2018). Many of those theories such as thermal benefits (Vulinec, 1990), information center (Bijleveld et al., 2010), and aposematism (Turner, 1975) do not apply to a large number of insect groups (Grether and Switzer, 2000). The predator dilution theory as an antipredator defense mechanism; however, is one of the most applicable hypotheses to a wide range of taxa (Lack, 1968), including within insects (Vulinec, 1990). Studies have shown that species have specific preferences for the timing and location of communal roosting (Miller, 1989; Teng et al., 2012; Finkbeiner, 2014; Laughlin et al., 2014), often exhibiting high levels of philopatry in both vertebrates (Lewis, 1995; Beauchamp, 1999) and

invertebrates (Miller, 1989; Grether and Donaldson, 2007; Finkbeiner, 2014). However, our understanding of the implication of microhabitat selection within roosting sites for the survival and fitness of individuals has not attracted comparable research attention.

Odonates are integral components of freshwater systems (Corbet, 1999; Martin and Maynou, 2016), occupying both terrestrial and aquatic habitats, and interacting with a wide range of taxa (Kaunisto et al., 2020). As adults, both dragonflies and damselflies spend the daytime foraging and reproducing near the water, however, at night, they occupy their roosting sites which are either near or far from the water (Corbet, 1999). Odonates are suitable organisms for the study of roosting behavior because they can be easily marked, recaptured, measured, and surveyed in the field throughout their entire lifespan (Cordero-Rivera and Stoks, 2008). Damselflies in particular perform mostly short-range movements and do not disperse frequently. There have been several records of communal roosting behavior in odonates (Neubauer and Rehfeldt, 1995; Grether and Switzer, 2000; Switzer and Grether, 2000; Rouquette and Thompson, 2007; Hykel et al., 2018), but only a few studies have explored microhabitat choice, site fidelity, and the potential fitness implications of roosting site selection.

Calopteryx exul is an endemic damselfly listed as Endangered on the IUCN Red list (Boudot, 2018). The species has a relatively patchy distribution with populations spanning from Morocco in the west to Tunisia in the East. In Algeria, the species had not been recorded for almost a century, from 1910 to 2007 (Khelifa et al., 2011). In later years, multiple subpopulations have been discovered in the Seybouse river, but several of them have perished following habitat degradation (Khelifa and Mellal, 2017). In more recent years, new sites have been recently discovered in the central North and east of Algeria (Chelli et al., 2019; Elafri, 2022), improving our understanding of its geographic distribution in the region. The historical sites of the country have encountered severe changes due to habitat destruction, exploitation (water pumping for irrigation), pollution (pesticides and fertilizers for agriculture), and climate change (severe drought and extreme heat) (Khelifa et al., 2021). Studies on the life history, reproductive behavior, habitat requirements, and geographic range dynamics have been carried out during the last decade (Khelifa, 2017; Mellal et al., 2018; Khelifa, 2019), furthering our understanding of the species ecology and behavior. However, there has not been any study on the roosting behavior in *C. exul*, restricting our holistic understanding of habitat preferences of the species. Filling in this gap of knowledge is crucial for the better management of natural habitats and maintenance of populations in their natural environment.

In this study, we investigate the roosting behavior of *C. exul* using capture-mark-recapture in the Seybouse river, Northeast Algeria. We marked individuals across a 100 m transect of the watercourse and surveyed their vertical stratification, horizontal distribution, timing of occupancy of roosting sites, and lifespan. We aim to test whether: 1) vertical and horizontal distribution differed between sexes, 2) vertical stratification and timing of roosting is correlated with fitness components (lifespan); and 3) temperature influences the timing of roosting. We hypothesize that: 1) there is sexual segregation in space and time due to behavioral differences

between sexes; 2) vertical stratification and the timing of roosting are correlated with lifespan because better spatiotemporal choices have fitness consequences; and 3) timing of roosting depends on temperature such that individuals roost later on warm days.

Materials and methods

Roosting behavior

Mature adults of *C. exul* spend their daytime mating in patches of vegetation floating on the water (territories). At the close of the day, the damselflies gather in specific areas along the watercourse, both males and females joining together in a communal roosting site. These areas are often nestled amidst the bank vegetation, providing foraging, resting, and roosting sites. Prior to roosting, damselflies perched on stems or leaves to forage using a sit-and-wait tactic and seize the passing insects that fly during the dawn. When it becomes dark, damselflies take their roosting position and posture (Figure 1), spreading their wings open and remaining in the same posture until sunrise. Thus, this behavioral display allows us to identify roosting individuals and investigate intraspecific variation in spatiotemporal distributions of roosting behavior.

Study site

The research was conducted in the Seybouse river in the northeastern region of Algeria. The local climate is Mediterranean with hot and dry summers and cool and wet winters. In the Seybouse river, the mean annual rainfall varies between 350 mm upstream and 608 mm downstream (ABHCSM, 2009). The hydrology displays a wet season that encompasses the period from October to May, followed by a dry season that extends from

June to September. The behavioral study was carried out upstream of the Seybouse River, approximately 5 km west of Guelma city (36° 28'02.16"N and 7°22'032.73"E; 210 m elevation). The watercourse was a stream with a shallow depth and a 2–4 m width. The vegetation along the banks predominantly comprises *Typha angustifolia* L., *Cyperus longus* L., *Juncus maritimus* Lam., and *Paspalum distichum* L. In the same site, odonate assemblage is dominated by *C. exul*, *C. haemorrhoidalis*, *P. subdilatata*, and *G. lucasii*.

Capture-mark-recapture

We took advantage of the daily capture-mark-recapture scheme that took place between 9:30 AM and 4:00 PM between late April and mid-July 2011 (total individuals marked 1417) as described in Khelifa et al. (2016). Six researchers carried out captures of adults with a hand net across a transect of 2 km. Adults were marked on the hindwing using permanent markers (Edding paint marker 780). Thus, a large proportion of individuals were marked throughout the flight season, which facilitated behavioral surveys of roosting behavior. Using repeated resightings, we were able to estimate the lifespan of individuals as the number of days between the first capture and the last resight.

Behavioral survey

To assess the roosting behavior of *C. exul*, we selected a transect of 100 m where the largest number of individuals occurred. A prior behavioral survey on the reproduction of the species took place in the same location (Khelifa, 2019). Two observers performed all behavioral surveys (each observer surveyed 50 m). To locate individuals within the studied area, we segmented the transect into 10 m sections using flags.



FIGURE 1

A roosting mature male (left) and female (right) of *Calopteryx exul* adult early in the morning in the Seybouse river, Northeast Algeria. Wing spreading occurs only when individuals are roosting. The typical wing posture when individuals are perched is joint wings.

The location within each 10 m-section was estimated visually to the nearest meter. The spatial and temporal distribution of roosting behavior was surveyed in the early morning between 5:00 am and 09:00 am and in the late afternoon between 05:30 pm and 09:00 pm for seven days (18–27 May 2023). We carried out scans every 10 minutes across the 100 m transect where we recorded the time of the day, individual ID, sex, location within the transect, and vertical stratification on the perching site. To estimate the vertical height of perching and roosting sites, we provided gridded sticks at different parts of the transect which allowed an estimation to the nearest 1–5 cm. The perching height of unmarked individuals was also estimated to determine the vertical stratification (involving a total number of observations of marked and unmarked individuals of 2357 and 589, respectively). Uniquely marked individuals included 122 adults, involving 70 females and 52 males.

Statistical analyses

We used R 4.2.2 to perform our statistical analyses (R Development Core Team, 2023). All mixed effects models (LME) were carried out using lme4 (Bates et al., 2015). To assess sexual differences in the vertical and horizontal distribution of individuals across the watercourse, we carried out a two-sample Kolmogorov-Smirnov test. To determine the temporal change in vertical stratification in the morning and the evening, we used a repeated measure correlation using the rmcrr package (Bakdash and Marusich, 2017). To assess philopatry to roosting sites and vertical stratification, we also analyzed the repeatability of location across days using the rpt function of the rptR package (Stoffel et al., 2017) with an LME including only the random effects of individual ID and sampling date. To determine whether there is a difference in the vertical stratification of individuals at communal roosting sites between sexes, marked and unmarked individuals, and time, we conducted an LME with sex, marking (marked or unmarked), and time of the day as explanatory variables, the height of roosting individuals as a response variable, and individual ID and sampling date as random effects. To test whether lifespan was correlated with vertical stratification, we used a generalized mixed-

effects model (with negative binomial errors) that includes lifespan as a response variable, average roosting height (mean across days) and sex as explanatory variables, and individual ID as a random effect. To determine whether the temporal pattern of roosting differed between sexes and temperatures, we conducted a generalized LME (with binomial errors) for each period (morning and evening) with the presence/absence of roosting behavior as a response variable, time, sex, and average daily temperature as explanatory variables, and individual ID and sampling date as random effects. We used DHARMA package (Hartig, 2022) to perform residual diagnostics and check for the assumptions of the mixed-effects models (Supplementary material). Values shown in the text are mean \pm SD.

Results

Vertical stratification

During the sampling period, adults occupied an average height of 65.6 ± 40.6 cm ($n = 2946$; range = 1–200 cm) strata. On average, males occupied significantly higher strata (70.0 ± 42.4 cm) than females (62.5 ± 39.0 cm) (two-sample Kolmogorov-Smirnov test: $D = 0.09$, $P < 0.0001$) (Figure 2). Vertical stratification showed a temporal decline in the morning (from dawn to early morning) ($r = -0.20$ [95% -0.24 – -0.15], $P < 0.0001$) whereas a temporal increase in the evening (from late afternoon to dusk) ($r = 0.45$ [95% 0.40 – 0.50], $P < 0.0001$).

In roosting sites, when we consider only marked individuals, we found that there was no significant difference in vertical stratification between sexes (LME: $\chi^2 = 2.25$, $P = 0.13$) and across days (LME: $\chi^2 = 1.58$, $P = 0.20$). In fact, vertical stratification of roosting behavior showed a low but significant level of repeatability across days ($R = 0.13$ [0–0.38], $P = 0.008$). Interestingly, there was a significant negative correlation between the average height of roosting and the lifespan of individuals (GLME: $\chi^2 = 4.54$, $P = 0.03$), revealing that individuals that had longer lifespans occupied lower strata (Figure 3).

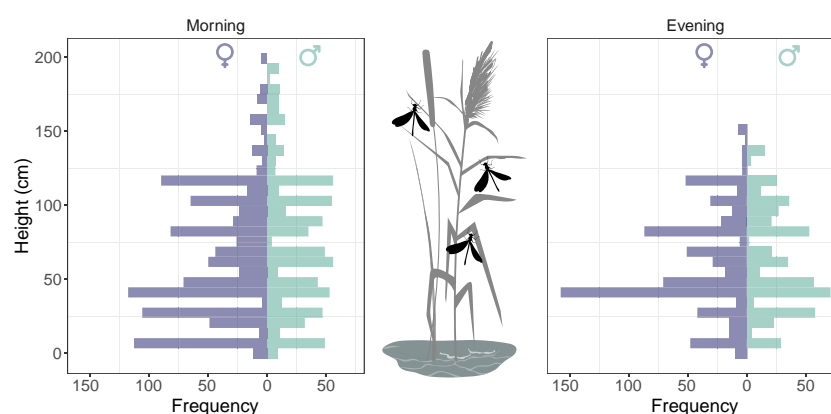
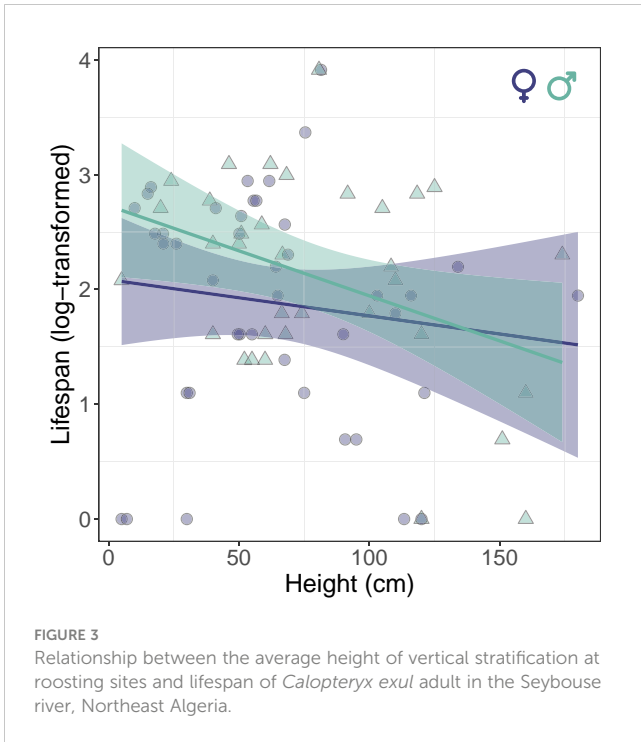


FIGURE 2

Vertical stratification of *Calopteryx exul* adult in roosting sites in early morning and evening in the Seybouse river, Northeast Algeria.



Timing of roosting behavior

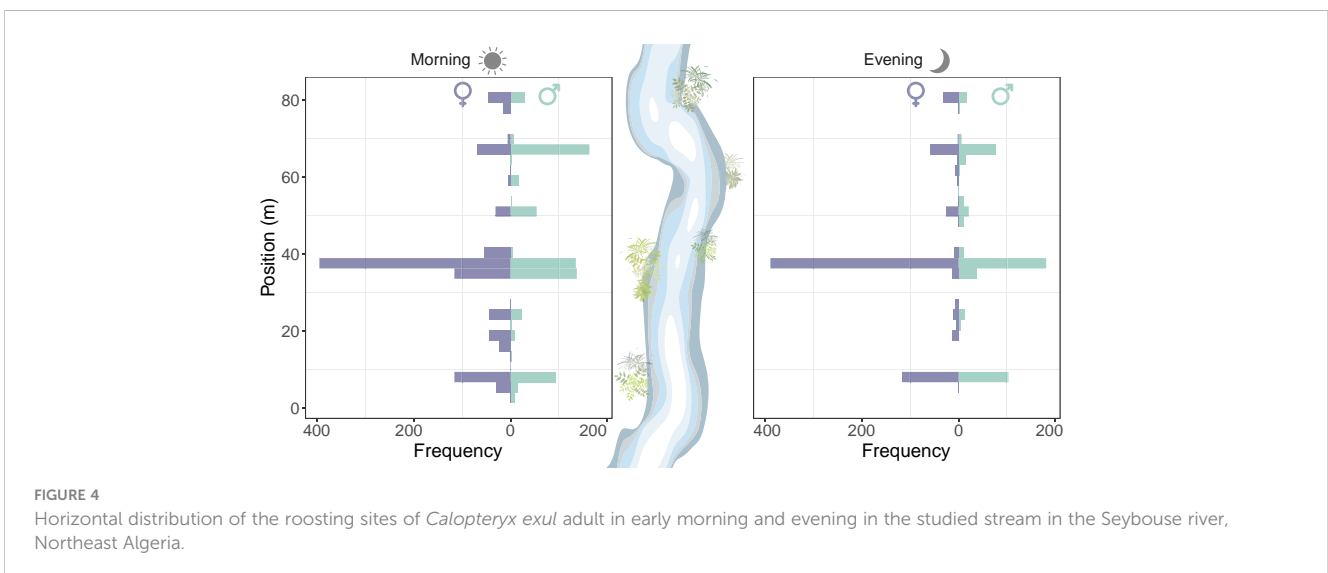
There was intraspecific variation in the timing of the beginning (in the evening) and ending (in the morning) of roosting. The proportion of roosting individuals increased gradually with time in the evening (LME: $\chi^2 = 58.8, P < 0.0001$), and decreased in the morning ($\chi^2 = 88.4, P < 0.0001$) (Figure 5), revealing a gradual chronological shift in the proportion of roosting individuals. The absence of time-by-sex interaction in the morning indicates that males and females had similar timing of roosting ($\chi^2 = 0.03, P=0.84$), but in the evening the rate of roosting was slightly but not significantly faster in females than males ($\chi^2 = 0.71, P=0.39$). Timing of roosting interacted significantly with the average temperature of the day in the morning ($\chi^2 = 58.1, P < 0.0001$) and the evening ($\chi^2 = 32.6, P < 0.0001$), revealing that individuals ceased the roosting posture earlier in the morning and started the roosting posture later in the evening in warmer days (Figure 5). There was a marginal negative correlation between the timing of roosting and lifespan in males but not in females, as revealed by the marginal interaction of lifespan and sex ($\chi^2 = 3.19, P = 0.08$) (Figure 6).

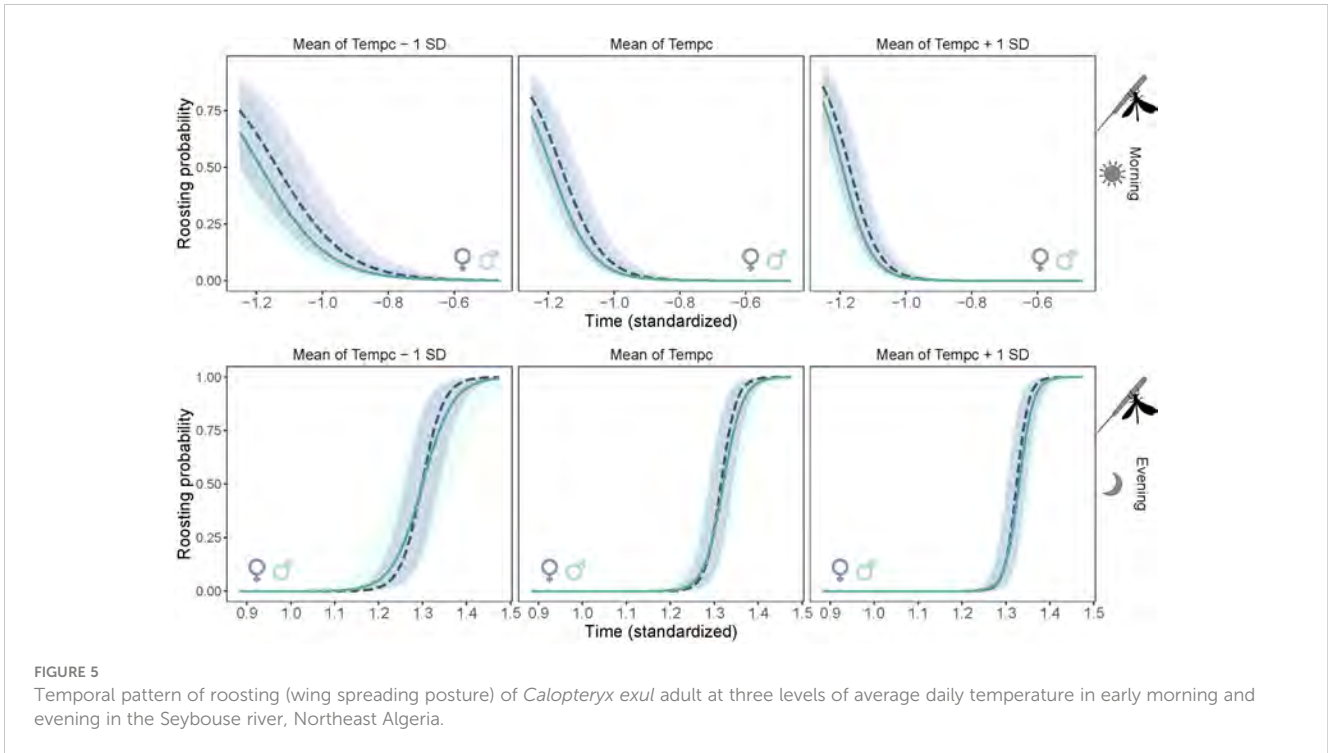
Discussion

Although communal roosting behavior in odonates has been documented in both damselflies (Grether and Switzer, 2000; Rouquette and Thompson, 2007) and dragonflies (Miller, 1989), the study of its vertical stratification and timing and its potential fitness consequences has not attracted much research attention. In this study, we investigated the roosting behavior of *C. exul*, an endangered endemic damselfly that lives in lotic habitats of North Africa. Our behavioral survey showed that 1) roosting sites were restricted to small areas in the watercourse; 2) adults were philopatric to roosting sites but less so to vertical stratification; 3) vertical stratification and timing (marginal) of roosting were

Horizontal distribution

Roosting sites had a patchy horizontal distribution across the vegetated areas of the watercourse. Overall, males and females had a similar horizontal distribution of roosting sites in the evening (two-sample Kolmogorov-Smirnov test: $D = 0.21, P=0.06$) (Figure 4). Roosting site selection across the watercourse was significantly repeatable from one day to another ($R=0.49 [0.03-0.77], P < 0.0001$). Almost all individuals (94%) were recorded near the water with one individual (<1%) recorded roosting at 10 m away from the water.



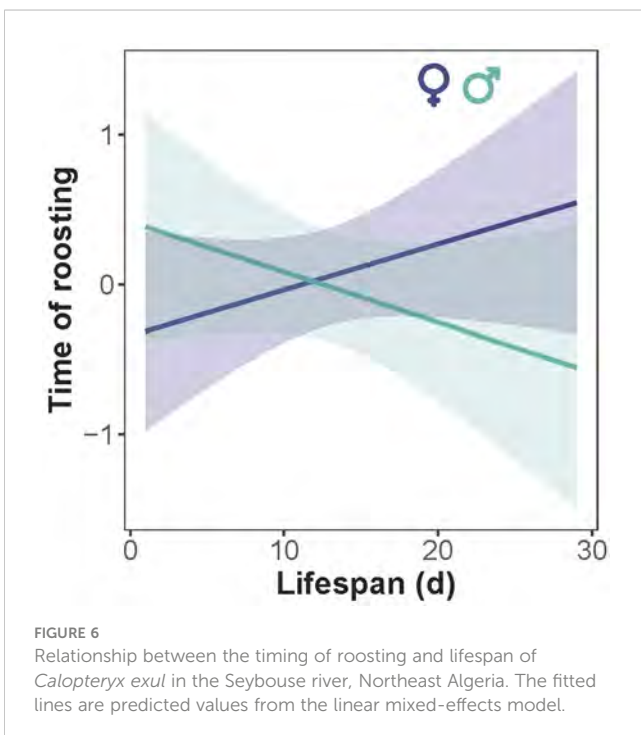


negatively correlated with lifespan; and 4) temperature of the day influenced the timing of roosting. This is the first study that investigates the beginning of roosting behavior was marginally correlated with individual lifespan.

In our study species, the non-random horizontal distribution of individuals suggests that the species exhibits site preferences for communal roosting. These roosting areas were relatively dense vegetated areas on the banks of the watercourse, which likely

provided shelter against predators and resilience to withstand adverse nocturnal weather conditions (wind and rain) (Rouquette and Thompson, 2007; Hykel et al., 2018). Concordant with our hypothesis of site fidelity, we found that individuals were philopatric to roosting sites, which is similar to other species of Calopterygidae displaying comparable communal roosting behavior (Grether and Switzer, 2000). Grether and Switzer (2000) suggest that the location of the roosts is, at least partly, socially learned (i.e., traditional rather than habitat-related). In an experimental study on philopatry to roosting sites in a harvestman, Grether and Donaldson (2007) found that past communal usage was the best predictor of roosting site selection despite the occurrence of other similar sites (Grether and Donaldson, 2007). In many insects and other animal groups, philopatry is suggested to have evolved because of its fitness benefits (Stacey and Ligon, 1991; Hendry et al., 2004), which include familiarity with the environmental conditions including competition and predation risks, and minimization of the time and energy allocated to searching new locations (Switzer, 1993). Those benefits could also explain the occurrence of philopatry of odonate adults not only to roosting sites, but also to reproductive and emergence sites (Dolný et al., 2013).

In addition to selecting a particular location of roosting sites, adults of *C. exul* were also selective of vertical strata. The similarity in the vertical stratification between males and females (absence of sexual segregation) and the absence of mating attempts strengthens the hypothesis that vertical stratification is not directly related to mating (Grether and Switzer, 2000). There are many studies that show intraspecific and interspecific variation in the vertical distribution of adults during the active period of the day (Worthen and Jones, 2006; Worthen and Morrow, 2016), as well as larvae during emergence (Cordero, 1995; Hadjoudj et al., 2014).



These studies suggest that the selection of heights has many fitness implications, including avoidance of predators, coping with harsh weather conditions, reducing competition, and exposure to sunlight (Switzer and Grether, 2000; Khelifa et al., 2013). Some of these benefits may apply to the vertical stratification of *C. exul* at roosting sites. In particular, roosting in specific strata may allow individuals to receive the first sunlight in the morning (Switzer and Grether, 2000), which could prolongate their hunting period. Importantly, our results support the hypothesis that lower strata likely provided better ecological conditions to roosting adults. In fact, we found a negative correlation between lifespan and vertical stratification of individuals at roosting sites, suggesting survival costs related to the selection of higher strata. It is likely that individuals that roosted in higher strata were more conspicuous to predators and thus more exposed to higher rates of mortality. This hypothesis goes in line with studies showing that more conspicuous individuals of Calopterygids are more often predated by birds (Svensson and Friberg, 2007). Further studies need to be conducted to assess whether the benefits of vertical stratification is condition-dependent, that is, lower strata could be less beneficial in some sites compared to others due to differences in predation or interspecific competition.

Unlike other species of Calopterygidae (Grether and Switzer, 2000), where foraging and roosting sites are distinct patches of vegetation, we found that roosting sites were often used as foraging sites for both males and females of *C. exul*. In the same roosting area, foraging was carried out prior to roosting in the evening and after becoming active in early morning, similar to other Calopterygidae (Switzer and Grether, 2000). However, the vertical strata used for both activities were quite different. As indicated by the temporal decline of vertical stratification in the evening and its gradual increase in the morning, the roosting strata were often lower than the foraging strata in *C. exul*. This might be a behavioral strategy to not only maximize foraging success at higher strata prior to or after roosting, but also reduce detectability and avoid predation at night during roosting. Interestingly, a high proportion of individuals concentrated near the water when roosting although there were vegetated areas farther from the water. Unlike other odonate species that roost away from the water (Rouquette and Thompson, 2007; Hykel et al., 2018), the nocturnal aggregation of individuals near the water renders the bank aquatic plants vital resources for feeding, resting, roosting, and emergence for *C. exul*.

Another finding in our study was that the average temperature of the day influenced the timing of roosting. On warmer days, both males and females started roosting later in the evening and became active earlier in the morning. As an ectotherm, damselfly activity is highly dependent on temperature (Angilletta, 2009), such that as body temperature increases earlier in the morning, individuals become active earlier (May, 1979). On warmer days, individuals also roosted later in the day probably because they spend more time mating and foraging. It is important to note that, since our survey was carried out in the spring, warmer days did not involve extreme heat. A similar influence of weather conditions on the timing of communal roosting behavior was recorded in a social bird (cattle egret) (Youcefi et al., 2019). This finding suggests that climate

change could influence the diel pattern of activity and spatial distribution of the studied species (Yang et al., 2021).

Our results showed a marginal negative correlation between the timing of roosting and lifespan in males but not in females. It is likely that the temporal variation in roosting suggests competition for space at roosting sites. It is well known that high-quality males arrive earlier in breeding sites in birds and other taxa (Kokko, 1999; Morrison et al., 2019). If this hypothesis is true, we believe that such competition is more scramble than interference competition due to the rare intraspecific interactions between individuals at roosting sites. This is unlike the interspecific competition for space in perching sites usually recorded in different odonate assemblages where larger species tend to exclude smaller species from preferred habitats (Worthen and Jones, 2006; Worthen and Morrow, 2016). An alternative explanation is that, since foraging often precedes roosting, it is likely that individuals who are more fit (better at surviving longer) are more effective at foraging, thus roosting earlier than other individuals. Further studies are needed to shed light on the mechanisms underlying the negative relationship between the timing of roosting and fitness.

Our study presented some limitations due to the technical difficulty of performing field observations early in the morning and in the evening. Due to the rarity of the species and security issues, we could not perform the behavioral survey on multiple sites and throughout the entire season. We did not measure morphological traits such as body size and territoriality to determine their implication in vertical stratification and roosting behavior. Nevertheless, we believe that our fitness measure (lifespan) is a good proxy for quality because it captures the ability of individuals to survive and live longer. Further studies on roosting behavior need to explore potential behavioral variations of roosting across space and time.

Conservation implications

Our results on the potential fitness consequences of roosting microhabitat selection highlight the importance of investigating roosting behavior and ecology. The dual function of roosting sites as both foraging and roosting areas makes them vital habitat elements and likely key criteria in habitat selection for *C. exul*, and other odonates. Studies have highlighted the pivotal role that bank vegetation and hydrophytes provide for the reproduction of damselflies (Oliveira-Junior et al., 2017), including *C. exul* (Khelifa, 2013; Mellal et al., 2018). Our results, together with the existing literature, highlight the importance of understanding the function of the bank vegetation of aquatic habitats (Guillermo-Ferreira and Del-Claro, 2011; Vilenica et al., 2022) and the ecological implications of its degradation on the aquatic community and ecosystem functioning (Da Silva Monteiro Júnior et al., 2013). The conservation plan for threatened species such as *C. exul* should not only focus on reproductive sites but also consider roosting sites as integral parts of the habitat requirements for the species (Rouquette and Thompson, 2007; Hykel et al., 2018). The conservation of these habitats probably has an umbrella effect on a diversity of terrestrial and aquatic taxa, thus promoting biodiversity

and protecting the integrity of ecosystems. Future studies need to investigate the interplay between reproductive behavior, habitat preferences, foraging success, intrinsic traits, and lifetime mating success.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://figshare.com/s/b49f4f90592f2628def9>.

Ethics statement

Ethical review and approval was not required for the study on animals in accordance with the local legislation and institutional requirements.

Author contributions

HM: Data curation, Writing – original draft, Writing – review & editing, Formal Analysis, Visualization. RZ: Data curation, Writing – review & editing, Conceptualization, Investigation. HA: Data curation, Investigation, Writing – review & editing. SB: Data curation, Investigation, Writing – review & editing. AZ: Investigation, Writing – review & editing. AY: Data curation, Investigation, Writing – review & editing. RK: Writing – review & editing, Conceptualization, Data curation, Supervision, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1267705/full#supplementary-material>

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