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Demographic Traits and Behavior of *Hetaerina cruentata* (Odonata: Calopterygidae) in Ecosystems of the Andean Region of Colombia

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Abstract: Demography and territorial behavior of *Hetaerina cruentata* was studied along three lowland streams located at Norte de Santander department in the Colombian Andean region. Adult damselflies (N: 278) were individually marked, and using their recapture histories we estimated survival, longevity, sex ratio, age groups and population size at each location. We found no evidence for survival differences between ages and sexes. However, the proportion of resighted individuals was lower for females, and the sex ratio was male-biased in all populations. Although we recorded few reproductive events, a high number of male-male agonistic interactions were registered around midday. During reproductive behavior, we observed brief wing displays as signals between males and females, and the formation of the tandem position, followed by the intra-male sperm translocation and copulation (mean duration 11.3 min). After copulation, the pair in tandem looked for suitable sites to oviposit, and then the male broke tandem and perched on the vegetation while the female laid eggs partially or completely underwater. The recapture probability was time-dependent, which suggests that the alternation of rainy and sunny days during the study may be generating differences in the demography of the three *H. cruentata* populations.

Keywords: Dragonfly, damselfly, Zygoptera, mark-recapture, Neotropics

Introduction

Our knowledge of population ecology of wild animal populations has improved in recent years, thanks to the development of approaches based in maximum likelihood models that allow the estimation of demographic parameters using recapture histories of marked individuals (Lebreton, Burnham, Clobert, & Anderson, 1992). These methods consider the imperfect detection of individuals that otherwise would bias the estimates of population sizes and survival rates (Kéry & Schaub 2012). Dragonflies and damselflies have been widely studied using mark–recapture methods in temperate regions (reviewed by Cordero-Rivera & Stoks, 2008), but research about Neotropical species has lagged behind until recently (Altamiranda-Saavedra & Ortega, 2012; Palacino-Rodríguez, 2016; Cordero-Rivera et al., 2019).

Understanding the effects of environmental variations is crucial for elucidating the mechanisms that structure the populations (Barretto, Cultid-Medina, & Escobar, 2018). For instance, a comparison of a shaded and a sunny (modified) stream revealed differences in survival and body size in *Heteragrion cooki* Daigle & Tennessen, 2000*,* even if both streams were only 7.6 km apart (Rivas-Torres et al., 2017), suggesting local acclimation. By studying several populations, it is possible to evaluate the vulnerability of species to the alteration of environmental conditions (Lemoine et al., 2007), because factors like sun exposure or population density are expected to affect the behavior of odonates, particularly behaviors that occur at the breeding site (Lambret & Stoquert, 2011). Human alteration of riverine habitats (e.g. pollution, flow modifications, exotic species, harvesting) has been found to

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negatively affect demographic traits of Neotropical odonates (Fincke & Hedström, 2008; Palacino-Rodríguez et al., 2012; Palacino-Rodríguez et al., 2020a, b).

Although damselflies can be easily captured, marked and individually recognized (Cordero-Rivera & Stoks, 2008), in tropical habitats reproductive activity is rarely observed in many species (e.g. Cordero-Rivera et al, 2019; but see Fincke, 1992), perhaps because animals survive for long periods but only reproduce when conditions are appropriate (Altamiranda-Saavedra et al., 2014; Palacino-Rodríguez et al., 2020a; Rivas-Torres et al, 2017; Sanmartín–Villar & Cordero–Rivera, 2016; but see Cordero-Rivera, et al., 2019). Several studies have been published about the reproductive behaviour of temperate calopterygids (e.g. Bick & Sulzbach, 1966; Cordero-Rivera, 2017a; reviewed by Córdoba-Aguilar & Cordero-Rivera, 2005; Khelifa, 2019), but studies about the genus *Hetaerina* Hagen in Selys, 1873 (Odonata: Calopterygidae) have been mainly limited to Mexico and the United States, with scattered studies in other countries (e.g. Lefevre & Muheter, 2004; Peixoto & De Marco, 2009; Gabela-Flores et al., 2019). This genus comprises about 40 species abundant in Neotropical riverine ecosystems (Garrison, 1990). Previous studies have shown that the behavior of males of *Hetaerina* includes: i) territorial or nonterritorial tactics to obtain matings, ii) signals indicating their corporal condition, using their wing pigmentation, iii) displacement of the sperm that the female has stored from previous matings, and iv) after copulation, guarding of females to prevent other males from copulating with them (Córdoba-Aguilar & Cordero-Rivera, 2005). Gabela-Flores et al. (2019) studied the demography and territorial behaviour in populations of *Hetaerina aurora* Ris, 1918; *Hetaerina caja* (Drury, 1773), and *Hetaerina fuscoguttata* Selys, 1878 from tropical populations in Ecuador. They recorded only a few reproductive events, but a high number of male-male agonistic interactions, with territoriality, site fidelity and non-territoriality as male mating strategies.

Behavior and territorial competition of *H. cruentata* (Rambur, 1842) (Figure 1a) males has been studied in Mexican temperate rivers by Córdoba-Aguilar (1995), who found resource-defense polygyny and three male territorial tactics: aggressive residents, aggressive sneakers, and floaters that rarely fight. Given the influence of local factors on general and reproductive behavior of calopterygids (Córdoba-Aguilar & Cordero-Rivera, 2005), multiple studies are needed to fully understand the extent of behavioral diversity, both at the intra- and interpopulation levels (Cordero-Rivera, 2017a).

We would like to highlight that the knowledge of population dynamics of tropical damselflies is still very limited, and therefore many more studies of field observations are needed to be able to build up a "big picture", using basic data for future meta-analyses. Here, we present the results of a demographic and behavioral study of *H. cruentata* in Neotropical populations of the Colombian Andes, including localities affected by human activities. Our aims included: i) to estimate population size, sex ratio, survival, and life expectancy; ii) to compare demographic traits between groups by age and between populations, and iii) to describe general and reproductive behavior, and compare with previous studies.

Figure 1. ***Hetaerina cruentata*****. A. male, Photo from C. Bota-Sierra, b. female. Photo from M. Altamiranda.**

Material and methods

Study area and study species

The fieldwork was done at three streams (Figure 2) of the Pamplonita municipality, situated at Norte de Santander Department in the Colombian Andean eastern mountains range (Table 1, Figure 3). Geographical coordinates and basin area are described in Table 1. The region is located in an altitudinal range of 1000 to 2000 m.a.s.l., and it is characterized by temperatures that range between 11 and 34 °C, with a bimodal annual rainfall of 1000 to 2000 mm and maxima in April-May; and from September to November (IDEAM, 2017). It belongs to the Sub-Andean forest biome, with native vegetation dominated by *Ficus* sp., *Piper aduncum* L., *Inga oerstediana* Benth., *Cinnamomum triplinerve* (Ruiz & Pav.) Kosterm., *Heliocarpus americanus* L., *Boehmeria caudata* (Burm.f.) J.J. Sm. ex Koord. & Valeton, and *Smallanthus riparius* (Kunth) H. Rob.

The genus *Hetaerina* exhibits sexual dimorphism (Figure 1). Mature males have a reddish body, with a red spot at the basis of the wings. Females have amber-coloured wings, with greenish or yellowish bodies (Garrison, 1990). All the species of the genus are riverine, and can be found in high numbers at forested streams.

Figure 2. Stream ecosystems where *H. cruentata* was sampled in Norte de Santander department, Colombia. A, Galindo stream; B, Cucalina stream, C, Santa Helena stream.

Table 1. Basic information for localities in Norte de Santander department, Colombia

Population	Coordinates	Altitude (msnm)	*Total stream area (km^2)
Cucalina	7.45674, -72.60111	1700	50
Galindo	7.46179, -72.65480	1460	63
Santa Helena	7.44900, -72.59891	1600	68

*Total area refers to where the species was sampled, including stream area searched and perching locations.

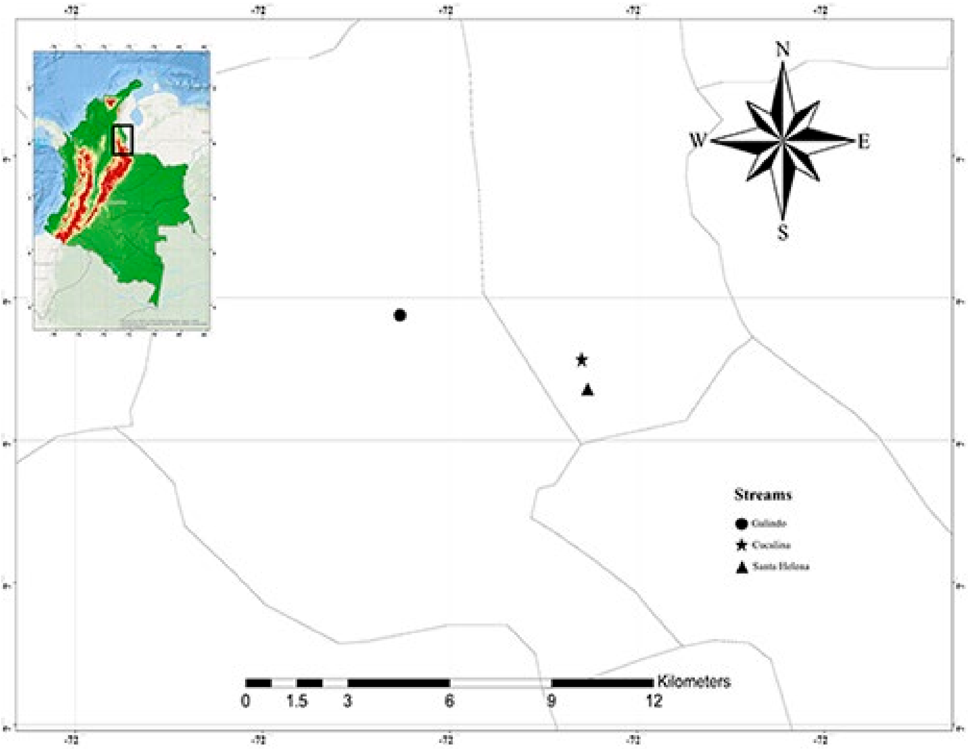

Figure 3. Location of the three sampled localities in the Norte de Santander department, Colombia. The thin black lines represent departmental limits.

Data collection

A transect of 200 m parallel to each stream was demarcated. Each individual observed was caught, marked (at first capture), and its sex, color (as an estimation of age; see below), and recapture data were recorded. Then, it was photographed and released at the site of capture. The whole process took less than 1 minute per individual (Álvarez-Covelli et al.,2015; Palacino-Rodríguez & Contreras-Sánchez, 2014). Following a similar method as in Plaistow & Siva-Jothy (1996) individuals were classified into two age categories: i) Sexually immature: individuals with soft hyaline wings lacking well-defined general body pigmentation, and individuals with wings entirely flexible, or flexible from the node to the tip, with a pale body color; and ii) Sexually mature: individuals with hard and opaque, inflexible wings, body color well defined. Fieldwork was done from 08:00 to 15:00 hours from 28 January to 11 February at Galindo, 12 to 26 February at Santa Helena and from 29 February to 14 March 2020 at Cucalina. Damselflies were captured with aerial nets and individually marked with a fine-tip Sharpie® black marker on the right forewing using four-digit numbers. A total of 162 h of sampling person effort was used in each locality.

Behavioral study

The observations followed the focal animal temporal sampling technique (Altman, 1974). Each session occurred from 08:00 to 15:00 h (seven hours daily) Colombian time (COT, UTC-5), divided into periods of 10 min (per individual), in which the sequence and changes in behavior were observed and recorded. Ten minutes later, a different marked animal was observed. A total of 1500 min by locality were used for observation and collecting observational data into the breeding area or territory. We sorted our observations into the following categories: i) mating strategy; ii) foraging; iii) tandem; iv) mating; v) oviposition; vi) male interactions: a) siege: an individual approaches another to prevent its passage or scare it away; b) pursue: and individual follows another to move it away from the territory; and c) contest: a continuous sequence of agonistic actions initiated inside the territory (at the perch or in flight) and finalized by a return to a perch (Baird & May, 2003). Observations were done with the naked eye or using 10×50 JHOPT™ binoculars (Brighton, CO, USA). We followed Kaufmann (1983) and define a territory as a fixed area that an individual defends from conspecifics because it includes one or more resources that increase the fitness of the individual. According to this definition, and considering the proposal of Raihani, Serrano-Meneses, & Córdoba-Aguilar (2008), we classified male mating strategies as: i) Territorial: when males remain in the same territory and defend it; ii) site fidelity: when males remain in the same territory, but do not defend it; and iii) non territorial: males fly to different locations into the study area, and do not remain for long time in any site.

Statistical analysis

We calculated the overall proportion of resighting (PR) for males and females (immature and mature) by locality. A chi-square test (χ^2) was used to compare PR of these groups using SPSS 25.0 software (IBM Corp., 2017). We used Cormack–Jolly–Seber (CJS) capture–recapture models to estimate survival and recapture probabilities for four groups: (i) immature males, (ii) mature males, (iii) immature females, and (iv) mature females in the field. These models dissociate survival from recapture probabilities (Lebreton et al., 1992), and we ranked models using the Akaike Information Criterion (AIC) (White & Burnham, 1999). The goodness-of-fit (GOF) of the saturated model (the model including time and sex variation and their interaction) was calculated using RELEASE program within MARK. TEST 2 was used to test the assumption of 'equal catchability' of marked animals, and TEST 3 to test that all marked animals alive on day (i), have same the probability to survive to day (i+1) (White & Burnham 1999). These tests were not significant in any population (Test 2 + Test 3, Galindo stream χ^2=93.07, df = 107, p = 0.82; Santa Helena stream χ^2= 43.62, df = 62, p = 0.96; Cucalina stream χ^2=19.95, df = 41, p = 0.99). Thus, the saturated model in our datasets is a good approximation for parameter estimation. To estimate the variance inflation factor, we checked for overdispersion with the median c-hat approach in the global model. Overdispersion factors greater than 3 may indicate structural deficiencies in the models (Lebreton et al, 1992). Our models were far below this threshold. For the Galindo stream overdispersion was 1.12, for Santa Helena stream was 1.23, and for Cucalina stream was 1.27. These values were employed to correct AIC estimates ($QAIC_c$; Burnham & Anderson, 2002) to select the most supported model (i.g. the model with the lowest $QAIC_c$ value; see Supplementary tables 2-4). We employed MARK 6.2 software to estimate these capture–recapture models (White & Burnham, 1999). We estimated adult life expectancy (le) with the equation $le = -1 / \log_e$ (average daily survival rate) provided by Cook & Brower (1967), and population size using Jolly-Seber (Jolly, 1965) and Manly-Parr (Manly & Parr, 1968) models by means of POPAN software (Arnason, Schwarz & Boyer, 1998).

Results

Population size, age, and sex-ratio

Overall, we marked a total of 278 individuals, and found male-biased sex ratio (164 males, 58.99%; 114 females, 41.01%, χ^2= 17.34, $p<0.001$; Table 2). Twenty percent of individuals were never recaptured, 52% were recaptured 1-5 times, and 24% were recaptured 6-12 times (Supplementary material Table 1). The proportion of resighted individuals was lower for females in all populations and ages (Table 2; see also Table 3). The proportion of immature males, immature females and mature males was significantly different among Galindo and the remaining two localities, but not between Santa Helena and Cucalina (Table 3). The proportion of mature females resighted was not significantly different among localities. Likewise, significant differences were found in sex-ratio in Santa Helena and Cucalina, but not in Galindo stream (Table 3). Using POPAN-5 software, we estimated a mean population size of 45±2.62 males and 23.57±2.35 females for Galindo; 23±1.81 males and 16±2.03 females for Santa Helena; and 19±2.75 males and 10±2.00 females for Cucalina.

Table 2. Number of individuals in each group of age in each locality. n, number of individuals captured; RC, number of individuals recaptured; PR, proportion resighted, G, Galindo; SH, Santa Helena; C, Cucalina.

Group	Immature male			Mature male			Immature female			Mature female			Sex ratio
Population	n	RC	PR	n	RC	PR	n	RC	PR	n	RC	PR	
Galindo	24	21	0.87	61	54	0.88	38	21	0.55	22	15	0.68	1.4
Santa Helena	11	10	0.90	29	25	0.89	10	8	0.80	22	18	0.81	1.3
Cucalina	9	7	0.77	30	27	0.90	6	4	0.66	16	14	0.87	1.7
Overall	44	38	0.84	120	106	0.89	54	33	0.40	60	47	0.80	1.4

Table 3. Chi square test (χ^2) comparing proportion resighted (PR) in each sex by age group, p, probability

	Immature groups between localities				Mature groups between localities					
	PR Males		PR Females		PR Males		PR Females		Sex ratio	
Populations	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
G vs SH	7.81	0.005	11.66	<0.001	21.29	<0.001	0.55	0.46	0.02	0.89
G vs C	14.00	<0.001	23.12	<0.001	18.0	<0.001	0.07	0.79	0.14	0.71
SH vs C	1.06	0.302	2.671	0.102	0.154	0.693	1.004	0.316	0.061	0.802
	Mature/immature males		Mature/immature females							
	χ^2	p-value	χ^2	p-value						
Galindo	29.04	<0.005	2.00	0.15						
Santa Helena	12.86	<0.001	7.69	0.005						
Cucalina	23.53	<0.001	11.11	<0.001						

Survival, life expectancy, and recapture rates

The model that included constant survival, but differences in recapture rates between sexes [Phi(.) p(sex)] was the first or second most supported in all populations (Supplementary material Tables 2-4). The estimates derived from Phi(.) p(sex) model, for survival and life expectancy (le) were similar among populations: Galindo (Phi= 0.915 ± 0.011; le=11.21 days), Santa Helena (Phi= 0.916 ± 0.015; le= 11.35 days), and Cucalina (Phi= 0.903 ± 0.019; le= 9.76 days). The estimated recapture rate was higher for males than females in Galindo and Santa Helena populations, but was higher for mature females in Cucalina population (Table 4).

Table 4. Recapture rate (±SE) estimated from the model Phi(.) p(g) in each population. NA: Not available because the number of individuals was too low.

Population	Immature males	Mature Males	Immature Females	Mature Females
Galindo	0.611 ± 0.047	0.653 ± 0.028	0.494 ± 0.049	0.520 ± 0.066
Santa Helena	0.852 ± 0.054	0.752 ± 0.036	0.616 ± 0.115	0.609 ± 0.051
Cucalina	0.552 ± 0.113	0.791 ± 0.038	NA	0.833 ± 0.049

Behavior

The following traits of *H. cruentata* behavior in tropical ecosystems from Colombia are based on observations on 65 individuals in total across all localities. Between 11:00 and 13:30 h individuals perch near to water in spots where sunlight enters. Our observations indicate low activity. Teneral individuals perch on leaves and logs, while mature individuals perch on leaves, logs, and rocks. Some teneral individual changed perches in less than 1 min and they tended to fly away from the stream. Individuals were seen perching at a height of 0 to 5 meters (mean: 2.2 m, SD: 1.45 n: 45 (Galindo: 20, Santa Helena: 14, Cucalina: 11)), during a minimum of one minute, and a maximum of 60 continuous minutes (mean: 28.3 min, SD: 26.54). Teneral individuals visited the stream for periods of 1 to 15 min (mean: 12 min, SD: 4.00 n: 10 (Galindo: 5, Santa Helena: 2, Cucalina: 3)) but adult individuals could spend most of the day perching around the water. Several mature females may share the same perch, but this rarely occurs among mature males.. This behavior lasted 1 to 5 sec (mean: 4.25 sec, SD: 1.25 n: 20 (Galindo: 7, Santa Helena: 5, Cucalina: 8)). In the early hours in the morning and some hours in the afternoon (8:00-9:00 and 14:30-15:00), individuals selected as perching sites those spots near to water which receive sunlight. Commonly, focal individuals made short flights (less than 1 m; 3 – 10 sec. mean: 5.78 sec., SD: 2.49) returning to their perch. Territorial defense was seen during 80% of the time. Some of these flights were used to capture prey (mean: 9.00 sec; SD: 1.41, n: 5).

Mature males approached females with a short flight, lasting 3–5 s. Given the low frequency of these events, when a courtship was detected, we followed the pair until the end of oviposition. When the female was receptive, the tandem position was formed (mean: 11.80 min; SD: 3.32; N: 3). Then, intramale sperm translocation was observed, and copulation followed, for 5 to 20 min (mean: 11.25 min; SD: 6.56; n: 3). After copulation, the pair in tandem position looked for suitable sites to oviposit (mean: 12.65 min; SD: 5.32; n: 3). In two pairs, the male broke the tandem and perched on the vegetation while the female laid eggs completely underwater. In the other pair, the male remained in tandem when the female laid eggs partially underwater. Oviposition lasted for 6–20 min (mean: 10.90 min. SD: 5.72; n =5). In two cases, when the emergent vegetation was scarce, females took up to 2 h to return to the surface.

Discussion

Our results indicate male-biased sex ratio in *H. cruentata* for all localities of the study. At rendezvous sites, it is known that males are slightly more frequent in number at the emergence among Zygoptera

(Corbet & Hoess, 1998), and much more common among the adults (reviewed by Cordero-Rivera & Stoks, 2008). Likewise, Cordero-Rivera & Stoks (2008) found higher female than male survivorship in Calopterygids. Therefore, our results are in line with previous research. It is possible that a sampling bias, due to the more conspicuous coloration of males, may contribute to the male-biased sex-ratios found when adult damselflies are marked in natural populations. Males not only present more striking colors, but they also concentrate near to water and show a closer association with riparian vegetation. These characteristics could make males more visible during sampling, generating involuntary biases in the data. On the other hand, recapture rates estimated from CJS models were higher for males in Galindo and Santa Helena populations (Table 4), but not in Cucalina, suggesting that, in general, males are more easily detected. Thus, we agree with Gabela-Flores et al,. (2019), who suggested that male-biased sex ratio found in *Hetaerina* could be explained by females commonly perching in higher forest strata (≥ 3 m), where they are difficult to sight and capture. Male-biased sex ratio in other Neotropical species of Odonata has been attributed to the presence of dense perch areas near to water, where males are more common (Palacino-Rodríguez et al., 2020a,b) and to the aggregation of males at the stream waiting by females, whereas females only appear for oviposition (Altamiranda-Saavedra et al., 2014). In fact, the aggregation of males in a lek-like mating system has been reported in *Hetaerina* species, including *H. cruentata* (Córdoba-Aguilar et al., 2008; Gabela-Flores et al., 2019), which supports our findings.

The alternation of rainy and sunny days during our fieldwork (Palacino-Rodríguez et al., 2012) may explain why the most supported model in Cucalina and Santa Helena was [Phi(.) p(t)], which indicates that recapture rates were different between days. Unfortunately, due to logistic limitations, our study was short at each locality, and did not cover several times the mean life expectancy of adults (e.g. 45 days), as previous studies have suggested for Calopterygidae (Cordero-Rivera & Stoks, 2008). However, even with these limitations, our longevity estimates are higher than the values averaged for Zygoptera (mean: 7.6 days; Corbet, 1999) in the three localities. These values are similar to the maximum life expectancy observed in other damselflies from temperate and tropical regions (5-38 days; Cordero-Rivera & Stoks, 2008; Cordero-Rivera et al., 2019). Since life expectancy is linked to survival, it is probable that in our populations lifespan was even higher, but longer periods of fieldwork will be necessary to record maximum longevities.

The recapture rates were lower for immature females compared to mature females and males in all populations (Table 4). We have two possible explications for these results. First, although marking in this study was performed with great care to avoid damaging the individuals (Palacino-Rodríguez & Contreras-Sánchez, 2014), an increase in the mortality due to handling and marking of individuals in the teneral state has been reported by several authors (Uéda & Iwasaki, 1982; Nomakuchi, Higashi, & Maeda, 1988; Fincke, 1988). Secondly, handling during the marking procedure could induce dispersive behavior (Mallet et al.,1987), leg loss affecting survival (Cordero Rivera et al., 2002) and elicit nervous behaviour, as some species quickly escape when humans approach (Cordero-Rivera et al., 2019). Teneral individuals were observed to perform continuous changes of perch and brief visits to the stream, making them less likely to be detected.

In accordance with Córdoba-Aguilar (1995), *H. cruentata* populations studied by us showed intense male competition for territories around midday, when density was higher. Male-male aggression, persecution, and fights were constantly seen, and their duration was variable (10 sec. to 25 min.). However, territorial individuals defended and held their territories in all cases. The differential ability of males to defend territories can promote alternative male territorial behaviors (Conrad & Pritchard, 1992), associated with different energetic costs. Similar to calopterygids from temperate regions, in tropical populations of *H. cruentata*, males retain the territory for long periods of time (up to 15 days), and spend several hours every day defending it (Córdoba-Aguilar, 1995). Thus, high energetic demands, and physiological and injury costs for territorial males are expected. Therefore, we hypothesize that territorial males in *H. cruentata* are mostly middle-aged individuals in possession of high fat reserves (reviewed by Suhonen, Rantala, & Honkavaara, 2008).

Despite the high number of males observed near to water, we only recorded eleven pairs in copula, indicating very low reproductive activity, as is usual in some tropical damselflies (e.g. Gabela-Flores et al., 2019; Rivas-Torres et al., 2017; Sanmartín-Villar & Cordero-Rivera, 2016). The duration of tandem, copulation and oviposition were considerably longer than in other tropical *Hetaerina* populations (Cordero-Rivera et al., 2019). Although variation in the pre-copulatory behavior has been reported for several calopterygid genera, in *Hetaerina* spp., females are taken by males without any apparent courtship (Weichsel, 1985; Cordero-Rivera et al., 2019). Brief wing displays were observed as signals between males and females in our study. Long copulations and postcopulatory behaviors in damselflies allow males to guard their mate, impeding other males to take over the female (Cordero-Rivera, 1990). In our populations, males copulated for an average of 11 minutes, time during which territorial defense cannot be done. Spending long time in copulation by territorial zygopteran males can only be evolutionary stable if males are able to regain the territory after copulation (Córdoba-Aguilar, Serrano-Meneses, & Cordero-Rivera, 2009). In fact, copulation is shorter in territorial than in non-territorial odonates (Córdoba-Aguilar et al., 2009). In *Hetaerina americana*, some territorial males abandon the territory for several days and after return to regain it (Raihani et al., 2008). We observed several territorial males in all localities that were marked, disappeared by one or two days, and then, returned and won territorial disputes. It is possible that long copulation duration in territorial males of *Hetaerina* could be associated to their sperm manipulation ability (Córdoba-Aguilar & Cordero-Rivera, 2005). We speculate that the long duration of reproductive behaviors in *H. cruentata* could be occasioned by the continuous disturbance of males to pairs in reproduction, because male disturbance prolongs copulation in other odonates (e.g. Utzeri & Ercoli, 2004). This behaviour might also induce copulating pairs to perch higher in the vegetation, thus diminishing our ability to detect mating pairs. Due to the rarity of copulation behaviour, we could not identify which phenotypic characteristics are associated with high reproductive success, but in other calopterygids wing pigmentation is under female selection (Pena-Firme & Guillermo-Ferreira, 2020), and something similar could occur in *H. cruentata*. Further research is needed to test these ideas in Neotropical populations of *H. cruentata*.

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