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The Effect of Age on Survival Is Similar in Males and Females of an Aquatic Insect Species

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Abstract: Age is a critical intrinsic factor that influences the probability of survival of organisms on Earth. In many animals, the lifestyles and habitat occupancy of males and females are so different that the effect of age could be sex-dependent. To reveal such patterns in wild animal populations, we here use a natural population of the Mediterranean demoiselle *Calopteryx haemorrhoidalis* Vander Linden (Calopterygidae: Zygoptera) in Northeast Algeria to analyze the influence of age and sex on survival probability using daily capture–mark–recapture. We used stepwise model selection on Cormack–Jolly–Seber models that explain recapture and survival probability, including age and sex as covariates. We marked a total of 214 adults throughout the study period (41 days). The sex ratio did not deviate from unity. Recapture probability depended on sex and time, with a slightly higher recapture probability in males (0.30 [95% CI: 0.27–0.35]) than females (0.26 [0.22–0.30]). The survival probability was slightly higher in females (0.89 [0.86–0.91]) than males (0.86 [0.82–0.88]). The best model for the survival probability included an additive effect of sex and age, indicating that the survival probability of both sexes declined with age. Interestingly, the lifespan of some individuals reached 119–130 days, which is surprisingly long compared to other temperate damselflies.

Keywords: damselfly; capture–mark–recapture; lifespan; lotic; Mediterranean

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1. Introduction

Empirical studies have documented the effect of age on survival and fecundity in many animal taxa [1–3]. One typical age effect is a decrease in survival rate with chronological age [4]. The literature on senescence in wild populations is dominated by studies on vertebrates such as mammals and birds, but invertebrates like insects remain relatively less documented [5]. Studies on senescence have been conducted in some insect groups, including dipterans [6,7], hymenopterans [8], orthopterans [9], and odonates [10,11]. There are various intrinsic and extrinsic factors that could influence the effect of age on individuals. For instance, the magnitude and direction of the effect of age could differ between males and females [12,13], especially in species where sexes differ substantially in lifestyle and habitat use [14,15]. This hypothesis on the differential age effect on sexes warrants investigation in wild populations of insect species with long lifespans.

Odonates are suitable for capture–mark–recapture (CMR) studies because they are relatively easy to capture, mark, and survey throughout their lifespan [16]. Many studies have applied the CMR technique on damselflies to answer ecological and evolutionary questions because they are easy to catch and likely to stay in the same area after release [17–19]. The effects of sex and age on the survival rate have been investigated in various studies on damselflies [20]. A recent meta-analysis investigating drivers of survival rate showed that age showed a significant effect, whereas sex did not [20]. This finding confirms the conclusions of Sherratt, Laird, Hassall, Lowe, Harvey, Watts, Cordero-Rivera, and Thompson [10], who found that age-dependent models of survival performed better than those without age dependence at explaining the CMR data on various dragonflies and damselflies. The direction of the effect of age on the survival rate of odonates varied across studies. For instance, in *Platycnemis subdilatata* Selys, tenerals (recently emerged adults) and immature individuals had lower survival probabilities than mature individuals [21]. Studies on mature damselflies showed that the effect of age was negative [10,22], indicating a lower survival rate in older individuals. Despite the large number of CMR studies, only a few studies have investigated the differential effect of age in males and females [12,13].

Although CJS models are suitable for CMR of odonates, their estimates of apparent survival could be slightly biased due to individual emigration. In fact, the spatial and temporal (season) coverage of the CMR sampling should determine the accuracy of the survival and lifespan estimates [16]. First, a meta-analysis of 39 species showed that the longer the CMR survey, the more accurate the estimate of survival probability [20]. Second, the larger the sampling area, the more likely marked individuals are resighted and the less likely emigration occurs [23]. Thus, to avoid these shortcomings, CMR surveys should be carried out across larger areas and for longer periods. However, most CMR studies have targeted small areas (<1 km transect), and span only a few weeks, which may result in an underestimation of the survival, the lifespan, and the effect of age on survival of individuals.

Calopteryx haemorrhoidalis Vander Linden is a Mediterranean damselfly that is native to North Africa (Algeria, Tunisia, and Morocco) and western Mediterranean Europe (Iberia, Southern France, Italy, and Monaco) [24]. The species is listed as Least Concern in the IUCN Red List. Across its range, the species is very common in various lotic habitats, particularly in rivers and streams. Its flight period is relatively long, from May to September in Europe [25,26] and slightly longer in North Africa (late March to October) [27,28]. The available CMR-based estimates of maximum lifespan of the species are 43 days in Spain [29] and 39 days in France [30]. Compared to other congeneric species that exist across its range (e.g., *C. splendens* Harris, *C. virgo* Linnaeus, *C. exul* Selys), *C. haemorrhoidalis* has received less research attention. In North Africa, most research on the life history, behavior, and ecology of *Calopteryx* focuses on the endemic endangered *C. exul* [31–33] and rarely on *C. haemorrhoidalis* [34]. To our knowledge, capture–mark–recapture studies on *C. haemorrhoidalis* have been exclusively carried out in Europe [29,30,35–37], and not in North Africa.

In this study, we aim to assess the effect of sex and age on the survival of the damselfly *C. haemorrhoidalis* in the Seybouse River, Northeast Algeria. We used daily CMR from late April to early June across a 2 km stretch of the river. We specifically assessed the seasonal pattern of abundance of the species. Then, using Cormack–Jolly–Seber models, we determined the best model for recapture and survival probability using different covariates that include sex and age. Finally, we reported unusually long lifespans for this species by recording individuals that we marked in summer during the autumn. We hypothesize that age will have a similar effect on males and females because the latter do not typically show spatial segregation at the adult stage even during maturation [29].

2. Materials and Methods

2.1. Study Area

We carried out this study in the Seybouse River, northeastern part of Algeria. The region has a Mediterranean climate (Csa Köppen climate classification) with hot and dry summers and cool and wet winters. The annual rainfall varies between 350 mm upstream and 608 m downstream. The study location was upstream of the Seybouse River, about

5 km west of Guelma city, and at a 210 m elevation (36°28′023.16″ N and 7°22′032.73″ E). The odonate assemblage consisted mainly of *C. exul*, *C. haemorrhoidalis* Vander Linden, *Platycnemis subdilatata* Selys, and *Gomphus lucasii* Selys. *C. exul* and *Platycnemis subdilatata* were more abundant than *C. haemorrhoidalis* [38]. The bank vegetation was dominated by *Typha angustifolia* L., *Cyperus longus* L., *Juncus maritimus* Lam., and *Paspalum distichum* L. Weather data (daily minimum, mean, and maximum temperature) were obtained from a weather station 8 km away from the study site (Belkhir province, Guelma).

2.2. Capture–Mark–Recapture Protocol

To assess the survival probability of C. *haemorrhoidalis,* we conducted daily capture–mark–recapture on adults across a stretch of 2 km from 27 April (the start of the flight season) to 7 June 2011. The sampling started at 9:30 h and ended at 16:00 h. Some sections of the river were not accessible because of the dense bank vegetation (mainly dense trees of *T. gallica*). Thus, we divided the river into 10 sections that were visited daily for marking and recaptures. Adults were captured with a hand net, then marked with a permanent marker. We used an alphanumeric code to give an individual mark for each adult (Figure 1). We categorized the age of individuals at first capture, using morphological features (rigidity of the wings and body, body coloration, and presence of pink color in the underside of the few last abdominal segments of the males), into three age classes: teneral (<24 h), immature, and mature. We released the marked individuals at the same locations by gently depositing them on the bank vegetation. Those individuals were not captured again, but just resighted on subsequent sampling occasions. Because the estimation of adult abundance on every occasion was challenging, we used a proxy which consisted of summing the number of newly marked individuals and the number of recaptured individuals. Those estimates were used to assess the seasonal pattern of abundance.

Figure 1. A reproductive pair of marked *Calopteryx haemorrhoidalis* in the Seybouse River (2011).

2.3. Capture–Mark–Recapture Modeling

We used the capture–mark–recapture data to design a capture–recapture history for each marked individual, which is a series of consecutive sampling occasions (days) with 1s (presence) and 0s (absence or non-detection) [39]. A capture–recapture history of "1101" means that the individual was captured on the first occasion, resighted on the second occasion, not detected on third occasion, and resighted again on the fourth occasion. We used CJS models to analyze our CMR data [40]. This model estimates two main parameters: recapture probability (p), which is the probability that a marked damselfly (alive) is resighted again during subsequent sampling occasions; and apparent survival probability (Phi), which is the probability that the marked damselfly (alive) survived (and has not emigrated) from occasion t to $t + 1$.

We designed candidate models for both p and Phi, starting with the simplest model (Phi(.) p (.)) that assumes that both parameters are constant. To determine the best model for p, we set Phi as constant and varied p with time, sex, daily average temperature (temp), and age class (age class at first capture). We gradually increased the complexity of the models by adding more covariates to the model. We used additive models such as Phi(.) p (time + sex + temp + age class). We also included two-way interactions between time and sex, as these were recorded in previous studies [12,20]. We performed model selection using the corrected Akaike criterion (AICc) [41]. We selected the most parsimonious model from the list of models that has ΔAICc < 2. After determining the best model for p, we fixed it in the CJS model and varied Phi with sex, time, age class, and age (age since the first capture). We used both the linear (age) and quadratic terms for age (age^2) to assess the potential complex effect of age on survival rate. We used increasingly complex additive models, going from the least complex (p(.)) to the most complex (time + sex + temp + age class + age + age^2). Because age could have different effects on males and females, we also tested for the two-way interaction between age and sex.

2.4. Lifespan

In autumn 2011, during a study on *Chalcolestes viridis* Vander Linden [42] in a nearby stream (1 km away) that flows into the Seybouse River (36°28′18″ N, 7°22′18″ E), we resighted the marked individuals from our CMR of *C. haemorrhoidalis*. This wetland is a small stream, 7 cm deep and 120 cm wide. The banks are dominated by bushes of Oleander trees (*Nerium oleander* L). At this time of the year, the odonate assemblage consisted mostly of *C. viridis*, *C. haemorrhoidalis*, *P. subdilatata*, and *Orthetrum chrysostigma* Burmeister. The watercourse was surveyed from 09:00 to 17:00.

2.5. Statistical Analyses

All our statistical analyses were carried out using R 4.3.1 [43]. We used the RMark 3.0.0 package [44] to analyze CMR data. To determine whether the seasonal distribution differed between males and females, we computed a two-sample Kolmogorov–Smirnov test. We used the MASS package [45] to compute a negative binomial model that assesses the seasonal pattern of abundance in males and females. The model included sex and the linear and quadratic term of Julian date to account for the typical hump-shaped seasonal distribution of adults [46]. We used the DHARMa package [47] to check the goodness of fit of our model. To assess the goodness of fit of our CJS model, we used the release.gof function from the RMark package, which computes three tests (TEST2, TEST3, and TEST2 + TEST3) that test whether the data meet the assumptions of the model [48]. Values are mean ± SD.

3. Results

A total of 214 individuals were captured and marked during the study period. The sex ratio of the captured individuals was 50% (107 males and 107 females). A total of 131 (61.2%) were recaptured at least once. Males were recaptured on average 2.85 ± 2.09 times with a maximum of 15. Similarly, females were recaptured on average 2.78 ± 2.75 times with a maximum of 10.

3.1. Seasonal Pattern of Abundance

The average number of adults recorded across sampling occasions did not differ between sexes (negative binomial: $z = 0.33$, $p = 0.74$). There was an average of 7.82 ± 6.76 females and 8.03 ± 4.79 males recorded across the study period. Although abundance fluctuated across sampling occasions, the overall seasonal pattern was hump-shaped (negative binomial: Julian date, z = 5.07, $p < 0.0001$; Julian date^2, z = −5.27, $p < 0.0001$), with an increase early in the season (late April–early May), then a decline later in the season (late May and early June) (z = −5.80, $p < 0.0001$) (Figure 2). Males and females had significantly different seasonal distributions of adult abundance (D = 0.135, $p = 0.004$). The average abundance in the first week of sampling (late April–early May) was 9.80 ± 5.81 males and 4.83 ± 3.19 females, and in the last week of sampling (early June) it was 2.00 ± 1.00 males and 3.00 ± 2.35 females.

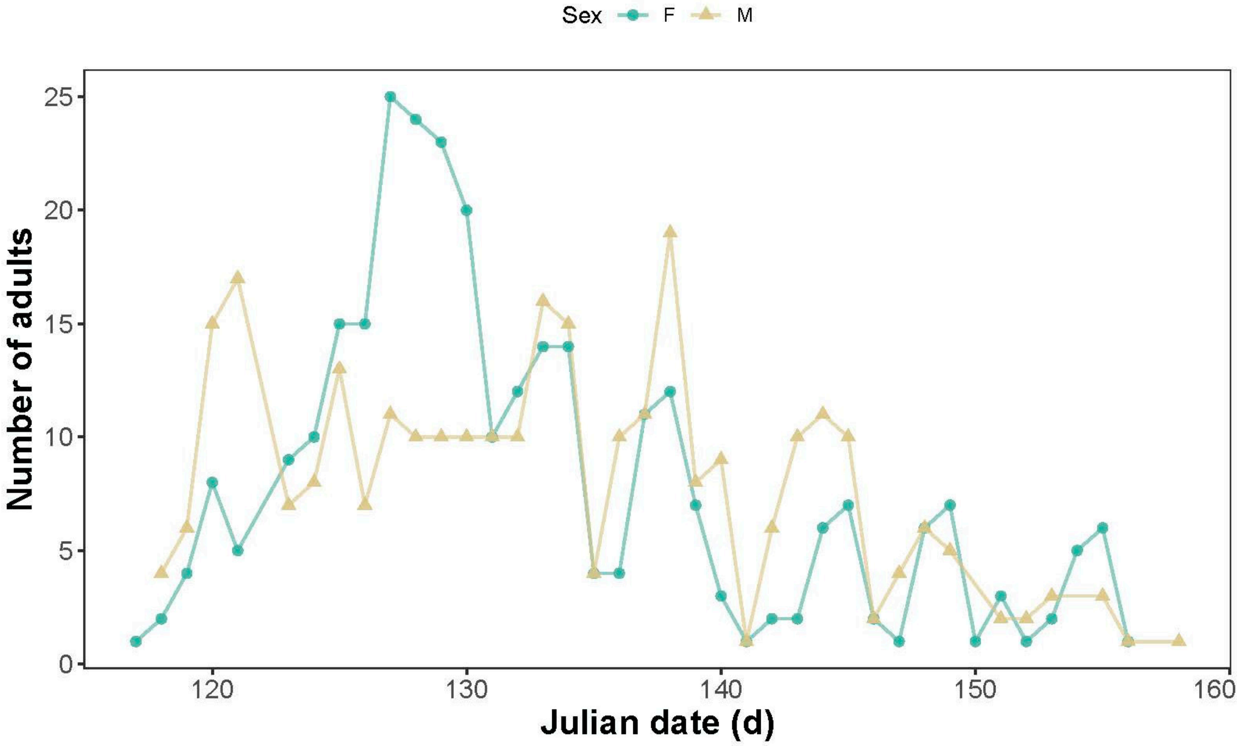

Figure 2. Temporal pattern of *Calopteryx haemorrhoidalis* adult males (M) and females (F).

3.2. Cormack–Jolly–Seber Model

The goodness-of-fit tests showed no significance (p = 0.99–1; Table S1); thus, the CJS model is suitable for our data. The average recapture rate based on a constant model was 0.28 [0.25–0.31]. We obtained two models with ΔAICc < 2, but the most parsimonious model included the additive effect of sex and time (Table 1). Recapture probability was on average slightly higher in males (0.30 [0.27–0.35]) than females (0.26 [0.22–0.30]). However, across the season, the recapture rate showed marked fluctuations (Figure 3).

The average survival rate based on a constant model was 0.87 [0.85–0.88]. The top model for survival included an additive effect of sex and age (Table 2), revealing that age influenced males and females similarly. Survival probability was on average slightly higher in females (0.89 [0.86–0.91]) than males (0.86 [0.82–0.88]). Our best model predicts that survival rate increases with age in both sexes (Figure 4). Survival models that included age class at capture were not ranked high, indicating that the age classes at capture had relatively similar probabilities of mortality.

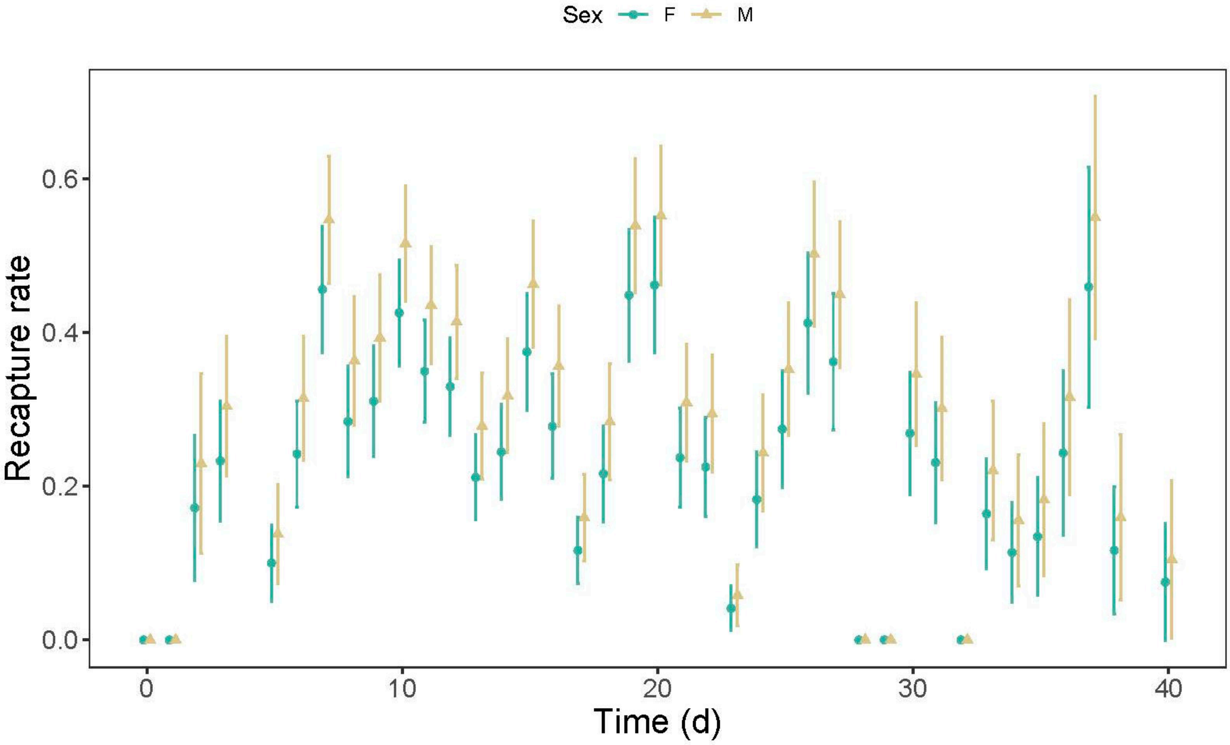

Figure 3. Recapture probability of *Calopteryx haemorrhoidalis* adult males (M) and females (F) across the season. Error bars are 95% confidence intervals.

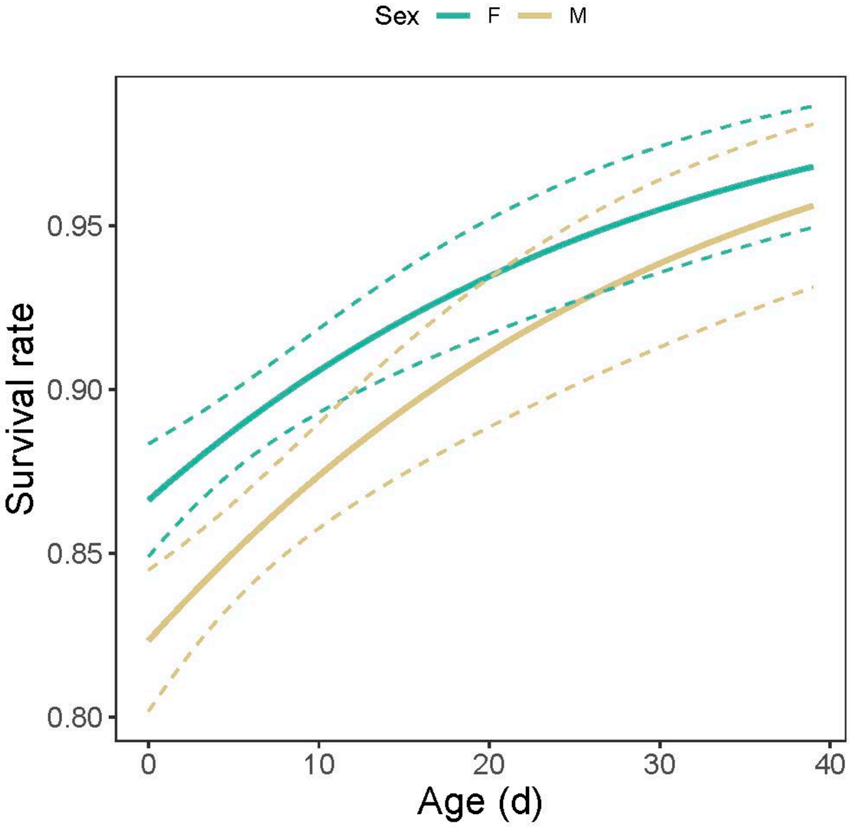

Figure 4. Survival probability of *Calopteryx haemorrhoidalis* adult males (M) and females (F) across age. Error bars are 95% confidence intervals.

Table 1. Model selection of the Cormack–Jolly–Seber model assessing the recapture probability. The survival probability was fixed to a constant model (Phi(~.)). Models are ranked based on their AICc (from lowest to highest values).

Model	npar	AICc	ΔAICc	Weight	Deviance
Phi(~.)p(~Sex + time)	**41**	**2012.9**	**0.000**	**0.563**	**1580.2**
Phi(~.)p(~Sex + time + Tempc)	42	2015.2	2.317	0.177	1580.2
Phi(~.)p(~Sex + time + Age_class)	43	2016.1	3.182	0.115	1578.8
Phi(~.)p(~time)	40	2016.2	3.263	0.110	1585.8
Phi(~.)p(~Sex + Tempc + time + Age_class)	44	2018.4	5.517	0.036	1578.8
Phi(~.)p(~Sex * time)	79	2046.3	33.427	0.000	1519.2
Phi(~.)p(~Sex * time + Tempc)	80	2049.0	36.102	0.000	1519.2
Phi(~.)p(~Sex * Time)	5	2071.0	58.060	0.000	1716.4
Phi(~.)p(~Sex + Time)	4	2073.2	60.315	0.000	1720.7
Phi(~.)p(~Time)	3	2074.3	61.362	0.000	1723.8
Phi(~.)p(~Sex)	3	2081.1	68.214	0.000	1730.6
Phi(~.)p(~.)	2	2082.2	69.267	0.000	1733.7
Phi(~.)p(~Sex + Tempc)	4	2083.0	70.058	0.000	1730.5
Phi(~.)p(~Tempc)	3	2084.1	71.157	0.000	1733.6
Phi(~.)p(~Sex + Age_class)	5	2085.1	72.197	0.000	1730.6
Phi(~.)p(~Age_class)	4	2086.0	73.079	0.000	1733.5
Phi(~.)p(~Sex + Age_class + Tempc)	6	2086.9	74.038	0.000	1730.4

Age_class: age class at capture (teneral, immature, and mature); Tempc: average daily temperature (centered). The dot (.) refers to a constant model. The best model is highlighted in bold.

Table 2. Model selection of the Cormack–Jolly–Seber model assessing the survival probability. The recapture probability was fixed to the best model (p(~time+sex)) (see Table 1). Models are ranked based on their AICc (from lowest to highest values).

Model	npar	AICc	ΔAICc	Weight	Deviance
Phi(~Sex * Age)p(~Sex + time)	44	2005.6	0.000	0.453	1565.9
Phi(~Sex + Age)p(~Sex + time)	**43**	**2007.6**	**1.989**	**0.168**	**1570.2**
Phi(~Sex * Age + Sex * Age^2)p(~Sex + time)	46	2007.9	2.343	0.140	1563.6
Phi(~Sex * Age_class + Sex * Age)p(~Sex + time)	48	2009.0	3.461	0.080	1559.9
Phi(~Sex + Age_class + Age)p(~Sex + time)	45	2009.4	3.817	0.067	1567.4
Phi(~Sex + Age + Age^2)p(~Sex + time)	44	2009.8	4.207	0.055	1570.1
Phi(~Sex)p(~Sex + time)	42	2011.7	6.113	0.021	1576.7
Phi(~Sex * Age_class + Age)p(~Sex + time)	47	2012.4	6.821	0.015	1565.7

Age_class: age class at capture (teneral, immature, and mature); Age: number of days since the first capture. The best parsimonious model is highlighted in bold.

3.3. Lifespan

While the expected lifespan based on our CJS model was 6.6 [5.0–7.8] days for males and 8.6 [6.6–10.6] days for females, we resighted three marked males and one marked female in September from our CMR survey in a nearby stream. The estimated lifespans (number of days since marking) were 130, 130, and 119 days. While one of the adults showed notable wearing of the wings, the other two did not.

4. Discussion

Our study investigated the effect of sex and age on the survival of adults of *C. haemorrhoidalis*, a widespread species in the lotic habitats of North Africa. The species had an equal sex ratio and a relatively asynchronous flight period. Recapture rate depended on sex and time, with males being more likely to be resighted than females. Survival probability was slightly higher in females, and showed a positive age dependence in both sexes. Interestingly, some of our marked males were recorded in the autumn, suggesting that the lifespan of the species could exceed four months.

As expected from previous studies documenting the long flight season of the species in North Africa [27,28,49], our records of the abundance of *C. haemorrhoidalis* throughout the season suggest that the species has an asynchronous flight period. The flight season started in late April, which is similar to the phenology recorded in other studies in North Africa [34,49] but earlier than that reported in Spain [26]. The species emerged at the same time as its sympatric congeneric *C. exul* [32] and *Gomphus lucasii* [50].

Our estimate of the proportion of recaptured individuals (61.2%) was higher than that estimated in Northwest Spain (48%) [29], suggesting that our marked individuals were less likely to leave the sampling area or were more readily detectable (e.g., because of vegetation structure, access to the watercourse). Unlike other studies on damselflies showing a male-biased sex ratio at the adult stage [20,51], our study showed no clear sex bias. The congeneric *C. exul*, which shows similar reproductive behavior, also exhibits no deviation in the sex ratio from 1:1 [52]. This could be explained by an equal sex ratio at emergence, a relatively similar survival rate during maturation (as we found here with the non-significance of age class on survival rate), and similar habitat use at the adult stage [32]. In territorial species like *Calopteryx* spp., males guard territories (patches of vegetation) where females aggregate to lay eggs, whereas non-territorial males and non-reproductive females perch on the bank vegetation farther from territories [53]. Thus, due to the lack of spatial segregation between sexes which often leads to a biased sex ratio [14], a transect across the watercourse results in an equal sex ratio. It is important to note that the decline in the abundance of the species in early June was at least partly due to flooding caused by dam water releases that affected the structure of the river in early June. In a study on *C. exul* on the same site and in the same year, flooding reduced the recapture rate of adults [54], suggesting emigration to other areas.

The recapture probability varied with sex and time. Various studies using capture–mark–recapture on different species found that recapture rate depends on sex and time [21,55,56]. Males often have a higher probability of recapture than females because they are more conspicuous morphologically and behaviorally. In *C. haemorrhoidalis*, the difference in recapture rate was relatively small, which is most likely due to the lack of spatial segregation (e.g., females remain near the water even for foraging). Recapture rate changes from one day to another, most likely due to weather conditions [12]. Adults are more likely to be active when the weather is optimal (warm and sunny) [46].

The survival probability depended on sex and age, two covariates that studies have shown to influence survival in odonates [20]. In this study, the survival probability of *C. haemorrhoidalis* was 0.89 in females and 0.86 in males, which is relatively similar to that recorded in a population in Italy (0.84 in males and 0.86 in females) [36]. However, this was slightly lower than the average survival rate estimated for odonates (0.895 for males and 0.898 for females) [20]. A relatively similar survival rate between males and females was observed in Calopterygidae [20]. Our observed higher survival rates in females could be due to the higher activity of males, who have a more conspicuous phenotype and exhibit territorial behavior (males interact with both males and females whereas females interact mostly with males), which could make them more likely to be detected by predators [57].

We did not find an effect of age class at capture on survival rate (teneral, immature, and mature individuals had similar survival rates), which is different than other studies on other damselflies [21]. This could be due to the similarity in habitat use across age classes (all age classes remain near the watercourse), a behavior that was also recorded in a Spanish population [29]. However, the similarity in survival rate among age classes at capture should remove potential biases in the chronological pattern of survival rates across continuous age since capture. Our best model for survival probability, however, included an additive effect of age (days since marking) and sex. This model predicted that the survival rate of males and females increased gradually with age in a similar manner, which confirms our prediction. This finding is different than those found for the damselfly *C. puella* [10], the honeybee *Apis mellifera* L. [8], the cricket *Teleogryllus commodus* Walker [13], and the neriid fly *Telostylinus angusticollis* Cresson [7], which showed a decline in survival rate with age. Our finding was similar to that recorded on the same species in one of the years of sampling [12]. One possible explanation for the observed increase in survival rate is an improvement in the environmental conditions with the season (abiotic and/or biotic conditions were better later in life). However, the absence of a decline in survival rate later in life is likely due to the long lifespan of *C. haemorrhoidalis*, which was not fully surveyed by our sampling.

Estimating the lifespan of odonates accurately in natural conditions is difficult because species can disperse due to environmental changes. Our CJS model yielded an expected lifespan of 6.6 [5.0–7.8] days for males and 8.6 [6.6–10.6] days for females, which is slightly lower than the expected lifespans of a Spanish population (10.6 days in males and 12.0 days in females), *C. maculata* Beauvois (11 days) [58], and *Mnais pruinosa* Selys (10.7 days) [59]. Nevertheless, our estimate of survival might be an underestimate because the CJS model estimates the apparent survival, which does not distinguish between emigration and mortality [39]. Two months after the end of our CMR survey, while visiting a nearby stream, we recorded three of our marked males, revealing that they were able to survive for more than four months (up to 130 days). These estimates are more than three times longer than those reported for the species ([29], max = 43 days in Spain; [30], max = 39 days in France). This is most likely the longest lifespan for the species and the family [20]. We are not sure whether this extended lifespan is specific to the North African region. Currently, it is difficult to have a clear account because studies on adult odonates that span multiple months are rare to non-existent [20]. One hypothesis to explain this long lifespan is that the local climate in North Africa is more favorable for the species to survive and reproduce compared to Europe. Another hypothesis is that a longer lifespan provides an evolutionary advantage in a climate where drought is common because adults can secure reproduction whenever the hydrological conditions are optimal [60]. The adaptive significance of this long lifespan needs further investigation.

This study is an important contribution to our understanding of the life history of *C. haemorrhoidalis* in its southern edge where the species has not attracted research attention. Future studies should investigate the frequency of prolonged lifespans in terms of space (geographic range) and time (season). Such a study could be easily carried out given the large abundance of the species in lotic habitats across its range and the relatively long flight season [25]. Given the widespread distribution of the species across elevations, it is worthwhile to assess whether the life history in general, and adult lifespan in particular, shows an elevational gradient.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/ecologies5030030/s1: Supplementary Material: Table S1: Goodness-of-fit tests for the Cormack–Jolly–Seber model of the analysis of capture–mark–recapture data of *Calopteryx haemorrhoidalis* in the Seybouse River.

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Conflicts of Interest: The authors declare no conflicts of interest.

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