

Demographics and behaviour of *Heteragrion cooki*, a forest damselfly endemic to Ecuador (Odonata)

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Damselflies adapted to forest habitats are expected to be negatively affected by the disturbance of riparian forests, due to the change in insolation when trees are cleared. In this paper, we compare survivorship and behaviour of two populations of *Heteragrion cooki* by means of mark-recapture methods and focal observations of adults. We found similar densities of males (but not of females) in both streams, and similar recapture rates, higher for males (50%) than for females (20%). Body size was also significantly different between populations, with smaller individuals in the shadiest stream. The analysis of daily survival rates indicated that in the shaded stream, males survived better than females, whereas in the sunnier stream survival was similar between sexes, but varied over time. Furthermore, in the sunny stream, body size was negatively correlated with survival. Males arrived earlier than females to the stream, with a maximum activity between 13 and 16 hours. They defended small patches of the stream, exhibiting high site fidelity and aggressive behaviour against conspecific males. Copulation, which was very rarely seen in the stream, lasted about six minutes. Pairs in tandem remained for an average of 45 minutes laying eggs on roots and lianas. We found that *H. cooki* was not drastically affected by the loss of riparian vegetation, maintaining similar densities of males in both streams, probably because small remnants of native forests were still found near to the stream.

Keywords: shade; survival; population density; body size; copulation; dragonfly

Introduction

Dragonflies are insects whose activity is highly dependent on insolation. They have a complex life cycle, with an obligate aquatic larval period and elaborate adult behaviour (for a recent review, see Suhling et al., 2015). Even if sunny habitats harbour high odonate species richness, some groups have specialised in living in forests, where both insolation and heat are limited (Cordero-Rivera, 2006). Overall, an estimated 1000–1500 species await discovery and description, most of them from tropical areas (Kalkman et al., 2008). In the Neotropical region, odonates are highly diverse, with more than 1600 species in the Amazon forests. Since 1970, a mean of 38 species have been described per year in this region, but the number of undescribed species is accumulating at a higher rate (Paulson, 2004). Entire families are restricted to tropical forest streams and the information available on these families is very limited: e.g. Amphipterygidae, Polythoridae, Dicteriadidae and Perilestidae in the Neotropics and Pseudolestidae, Devadattidae and Euphaeidae in Asia.

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The genus *Heteragrion*, which contains at least 46 species (Machado, 2006), is a typical forest-dwelling odonate (Garrison, von Ellenrieder, & Louton, 2010). Recently, molecular phylogenetic studies suggested that *Heteragrion* species compose a unique family, recognised as Heteragri-onidae (Dijkstra, Kalkman, Dow, Stokvis, & van Tol, 2014). Nevertheless, further ecological, ethological and morphological studies are needed to clarify the taxonomic position of the genus, as the integrative taxonomy proposes (DeSalle, Egan & Siddall, 2005). Previous ecological studies suggest that some *Heteragrion* species are sensitive to habitat disturbance (Monteiro-Júnior, Juen, & Hamada, 2015). This taxon is one of the most common genera in many tropical forests in South America (pers. obs.), but surprisingly only three species have been studied by ethologists and behavioural ecologists (González Soriano & Verdugo Garza, 1982; Loiola & De Marco, 2011; Shelly, 1982).

In a study of foraging behaviour and thermoregulation of two forest odonates, Shelly (1982) proposed the hypothesis that some species are adapted to shady conditions, whereas other species are specialists of sunny spots in the forest. This dichotomy would also reflect profound differences in physiology, with shady species being energy savers and sunny species high-rate foragers. This hypothesis can be extended to intraspecific variability, with shaded habitats favouring slower life modes and open habitats more active behaviours. These behavioural differences are expected to result in contrasting patterns of survivorship, due to their effects on male–male aggression and territoriality.

In this paper, we study two populations of *Heteragrion cooki* from Ecuador (Daigle & Tennessen, 2000), to describe general and reproductive behaviour and to compare survivorship between sexes and populations. We predicted that local habitat features, specifically insolation, would affect adult survivorship, with disturbed habitats (more open) being more unfavourable for this presumably shade-seeking species. Our aim is to contribute ethological information for future comparative studies, which can be used to test ideas about the behavioural diversity of Odonata, a level of biological diversity that remains poorly studied (Cordero-Rivera, 2017).

Methods

Study area

We performed fieldwork in two second-order streams around the Buenaventura Biological Reserve (Jocotoco Foundation; Piñas, El Oro, Ecuador), with similar physical properties (width: 1.5–2.1 m; depth: 10–25 cm; flow speed: 0.25–0.5 m s⁻¹) and running over a substrate mainly composed by sand and rocks. One of the streams (hereafter, shaded population) was found in a pastureland, adjacent to a teak (*Tectona grandis*) plantation, with small remnants of the riparian forest, and was on the edge of the reserve (– 3.653045 S, 79.800495 W; 307 m). This stream is a tributary of the principal river of the reserve, which runs parallel to the 585 road. The sampled section of this stream was about 70 m, estimated from GoogleEarth images. The sunlight did not directly illuminate most of this section of the stream, which was in a shady environment. This stream is therefore predicted to be of high quality for *H. cooki*. The second stream (sunny population) was situated in Moromoro, a little village at the south-western limits of the reserve (– 3.679222 S, 79.737258 W; 880 m). The stream ends in Moromoro River after crossing sugarcane (*Saccharum officinarum*), pineapples and other agricultural crops. Therefore, large areas were illuminated directly by the sun in this stream, although some remnants of forests were found in the vicinity. We sampled about 105 m of this stream. This sunny stream should be of lower quality for a shade-seeking species. The distance between the two streams was 7.6 km. They belong to different river systems, and therefore are considered here as different populations.

The climate of the region is tropical with an average annual temperature of 22.4°C and on average annual precipitation of 1477 mm (<https://climate-data.org>). A dry season occurs from June to November. We found that *H. cooki* shared the streams with *Argia oculata* and *Hetaerina fuscoguttata*, the same species pool documented in Pichincha province, western Ecuador by Daigle and Tennesen (2000).

Field methods

We carried out observations in the dry season, over 15 days between 26 June and 11 July 2016 with sunny or partially sunny weather, for a total of 89 hours. We collected individuals with an entomological net, marked them on the right hind wing with a code number, measured (total body length, including anal appendages, to the nearest 0.1 mm with a calliper) and released them. At the moment of marking, and in each subsequent recapture, we recorded reproductive activity (tandem, copulation or oviposition) and male–male interactions. We typically recorded re-sightings by eye or with the help of a close-focusing monocular rather than by re-capturing individuals.

We marked focal individuals after observations, unless they were already marked. Marking of tandem pairs interrupted their association, and this fact may have affected the frequency of reproductive events observed. During agonistic interactions, we considered a male as resident when another male (the intruder) approached his perch site. We considered the winner to be the male that returned to the perch after chasing the other off.

Statistical analyses

To estimate survival and recapture probabilities we analysed the recapture histories of marked animals using the software MARK 8.1 (White & Burnham, 1999). We included sex, time and their interaction as factors in the models. First, we tested the adjustment of the full time-dependent Cormack–Jolly–Seber model by groups (model $\text{Phi}(g \times t) \text{p}(g \times t)$, where g is sex and t is time) using program RELEASE. In both rivers, this model showed good adjustment (shaded population, goodness of fit results (TEST 2 + TEST 3) by group: $\chi^2_{15} = 16.24$, $p = 0.367$; sunny population: $\chi^2_{24} = 23.644$, $p = 0.482$). Then, we estimated the variance inflation parameter (c-hat) by dividing the c-hat obtained from model $\text{Phi}(g \times t) \text{p}(g \times t)$ by the mean c-hat of the bootstrap simulations in MARK, and we used the values obtained (shaded population: 1.37707; sunny population: 1.53314) to adjust parameter estimates and standard errors. In a first step, we ran models without individual covariates, to select the most supported model, as the one that minimises quasi Akaike's information criterion (QAIC). In a second step, we included body length as an individual covariate. We analysed shaded and sunny populations separately because no movements were detected between them. To estimate population size, we used the methods of Jolly (1965) and Manly and Parr (1968) by means of the program POPAN 5 (Arnason, Schwarz, & Boyer, 1998).

We calculated statistical tests (ANOVA, correlation) using XLSTAT software (www.xlstat.com). We present mean values with their standard error and sample size.

Results

Demography

The abundance of individuals and overall recapture proportions (about 50% of males and 20% of females) were similar between populations (Table 1). Individuals were larger (approximately

Table 1. The number of animals marked and recaptured in each population and their body size in mm. There were no differences in overall recapture rates between sexes, but individuals from the shaded population were smaller (see the text for details).

Population and sex	Shaded population		Sunny population	
	♂	♀	♂	♀
Marked	145	20	184	49
Recaptured	74 (51%)	4 (20%)	92 (50%)	11 (22%)
Mean body length	34.7 ± 0.10	30.2 ± 0.44	38.2 ± 0.10	33.2 ± 0.16
Range	30.3–37.9	26.9–34.2	34.8–41.2	30.9–35.8

Contingence chi-square comparing the proportion of recaptured individuals between populations by sex (males: $\chi^2_1 = 0.04, p = 0.852$; females: $\chi^2_1 = 0.05, p = 0.823$).

5 mm) in the sunny population (Table 1; ANOVA, population effect, $F_{1,394} = 639.55, p < 0.001$) and males larger than females (sex effect, $F_{1,394} = 626.59, p < 0.001$) in both populations (the interaction population \times sex is not significant; $F_{1,394} = 1.55, p = 0.214$).

The estimates of population size indicated that the number of adults was slightly higher in the sunny population, a mean of 129 males compared to 85 males in the shaded population, but taking into account the length of transects, density was virtually identical (1.2 males m^{-1} in both streams). The average number of females estimated was 37 and three individuals in the sunny and shaded populations, respectively (Figure 1).

The analysis of daily survival and recapture probabilities using MARK revealed clear differences between populations. The most supported model in the shaded population was {Phi(g) p(.)}, implying a sex effect on survival and constant recapture probability (Table 2). Introducing body length as an individual covariate did not improve the statistical support for the model (Table S1). Nevertheless, a model with the effect of body size as covariate is the second most supported model, at 0.65 QAIC units (Table S1). Examining the relationship between body size and survival from this model, the tendency is for larger individuals to have reduced survival, particularly in females. Therefore, in the shaded stream survival was higher in males than females (0.927 versus 0.710), and recapture rate relatively high (0.493) and not sex-biased (Table 2). In the sunny population, the best model indicates time-dependence in survival and a sex effect on recapture rate, model {Phi(t) p(g)} (Table 2). In this case, introducing a linear effect of body length on survival probability increased model fit by 0.80 QAIC units (Table S1). This was due to a negative effect of body length on survival, particularly on day 1 (29 June, Figure 2). Other models were situated at more than 6 QAIC units and have therefore low support (Table S1). The estimates derived from model {Phi(g) p(.)} for this population, although this model is not among the best candidates, suggest slightly higher survival for males than females (0.918 versus 0.883; Table 2).

Behaviour

On both streams, males arrived earlier in the day than females, around 08:00–09:00 (Figure 3). Solitary females were scarcer than males and rarely found at the streams before noon (Figure 3). The maximum activity of males in the shaded stream occurred in the afternoon, 13:00–16:00 hours. In the sunny stream, male abundance was maximum at 11:00–15:00. We frequently observed reproductive behaviour in the sunny stream, with a highest at 14:00–15:00 (Figure 4). Because we rarely observed reproduction in the shaded population, a comparison between populations could not be done. Therefore, the following results were derived combining the observations realised at both populations.

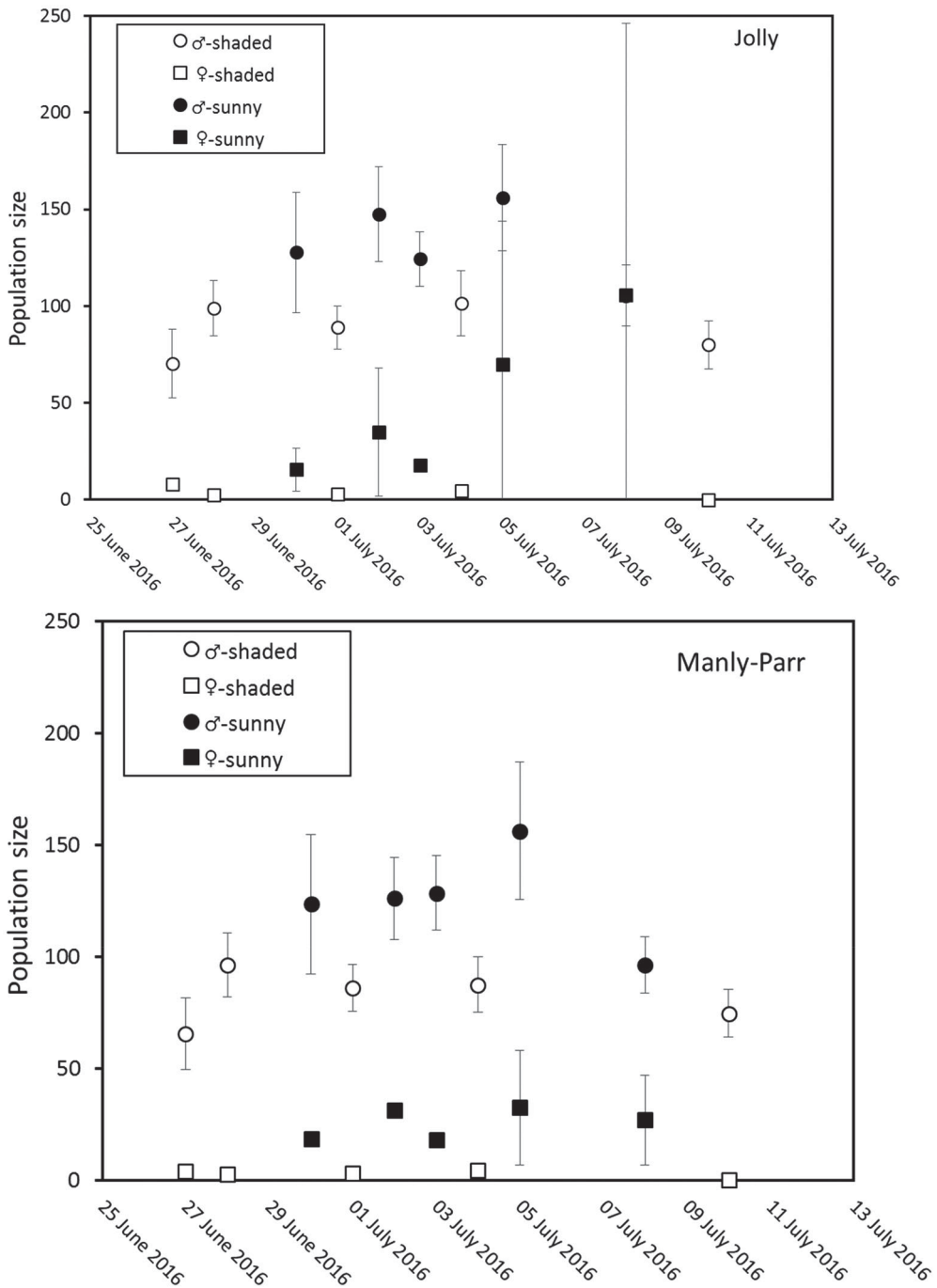


Figure 1. Estimates of population size (\pm SE) for the two populations (shaded and sunny), using the methods of Jolly and Manly-Parr. The number of males was slightly higher in the sunny population, and there are no clear seasonal trends. Females were scarce in both populations, particularly in the shaded stream.

Males defended small areas around their perches on both streams, exhibiting aggressive behaviour against conspecific males (and sometimes against *Argia* or *Hetaerina* males). These areas did not include oviposition substrates; they were not resource defenders. Male-male

Table 2. Estimates of survival (Φ) and recapture (p) probabilities from the most supported model for each population using MARK software. Results of model $\{\Phi(g) p(\cdot)\}$ for the sunny population were included for comparison, but this model was not among the most supported.

Parameter	Estimate	95% confidence interval		
		SE	Lower	Upper
Shaded population. Real function parameters of $\{\Phi(g) p(\cdot)\}$, corrected for $c\text{-hat} = 1.37707$				
Phi males	0.9271	0.0140	0.8945	0.9503
Phi females	0.7102	0.1040	0.4765	0.8684
p	0.4931	0.0458	0.4044	0.5822
Sunny population. Real function parameters of $\{\Phi(t) p(g)\}$, corrected for $c\text{-hat} = 1.53314$				
Phi 29 June	0.4553	0.0984	0.2775	0.6453
Phi 30 June	0.9440	0.0528	0.7043	0.9917
Phi 2 July	0.9472	0.1140	0.1706	0.9994
Phi 3 July	0.9916	0.0692	0.0000	1
Phi 5 July	0.9266	0.0537	0.7288	0.9834
Phi 8 July	0.9235	0.1865	0.0640	0.9995
p males	0.3605	0.0405	0.2855	0.4429
p females	0.1584	0.0538	0.0786	0.2934
Sunny population. Real function parameters of $\{\Phi(g) p(\cdot)\}$, corrected for $c\text{-hat} = 1.53314$				
Phi males	0.9186	0.0198	0.8703	0.9500
Phi females	0.8836	0.0554	0.7252	0.9562
p	0.3183	0.0352	0.2536	0.3909

agonistic interactions consisted in a face-to-face display (on average 29 ± 4 (10) s), hovering over the river, and slowly moving up and down. We observed 29 interactions involving 32 marked males. The resident male won 23 (79%) of these interactions. The average difference in body size between winner and loser was 0.25 ± 0.33 (24) mm, suggesting that body size was not relevant in the outcome of these interactions, but this effect could not be properly tested with the available data.

Individuals exhibited high site-fidelity. Over the period of study, most male recaptures and all female recaptures were in the same spot (within about 1 m) as the previous observation. In the shaded population, 64 out of 74 recaptured males and all four recaptured females were always found in the same site. In the sunny population, 90 out of 92 males and all 11 females remained in the same site. Given that we alternated observations between sites, it was not possible to determine exactly how long the individuals remained in the same spot, but an approximation can be obtained by calculating the time between the first and the last observation for males that remained in the same spot. These values were 6.8 ± 0.6 (68) days for males and 3.3 ± 1.3 (4) for females in the shaded population, and 5.0 ± 0.3 (92) days for males and 6.1 ± 0.8 (11) for females in the sunny population.

Males grasped females in tandem without precopulatory courtship ($N = 10$ tandem pairs observed since the start of their interaction). After tandem formation, all males performed sperm translocation and copulation followed shortly thereafter (Table 3). Copulatory activity showed two stages (see Miller & Miller, 1981). Stage I was always longer than stage II, occupying 92% of copulation (Table 3). After copulation, the pair perched on floating roots and lianas, and started oviposition, that may last for up to 1.4 h. In half of the ovipositing pairs observed ($N = 12$; Table 3) females continued ovipositing for up to 10 min after tandem separation. There was no assortative mating by size (correlation between male and female body length, $r = 0.32$, $N = 19$ pairs, $p = 0.179$).

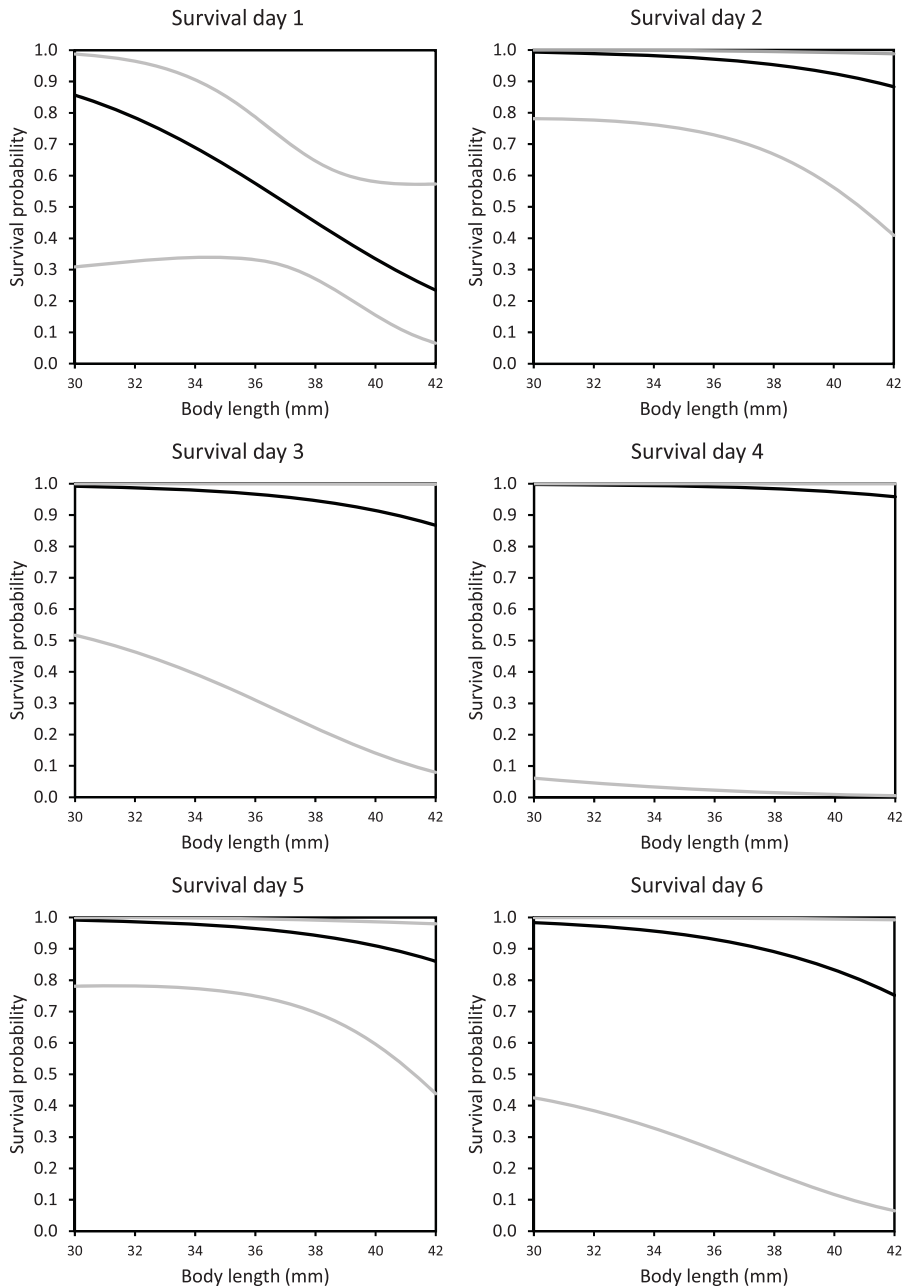


Figure 2. The estimated effect of body length on daily survival for adults of *H. cooki* of the sunny population. Grey lines indicate lower and upper confidence intervals. Survival was time dependent and clearly lower on the first day (29 June).

Discussion

Mark-recapture techniques offer the best spatial resolution for estimating survival and recapture rates of animal populations, and have been widely used in odonates (reviewed by Cordero-Rivera & Stoks, 2008). Our results indicate that both populations were relatively small, and had similar

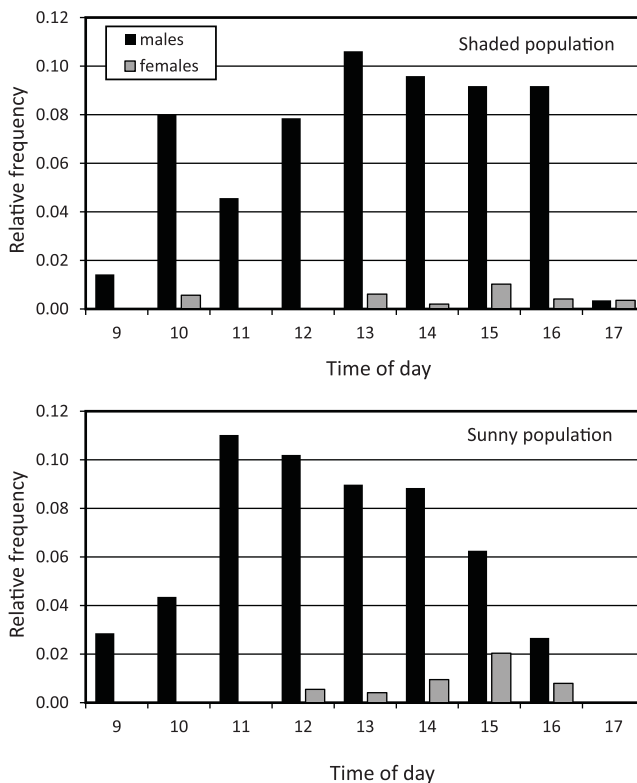


Figure 3. Abundance of males and females of *H. cooki* at the stream over the day. Frequency was calculated as the total number of individuals observed in each hour per metre of stream, divided by the number of days of observation at each hour interval. Females were almost never observed before noon. Due to logistic constraints, no observations were completed in the last interval (after 17 h) in the sunny population.

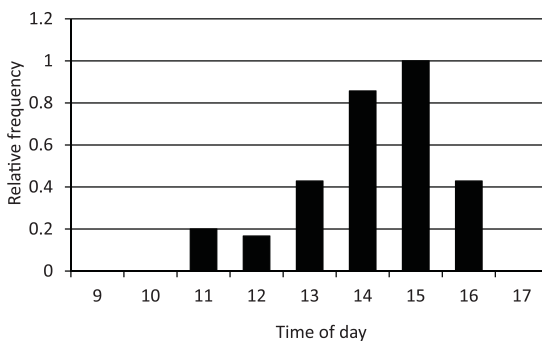


Figure 4. The relationship between time of day and reproductive activity (number of tandem pairs) in the sunny population. Values indicate the number of tandems observed at each hour interval divided by the number of days of observation at each hour. Not enough data were obtained for the shaded population.

global recapture rates, but differed in daily rates. The studied streams harboured fairly dense populations (1–2 males m^{-1}) compared to other populations of tropical stream odonates, which typically have very low densities (e.g. *Polythore* sp.; Sanmartín-Villar & Cordero-Rivera, 2016).

In the shaded population, sex affected survival but not daily recapture rates. Shaded population females had lower survivorship than males but did not differ from males in recapture rates (because although few individuals were recaptured, each of them was found several times). In

Table 3. Reproductive behaviour of *H. cooki*. Mean duration (\pm SE) of sperm translocation (ST) in seconds, copulation and oviposition (in tandem and female alone) in minutes with their standard error.

	ST	Copulation	Stage I	Stage II	Total oviposition	in tandem	female alone
Mean	11.20 \pm 1.00	5.86 \pm 1.08	5.39 \pm 1.10	0.48 \pm 0.05	45.83 \pm 5.23	43.87 \pm 5	3.92 \pm 1.61
N	10	9	9	9	12	12	6
Minimum	6	0.97	0.50	0.23	16.27	15.62	0.50
Maximum	15	11.05	10.63	0.65	84.23	77.30	10.12

N = sample size.

contrast, in the sunny population, survival was similar for both sexes and changed over time, with a negative effect of body size (Figure 2) and recapture rates were clearly higher in males. The negative effect of body size on survival was also found in the shaded population, but the model with body size as individual covariate was not the most supported (Table S1). Adults of the sunny population were larger. A similar result, with larger individuals and lower survival in more anthropic habitats compared to natural areas, was recently found in an amphibian species, *Bufo calamita* (Zamora-Camacho & Comas, 2016). Many factors can affect body size of adult odonates, including the amount of food available for larval growth, but unfortunately we have no information on larval food availability. Taken together, these results suggest that the sunny stream was not as unfavourable for *H. cooki* as we predicted (even if survival was slightly lower). Therefore, our working hypothesis of *Heteragrion* species as “shade-seeking” animals might be incorrect for *H. cooki*.

In territorial animals, including odonates, body size may confer advantages in reproduction, if it allows to maintain the territory for more time (e. g. Serrano-Meneses, Córdoba-Aguilar, Méndez, Layen, & Székely, 2007). In general, larger body size does not confer higher reproductive success in odonates, particularly in non-territorial species Thompson & Fincke, 2002). On the other hand, body size has been found to negatively correlate with wing beat frequency in damselflies, favouring small size at lower temperatures (Okuyama, Samejima, & Tsubaki, 2015). Species of the genus *Heteragrion* cannot be considered fully territorial if we define a territory as a defended area with resources needed for reproduction (see Baker, 1983 for a discussion of the concept), and therefore, no advantages associated with a large size were expected. In fact, agonistic interactions were won by the resident male, suggesting that residence is more relevant than size. The lower survival of larger animals in both populations needs confirmation with larger datasets. The complex three-dimensional structure of the vegetation where *H. cooki* is usually found may present challenges to agonistic encounters, increasing energy expenditure, or may difficult escape behaviours, increasing predation. However, Daigle and Tennesen (2000) highlight that *H. cooki* was difficult to collect due to the complex structure of vegetation in the sites it frequents, and this difficulty might also apply to natural predators. On the other hand, even if *H. cooki* might not qualify as a fully territorial species (in the above sense) it is certainly an aggressive species. Aggressive individuals are often involved in more fights and thus might have higher energy expenditure (Marden & Cobb, 2004). If larger males were more aggressive, this could explain their lower survivorship. Alternatively, the ecophysiological hypothesis of Shelly (1982) suggests that energy expenditure is directly proportional to body temperature, and therefore, in sunnier environments, these damselflies might be more food limited, selectively favouring for small size (see also Oliveira-Junior et al., 2015), but our data failed to support this alternative.

As Figures 1 and 3 show, the estimates of population size using mark-recapture methods and the daily counts of individuals in the two populations are concordant. The low number of females near the water is in agreement with sexual differences in behaviour and use of the space (e.g. Andrés & Cordero-Rivera, 2001), but the differences in female density between the two

streams are surprising. These differences affected reproductive activity, with almost no copulations observed in the shaded population. Adult activity at the stream was similar to the pattern of *Heteragrion consors* in Central Brazil (Loiola & De Marco, 2011) and *Heteragrion alienum* in Mexico (González Soriano & Verdugo Garza, 1982). The breeding activity showed its maximum peak from 13:00 to 16:00, as in *H. alienum* (González Soriano & Verdugo Garza, 1982). The fact that the individuals in the sunny environment started their activity at earlier hours compared to the shaded environment suggests that *H. cooki* is affected by insolation, allowing individuals to warm up earlier in the day. There is ample evidence in the literature for the effect of insolation (rather than temperature) on thermoregulation (May, 1976) and daily activity of odonates (De Marco & Resende, 2002), particularly in differences in foraging activity between species (Shelly, 1982). This effect may explain the dominance of Anisoptera in larger rivers compared to small streams (De Marco, Batista, & Cabette, 2015). In some Anisoptera, feeding is concentrated at sunrise, probably because many prey show swarms (for instance *Rhionaescha galapagoensis*; Cordero-Rivera, Encalada, Sánchez-Guillén, Santolamazza-Carbone, & von Ellenrieder, 2016), but in *H. cooki* feeding was observed (even if not quantified) throughout the day, as reported for other *Heteragrion* (González Soriano & Verdugo Garza, 1982; Loiola & De Marco, 2011; Shelly, 1982). As a shade-adapted species, *Heteragrion erythrogastrum* maintains similar activity patterns in sunny and overcast days (Shelly, 1982), and is therefore more independent of short-term climatic conditions than *H. cooki*.

Although we do not consider *H. cooki* a strictly territorial species (because it does not defend a territory with resources needed for reproduction), our results indicate that males and females show high site fidelity across different days (almost a week). Male fidelity to particular sections of the stream has been commonly found in other species of riverine damselflies (e.g. Sanmartín-Villar & Cordero-Rivera, 2016). Similar behaviour in females is less common, but it could indicate that females return to areas where suitable oviposition sites were found, or where attractive males were encountered.

We found that male body size seems of little relevance to establish who maintains the perch, because almost always the resident won the interaction, irrespective of size differences (as was reported for *Pyrrhosoma nymphula*; Gribbin & Thompson, 1991; but see Fincke 1992). In *Heteragrion* sp. site fidelity and defence does not ensure copulation, but a privileged position to be able to grab a female in tandem in flight, as soon as she is detected (González Soriano & Verdugo Garza, 1982), with no courtship displays (Loiola & De Marco, 2011). This probably explains why males arrive earlier to the stream than females. Once the male grasps the female, a copulation of about 6 min is completed, which is divided into two stages (Miller & Miller, 1981). Copulation in *H. cooki* was similar to *H. alienum* (8.3 min; González Soriano & Verdugo Garza, 1982) but shorter than *H. consors* (19 min; Loiola & De Marco, 2011). In the majority of odonates of the order Zygoptera, including other Megapodagrionidae *sensu lato* (Torres-Cambas & Fonseca-Rodríguez, 2009), the first stage corresponds to the removal of sperm from the female internal tract, and the second stage to insemination (Cordero-Rivera & Córdoba-Aguilar, 2010). Abdominal copulatory movements in *H. cooki* suggest that sperm removal was also taking place during stage I and insemination during stage II. On the other hand, our results indicate that there was no assortative mating according to size. This is what is expected in non-territorial species (Serrano-Meneses et al., 2007). After copulation, females oviposited in tandem with the help of the male for most of the time or even in its totality, as in the other species of the genus (González Soriano & Verdugo Garza, 1982; Loiola & De Marco, 2011). However, some females remained alone ovipositing, after the male ended the tandem, but for very short periods.

In our observations, males translocated sperm from the primary to the secondary genitalia before every mating, and after having grasped the female in tandem. This behaviour was described in similar terms for *H. alienum* (González Soriano & Verdugo Garza, 1982), but,

surprisingly, males of *H. consors* were described performing sperm translocation alone, with no females in the vicinity, and therefore never in tandem (Loiola & De Marco, 2011). This divergence in behaviour between similar species –if confirmed – highlights the relevance of ethological patterns in biodiversity studies (Cordero-Rivera, 2017). The adaptive significance of these differences open new avenues in comparative ethological research.

In conclusion, our study provides evidence for between-population differences in survivorship and body size in a forest damselfly, apparently related to human alteration of the riparian forests. However, both streams supported populations of similar density, a result at variance with our initial working hypothesis that considered *H. cooki* a shade-seeking species. This suggests that remnants of forests near the stream can be enough to maintain healthy populations of this species. A missing element in this discussion is whether larval density varied between sites, and therefore future studies should include the aquatic stages of the life cycle. Finally, survival was estimated by surveying the reproductive site, but females spend most of their time in the forest, where they are very difficult to find. A study including recaptures in the forest is needed for a better understanding of sexual differences in survivorship.

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Supplemental data

Supplemental data for this article can be accessed at <https://doi.org/10.1080/13887890.2017.1336495>.

References

- Andrés, J. A., & Cordero-Rivera, A. (2001). Survival rates in a natural population of the damselfly *Ceriagrion tenellum*: Effects of sex and female phenotype. *Ecological Entomology*, 26(4), 341–346. <http://doi:10.1046/j.1365-2311.2001.00338.x>
- Arnason, N. A., Schwarz, C. J., & Boyer, G. (1998). *POPAN-5. A data maintenance and analysis system for mark-recapture data*. Manitoba, Canada: Department of Computer Science, The University of Manitoba.
- Baker, R. R. (1983). Insect territoriality. *Annual Review of Entomology*, 28, 65–89.
- Cordero-Rivera, A. (2006). *Forests and dragonflies*. Sofia-Moscow: Pensoft.
- Cordero-Rivera, A. (2017). Behavioural diversity (ethodiversity): a neglected level in the study of biodiversity. *Frontiers in Ecology and Evolution*, 5:1–7. <http://doi:10.3389/fevo.2017.00007>
- Cordero-Rivera, A., & Córdoba-Aguilar, A. (2010). Selective forces propelling genitalic evolution in Odonata. In J. Leonard & A. Córdoba-Aguilar (Eds.), *The evolution of primary sexual characters in animals* (pp. 332–352). Oxford: Oxford University Press.
- Cordero-Rivera, A., Encalada, A. C., Sánchez-Guillén, R. A., Santolamazza-Carbone, S., & von Ellenrieder, N. (2016). The status of *Rhionaeschna galapagoensis* (Currie, 1901) with notes on its biology and a description of its ultimate instar larva (Odonata: Aeshnidae). *Animal Biodiversity and Conservation*, 39(1), 45–63.
- Cordero-Rivera, A., & Stoks, R. (2008). *Mark-recapture studies and demography*. In A. Córdoba-Aguilar (Ed.), *Dragonflies: model organisms for ecological and evolutionary studies* (pp. 7–20). Oxford: Oxford University Press. <http://doi.org/10.1093/acprof:oso/9780199230693.003.0002>
- Daigle, J. J., & Tennessen, K. J. (2000). *Heteragrion cooki* spec. nov. from Ecuador (Zygoptera: Megapodagrionidae). *Odonatologica*, 29(3), 255–259.
- De Marco, P. J., Batista, J. D., & Cabette, H. S. R. (2015). Community assembly of adult odonates in tropical streams: An ecophysiological hypothesis. *PLoS ONE*, 10(4). <http://doi.org/10.1371/journal.pone.0123023>

- De Marco, P. J., & Resende, D. C. (2002). Activity patterns and thermoregulation in a tropical dragonfly assemblage. *Odonatologica*, 31(2), 129–138.
- DeSalle, R., Egan, M.G., & Siddall, M. (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society of London, Series B Biological Sciences*, 360:1905–1916. <http://doi:10.1098/rstb.2005.1722>
- Dijkstra, K.-D. B., Kalkman, V. J., Dow, R. A., Stokvis, F. R., & van Tol, J. (2014). Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). *Systematic Entomology*, 39(1), 68–96. <http://doi.org/10.1111/syen.12035>
- Fincke, O. M. (1992). Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. *Ecology*, 73:449–462. <http://doi:10.2307/1940752>
- Garrison, R.W., von Ellenrieder, N., & Louton, J.A. (2010). *Damselfly genera of the New World*. Baltimore: Johns Hopkins University Press.
- González Soriano, E., & Verdugo Garza, M. (1982). Studies on neotropical Odonata: the adult behavior of *Heteragrion alienum* Williamson (Odonata: Megapodagrionidae). *Folia Entomologica Mexicana*, 52(52), 3–15. http://aims.fao.org/serials/c_7a11afdb
- Gribbin, S. D., & Thompson, D. J. (1991). The effects of size and residency on territorial disputes and short-term mating success in the damselfly *Pyrrosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Animal Behaviour*, 41, 689–695. [http://doi.org/10.1016/S0003-3472\(05\)80906-6](http://doi.org/10.1016/S0003-3472(05)80906-6)
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration: stochastic model. *Biometrika*, 52, 225–247. <http://doi:10.2307/2333826>
- Kalkman, V. J., Clausnitzer, V., Dijkstra, K. D. B., Orr, A. G., Paulson, D. R., & van Tol, J. (2008). Global diversity of dragonflies (Odonata; Insecta) in freshwater. *Hydrobiologia*, 595, 351–363. <http://doi:10.1007/s10750-007-9029-x>
- Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62(1), 67–118.
- Loiola, G. R., & De Marco, P. J. (2011). Behavioral ecology of *Heteragrion consors* Hagen (Odonata, Megapodagrionidae): a shade-seek Atlantic forest damselfly. *Revista Brasileira de Entomologia*, 55(3), 373–380. <http://doi:10.2307/2937171>
- Machado, A. B. M. (2006). Three new species of *Heteragrion* Selys, from Brazil with redescription of the holotype of *H. dorsale* Selys (Odonata, Megapodagrionidae). *Revista Brasileira de Zoologia*, 23(4), 1062–1070. <http://dx.doi.org/10.1590/S0101-81752006000400012>
- Manly, B. F. J., & Parr, M. J. (1968). A new method for estimating population size, survivorship, and birth rate from capture-recapture data. *Transactions of the Society for British Entomology*, 18, 81–89.
- Marden, J. H., & Cobb, J. R. (2004). Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites. *Animal Behaviour*, 68, 657–665. <http://doi.org/10.1016/j.anbehav.2003.09.019>
- May, M. L. (1976). Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecological Monographs*, 46, 1–32. <http://doi:10.2307/1942392>
- Miller, P. L., & Miller, C. A. (1981). Field observations on copulatory behaviour in Zygoptera, with an examination of the structure and activity of male genitalia. *Odonatologica*, 10(3), 201–218.
- Monteiro-Júnior, C. S., Juen, L., & Hamada, N. (2015). Analysis of urban impacts on aquatic habitats in the central Amazon basin: Adult odonates as bioindicators of environmental quality. *Ecological Indicators*, 48, 303–311. Retrieved from <http://www.sciencedirect.com/science/article/pii/S1470160X14003768>
- Okuyama, H., Samejima, Y., & Tsubaki, Y. (2015). Smaller damselflies have better flight performance at lower body temperature: implications for microhabitat segregation of sympatric *Mnais* damselflies. *International Journal of Odonatology*, 18(3), 217–224. <http://doi.org/10.1080/13887890.2015.1065517>
- Oliveira-Junior, J. M. B., Shimano, Y., Gardner, T. A., Hughes, R. M., De Marco, P. J., & Juen, L. (2015). Neotropical dragonflies (Insecta: Odonata) as indicators of ecological condition of small streams in the eastern Amazon. *Austral Ecology*, 40, 733–744. <http://doi.org/10.1111/aec.12242>
- Paulson, D. R. (2004). Critical species of Odonata in the Neotropics. *International Journal of Odonatology*, 7(2), 163–188. <http://dx.doi.org/10.1080/13887890.2004.9748208>
- Sanmartín-Villar, I., & Cordero-Rivera, A. (2016). Female colour polymorphism and unique reproductive behaviour in *Polythore* damselflies (Zygoptera: Polythoridae). *Neotropical Entomology*, 45, 658–664. <http://doi.org/10.1007/s13744-016-0417-7>
- Serrano-Meneses, M. A., Córdoba-Aguilar, A., Méndez, V., Layen, S. J., & Székely, T. (2007). Sexual size dimorphism in the American rubyspot: male body size predicts male competition and mating success. *Animal Behaviour*, 73(6), 987–997. <https://doi.org/10.1016/j.anbehav.2006.08.012>
- Shelly, T. E. (1982). Comparative foraging behavior of light- versus shade-seeking adult damselflies in a lowland Neotropical forest (Odonata: Zygoptera). *Physiological Zoology*, 55(4), 335–343. <https://doi.org/10.1086/physzool.55.4.30155861>
- Suhling, F., Sahlén, G., Gorb, S., Kalkman, V. J., Dijkstra, K.-D. B., & van Tol, J. (2015). Order Odonata. In J. Thorp & D. C. Rogers (Eds.), *Ecology and General Biology: Thorp and Covich's Freshwater Invertebrates* (4th ed., pp. 893–932). Amsterdam: Academic Press.
- Thompson, D. J., & Fincke, O. M. (2002). Body size and fitness in Odonata, stabilising selection and a meta-analysis too far? *Ecological Entomology*, 27:378–384. <http://doi:10.1046/j.1365-2311.2002.00419.x>

- Torres-Cambas, Y., & Fonseca-Rodríguez, R. (2009). Reproductive behaviour of *Hypolestes trinitatis* (Gundlanch) in Cuba (Zygoptera: Megapodagrionidae). *Odonatologica*, 38(3), 247–253.
- White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, 46 Supplem., 120–138. <http://doi:10.1080/00063659909477239>
- Zamora-Camacho, F. J., & Comas, M. (2016). Natterjack toads show shorter lifespan, but greater body size and reproductive investment in agrosystem than in natural habitat. In *Eco-Etología 2016. Congreso Internacional de la Sociedad Española de Etología y Ecología Evolutiva* (p. 94). Granada.