

**UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ**

**Colegio de Ciencias Biológicas y Ambientales**

**Demography and territorial behavior of three species of the genus *Hetaerina* (Odonata: Calopterygidae) along three tropical stream ecosystems**

**Proyecto de investigación**

**María Virginia Gabela Flores**

**Biología**

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**María Virginia Gabela Flores**

Calificación:

Nombre del profesor, Título académico

Andrea Encalada, Ph.D

Firma del profesor

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Quito, 7 de diciembre de 2016

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Firma del estudiante:

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Nombres y apellidos:

María Virginia Gabela Flores

Código:

00108113

Cédula de Identidad:

1716867260

Lugar y fecha:

Quito, 7 de diciembre de 2016

## RESUMEN

Estudiamos las características demográficas y el comportamiento territorial de tres especies de libélulas del género *Hetaerina* (*H. fuscoguttata*, *H. aurora*, *H. caja*) a lo largo de tres riachuelos en la costa del Ecuador. A través de una metodología de captura y recaptura, estimamos las tasas diarias de supervivencia, el radio de sexos y longevidad de la especie más abundante en cada localidad, al igual que el tamaño de cada población. De manera general, capturamos más machos que hembras y encontramos radios de sexos sesgados hacia los machos en las tres poblaciones estudiadas. A través de observaciones focales, analizamos el comportamiento territorial de los machos, al igual que el comportamiento reproductivo tanto de machos como hembras de las tres especies. Registramos un número bajo de eventos reproductivos en las tres especies. Por otro lado, registramos un número más alto de peleas territoriales entre machos de las tres especies. Sin embargo, no encontramos evidencia de que ciertos rasgos morfológicos están relacionados con el rol territorial de los machos.

**Palabras clave:** captura y recaptura, demografía, comportamiento territorial, Odonata, Ecuador

## ABSTRACT

We studied the demography and territorial behavior of three damselfly species of the *Hetaerina* genus (*H. fuscoguttata*, *H. aurora* and *H. caja*) along three lowland stream ecosystems in western Ecuador. Throughout a Capture-Mark-Recapture (CMR) methodology, we estimated the daily survival rates, sex ratio and longevity of the most abundant species on each location, as well as the respective population size. Overall, we captured more males than females and we found male biased sex ratios in all three studied populations. Throughout focal observations, we analyzed male territorial behavior as well as male and female reproductive behavior of the three *Hetaerina* species. We registered a low number of reproductive events in all populations. Conversely, we registered a higher number of male-male interactions of this territorial genus. However, we did not find evidence that certain morphological characters are related to a male's territorial role.

**Key Words:** mark-recapture, demography, territorial behavior, Odonata, Ecuador.

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## INTRODUCTION

Damselflies of the genus *Hetaerina* (Odonata: Calopterygidae) are endemic to the Americas and are highly diverse in tropical regions of South America (Garrison 1990). Currently, there are 37 described species of *Hetaerina* damselflies, which are often abundant and conspicuous in neo-tropical riverine ecosystems (Garrison 1990). Damselfly larvae dwell in stagnant water ecosystems, as well as in river and streams, where they are considered important predators of several aquatic taxa (Fincke et al. 1997, Johnson 1973). As adults, they are agile aerial predators and feed mostly on mosquitoes and other small flying insects; therefore, they are considered a key trophic link of lotic and terrestrial food webs (Corbet 1999). Moreover, in tropical countries, damselflies are crucial elements to control populations of mosquitoes associated with diseases such as malaria and dengue (Shaan & Canyon 2009). Damselflies are ideal organisms for demographic and behavioral studies because they can be easily marked and recognized without recapture (reviewed by Cordero-Rivera & Stoks in Córdoba-Aguilar 2008). However, most studies about the *Hetaerina* genus have been carried out in the United States and Mexico, and have focused primarily on *H. americana* and *H. titia*. Despite this and their ecological and evolutionary importance, there are few studies about their demography as well as their reproductive behavior in the Neo-Tropics (Córdoba-Aguilar 1994).

Demographic studies are useful to understand the variation and characteristics of a given population. Throughout mark-recapture studies, parameters such as survival rates and longevity can be estimated, as well as population density and abundance (reviewed by Cordero-Rivera & Stoks in Córdoba-Aguilar 2008). The sex ratio is another useful parameter to understand populations as well as female and male behavior. In odonates, for instance, changes in the sex ratio of a population can help predict which gender will be competing for

mating resources (reviewed by Kvarnemo & Ahnesjö 1996). Often, populations of odonates present male biased sex ratios, which could explain the territorial behavior of males as well as the intense competition between them for mating and oviposition resources (Hamilton & Montgomerie 1989). On the other hand, there are few populations with female biased sex ratios at oviposition sites (Donnelly 1990). However, in odonate populations where males are rare, females do not appear to adopt a territorial or aggressive behavior towards each other (Van Gossum et al. 2007). Nevertheless, knowledge about female territorial behavior in damselflies needs to be deepened and explored.

Conversely, territorial behavior of male calopterygid damselflies has been widely studied. This behavior is related to the males' mating tactics and reproductive success (reviewed by Córdoba-Aguilar and Cordero-Rivera 2005). A territory could be defined as a fixed area that an individual defends from conspecifics because it may hold one or more resources, such as water, food, shelter, space or receptive mates; all of which might increase the individual's fitness (Kaufmann 1983).

It has been proposed that calopterygid males achieve their higher reproductive success during periods when they are territorial. Therefore, the quality of the territory, which reflects the amount of resources and the duration which it is maintained, is a determinant factor of male reproductive success (Plaistow & Siva-Jothy 1996). To defend their territory, male odonates encounter other males in aerial contests or fights, which are energetically costly (reviewed by Suhonen et al. 2008). It is presumed that these aerial fights are more energetically demanding than other activities such as feeding and reproduction, since they require high speed chases and precise maneuvering in the air (Marden & Waage 1990).



There are some morphological, physiological and behavioral traits that allow territorial male damselflies to defend and maintain their territories. For instance, territorial males exhibit larger fat reserves in their thoraxes, which allows them to win fights and maintain their territories (Marden & Waage 1990; Fitzstephens & Getty 2000; Serrano-Meneses et al. 2007). Also, young male calopterygids with larger fat reserves may be able to displace older territorial males (Marden & Waage 1990). Additionally, wing pigmentation might communicate the males' energetic condition to other conspecific males during aerial fights (Contreras-Garduño et al. 2006). For example, in *H. americana*, territorial males exhibit more wing pigmentation than non-territorial males; this trait is correlated with fat reserves and immune ability, therefore, it is thought to function as a signal of the male's immune state (Contreras-Garduño et al. 2006).

Calopterygid males that are not able to win aerial fights cannot acquire nor secure a territory (reviewed by Córdoba-Aguilar and Cordero-Rivera 2005). Despite not owning a territory, non-territorial males can "sneak" into another male's territory and seize mating opportunities (Forsyth & Montgomerie 1987). Furthermore, some males might switch between roles (e.g. Switzer 1997) and generally older, previously territorial males become non territorial later in their lives because their fat reserves have been depleted (Forsyth & Montgomerie 1987; Plaistow & Siva-Jothy 1996). Additionally, in *H. americana* it has been observed that some non-territorial males can interchange between territorial and non-territorial roles (Raihani et al. 2008).

Although there is information of the relative abundance, demography and territorial behavior of some species of *Hetaerina*, in some tropical countries like Colombia and Brazil (Eberhard 1986, Peixoto & De Marco 2008), to our knowledge, there are no ecological studies of this

genus in Ecuador. In Ecuador, the *Hetaerina* genus has been reported in middle and low elevations in the Amazonian foothills as well as in rivers and streams close to the Pacific coastal areas (Garrison 1990, Cordero-Rivera Pers. Comm. 2015). Nevertheless, information about the specific habitats and ecosystems in which these damselflies can be found is scarce. Here, we present the first demographic and behavioral study of *Hetaerina fuscoguttata*, *H. aurora* and *H. caja* along three different lowland stream ecosystems of western Ecuador. In this context, the goals of our study were to (1) understand the population demography of three species of *Hetaerina* along three different lowland tropical ecosystems, (2) describe both male and female sexual and territorial behavior, and (3) analyze which morphological differences could be related to territorial and non-territorial roles of the three species of *Hetaerina* in three different stream ecosystems.

## METHODS

### Study Organisms

We studied the demography and behavior of three species of the *Hetaerina* genus: *H. fuscoguttata*, *H. aurora* and *H. caja*. Adult damselflies of this genus are sexually dimorphic, with males exhibiting a red wing spot at the base of each wing and females presenting a more cryptic coloration, generally consisting of amber colored wings as well as a green and yellow body coloration (Grether 1996a) (Figure 1). We identified males based on the shape and color of the apical wing spots: *H. fuscoguttata* males present apical brown spots on all four wings (Figure 1A), *H. aurora* males present red apical spots on all four wings (Figure 1C) and *H. caja* males present red apical spots on the hind wings only (Figure 1E) (Garrison 1990). The apical wing spot varies ontogenetically; this was evident on young individuals of *H. aurora* which did not exhibit the apical wing spots until approximately three days after emergence. Nonetheless, this identification method is more reliable than the comparison between the basal red wing spot among species (Garrison 1990). On the other hand, female identification on the field was much more complicated due to the phenotypic similarities between species (Garrison 1990).

### Study Areas

We studied the three species of *Hetaerina* in three different locations of Western Ecuador: (1) Tabuga (Province of Manabí) (Figure 2B), (2) Buenaventura (Province of El Oro) (Figure 2C) and (3) Moromoro (Province of El Oro) (Figure 2C). Since all Odonata larvae are restricted to aquatic ecosystems, and because most calopterygids are strictly lotic dwellers, we focused our study near streams and rivers of these lowland areas.

### *Tabuga*

We sampled the Tabuga river (Figure 3A) for 16 non-consecutive days between July 26 and August 10, 2015 and studied the population of *Hetaerina fuscoguttata* from 9h00-12h00. We carried out additional behavioral observations from August 11 to August 17, 2015. In January 2016, we repeated the sampling during the rainy season; however, we did not find any adult individuals during that time.

The Tabuga river is a coastal watershed (0.070136° S, 80.142022° W, 0 m.a.s.l), coming from the Jama-Coaque Coastal Mountain Range, a low size (500 m.a.s.l) secondary lift of the Andean Cordillera in north-western Ecuador. The Tabuga river is the main source of domestic water for the town of Tabuga ( $\approx$  1000 population size), which is located 15 km from the mid-sized coastal towns of Jama and Pedernales in the province of Manabí (Figure 2B). This river is located at sea level and runs for 2.5 km all the way to the Pacific Ocean. Water flow varies greatly throughout the year, with low flow values ranging from 0 to 31 m<sup>3</sup> s<sup>-1</sup>. In low flow season (May through November, Appendix 1), river width could vary from 0.45 to 3m and has mostly pool habitats and very few runs and riffles (Figure 2A). Although the river is anthropogenically modified in some reaches, it presented a relatively high Fluvial Habitat Index of 78 (modified from Pardo et al 2002) and a Pfankuch Index of 89, which indicates a fair stream stability (Pfankuch 1975). The sampled section of the river presented a neutral pH of 7.73, a temperature of 24.8°C and a standard conductivity of 535  $\mu$ S cm<sup>-1</sup>. During our study, we collected data of ambient abiotic factors in one hour intervals and obtained a mean environmental temperature of 27.9°C, a mean heat index of 33.21% a mean humidity of 81.8% and a mean wind speed value of 0.24 ms<sup>-1</sup>.

The Tabuga river is surrounded by a semi-deciduous tropical dry forest, one of the very last remnants of this type of forest in western Ecuador (Aguirre 2012). Contrary to other areas in Ecuador, this ecosystem is highly seasonal, therefore, it is primarily deciduous during the dry season, which is comprised between May and November (Appendix 1) (Pennington et al. 2000). We evaluated the quality of the riparian vegetation of the sampled section of the Tabuga river with the QBR index and obtained a value of 60, which indicates a fair quality (modified from Suárez 2002; Prat et al. 2003). This is mainly due to the fact that large trees located along the river shore were cut down for timber. Therefore, the riparian vegetation in this river was predominantly herbaceous and shrubby, with species mainly belonging to the *Arecaceae*, *Rubiaceae*, *Malvaceae* and *Piperaceae* families. Farther away from the river shore, the dominant tree genres were *Cecropia* and *Centrolobium* (Aguirre 2006).

### *Buenaventura*

We sampled the Buenaventura stream (Figure 3B) for 8 non-consecutive days between June 25 and July 11, 2016 and studied the populations of *H. fuscoguttata* and *H. aurora* from 9h00-14h00. The Buenaventura stream (3.657730° S, 79.763645° W, 525 m.a.s.l) (Figure 2C) is part of the Arenillas watershed and it is located within the Buenaventura Reserve (Cantón Piñas, Province of El Oro) which protects around 2,000 hectares of a seasonal foothill forest Catamayo-Alamor ecosystem in the west slope of the Andes. Although the forest in this ecosystem is not deciduous, there is a strong seasonality, with low precipitations between the months of June and November (Appendix 1). During low flow season, the width of the Buenaventura stream varied between 1.5 to 2.5 and it was 0.30m deep, with an estimated water flow of 30 m<sup>3</sup>s<sup>-1</sup>. The sampled section of the stream presented a neutral pH of 7.31, a standard conductivity of 117.9 µS cm<sup>-1</sup> and a temperature of 20.3°C. This stream is very well preserved, and it is composed of several small sized waterfalls and large boulders. We

estimated a value of 82 for the IHF Index, and a Pfanckuch index of 47, which indicate the excellent state of this stream.

Although the forest areas surrounding the Buenaventura Reserve have been intensively depleted and replaced with pasture land (Figure 2C) (Fundación de Conservación Jocotoco N.D), the area within the reserve is close to being pristine and the stream was surrounded by native forest, as indicated by a value of 100 for the QBR index. The riparian vegetation was comprised mainly of shrubby species belonging to the Heliconiaceae and Rubiaceae families and the surrounding forest included a variety of native tree species, distinctly of trees belonging to the Cecropiaceae family.

### *Moromoro*

We sampled the Moromoro stream (Figure 3C) for 7 non-consecutive days between June 29 and July 9, 2016 and studied the populations of *H. fuscoguttata*, *H. aurora* and *H. caja* from 10h30-15h30. The Moromoro stream (3.687193°S, 79.743370° W, 865 m.a.s.l) (Figure 2C) is also part of the Arenillas watershed and passes through the small-sized town of Moromoro (Cantón Piñas, Province of El Oro) (Figure 1C), where it is used for irrigation as well for domestic purposes and it also receives waste water from the surrounding houses. The sampled section of the stream was 1m wide and 0.40m deep, with an estimated water discharge of  $25 \text{ m}^3\text{s}^{-1}$ . We measured a neutral pH of 7.03 of the stream water, as well as a standard conductivity of  $117.9 \mu\text{S cm}^{-1}$  and a temperature of  $22.3^\circ\text{C}$ . Despite being next to a small town, this stream presented a high IHF index of 68 and a Pfanckuch index of 79, which indicate a good stream stability, due to the fact that the stream had not been modified and maintained its heterogeneity. However, the riparian vegetation has been extensively modified into cropland, mainly of sugar cane plantations and to a lesser extent, banana plantations. We

estimated a value of 30 for the QBR Index, which is the lowest value compared to the other two streams and which indicates a fair quality of the riparian vegetation.

### **Design for the Demographic study**

We conducted a capture-mark-recapture (CMR) methodology to analyze the population demographics of the three species of *Hetaerina* on the three sampled rivers. We captured male and female individuals and marked consecutive numbers with a permanent marker (Faber Castell Multimark 27®) on their left forewing (Figure 4A). We recorded the identification of each individual along with the date, time, location in the river, gender and age. To record the location of the individuals, we divided all three sampled rivers into sections. The age of the individuals was classified into four categories: **Age 0** individuals did not present a well-defined wing pigmentation and presented soft hyaline wings, **Age 1** individuals presented flexible wings all the way through, **Age 2** individuals presented flexible wings from the node to the tip, and **Age 3** individuals presented hard and opaque inflexible wings (based on Plaistow & Siva-Jothy 1996). After their manipulation, the damselflies were released on the same location where they were captured (based on Hagler & Jackson 2001).

Additionally, we took digital photos of each captured individual and recorded the following morphometric characteristics: 1) body length BL (including anal appendages); 2) forewing length WL; 3) thorax length TL; 4) thorax width TW; 5) eye distance ED of males and females; and also; 6) clasper length CL, as well as 7) wing spot length WSL of males only (Figure 4B).

### *Analysis of CMR data*

We analyzed the recapture histories of the individuals belonging to the most abundant species on each location, because a greater data availability allows us to estimate demographic characteristics more accurately. We used Cormack-Jolly-Seber models (CJS) implemented in the program MARK 6.2 (Cooch & White 2007), which is based on the Akaike Information Criterion (AIC) to explain the variability in the data (White & Burnham 1999). We tested the saturated model  $\text{Phi}(g^*t) p(g^*t)$ , where  $\text{Phi}$  is the survival rate and  $p$  the recapture probability, including two groups ( $g$ = males and females) (only for the Tabuga and Moromoro populations because we did not find enough females in Buenaventura) and time dependence ( $t$ ). We calculated the goodness-of-fit (GOF) of the saturated model with the program RELEASE from within MARK. The TEST 2 is used to test the assumption of ‘equal catchability’ of marked animals, therefore it can be considered as a recapture test (White & Burnham 1999). This test was not significant for the Tabuga population ( $\chi^2=43.41$ ,  $df= 33$ ,  $p=0.1062$ ), the Buenaventura population ( $\chi^2=1.41$ ,  $df= 5$ ,  $p=0.9231$ ) or the Moromoro population ( $\chi^2=3.83$ ,  $df= 6$ ,  $p=0.7002$ ). Moreover, the TEST 3 is used to test the probability of marked animals alive on day ( $i$ ) to survive to day ( $i + 1$ ) (White & Burnham 1999). This test was not significant for the Tabuga population ( $\chi^2=26.39$ ,  $df= 38$ ,  $p=0.9221$ ), the Buenaventura population ( $\chi^2=9.69$ ,  $df=11$ ,  $p=0.5585$ ) or the Moromoro population ( $\chi^2=4.68$ ,  $df= 15$ ,  $p=0.9945$ ).

We estimated the values of  $\hat{c}$  for each population, which indicates the extra-multinomial variance of the data, by dividing the value of the deviance of the saturated model by the mean deviance obtained from the bootstrap procedure executed by MARK. We adjusted the models with the  $\hat{c}$  value and ranked each model based on the Akaike’s quasi-criterion of



information (QAIC<sub>c</sub>) (White & Burnham 1999). Additionally, we estimated the population size of the three populations using the program POPAN from within MARK.

### *Statistical Analyses*

To determine if there were significant differences between the gender of the individuals and the age they presented on their first capture, we ran a Chi-Square test for the studied populations on each location.

### **Behavioral Study**

In all three sampled locations, we recorded the behavior that the individuals of each species presented at the time of their capture. We classified the behaviors into the following activity categories: Feeding Behavior (FB), Reproductive Behavior (RB), Fighting Behavior (FiB) and Perching Behavior (PB). Additionally, we carried out 10 minute focal observations of random individuals.

To analyze the territorial behavior of *Hetaerina* damselflies, we classified them into three categories: Territorial (T), Site Fidelity (SF) and Non-Territorial (NT). The individuals that remained in the same site for more than two consecutive days but were not observed defending it, were classified as males that exhibited “Site Fidelity” and individuals that remained in the same site and were observed defending it were classified as “Territorial” (based on Córdoba-Aguilar 2007). Finally, individuals that did not remain on the same site were categorized as “Non-Territorial”.

### *Statistical Analyses*

We classified the time of our behavioral observations into 15 time categories (starting from 8h30 until 16h00 in half hour intervals) and tabulated the number of male and female individuals that exhibited a particular behavior category. Since the distribution of male and female behavioral observations was not normal on either location (Shapiro-Wilk W Tests for Tabuga  $W=0.41$ ,  $p<0.001$ ; Buenaventura  $W= 0.13$ ,  $p<0.001$ ; and KSL Test for Moromoro  $D=0.52$ ,  $p=0.0100$ ), we ran a logistic regression analysis to determine significant differences between the activity of males and females, as well as the active individuals per time interval for each location. Additionally, we ran a series of correlations between different morphological measurements of male individuals. To determine significant differences between male territorial roles and morphological characters, we ran a generalized linear regression for each morphological measurement, with the factors being territorial role and stream site.

## RESULTS

### *Hetaerina* demography

We found *Hetaerina fuscoguttata* in all three sampled locations, *H. aurora* in the Buenaventura and Moromoro streams, and *H. caja* in the Moromoro stream (Figure 5). It is important to note that *H. caja* was present in the Tabuga river but individuals were found aggregated in patches outside the sampled section of the river, therefore, this species was not included in our analysis. *H. fuscoguttata* was the most abundant species in the Tabuga river and in the Buenaventura stream, whereas *H. aurora* was the most abundant species in the Moromoro stream (Figure 5).

### *Hetaerina fuscoguttata* in the Tabuga River

The capture and recapture curves of *H. fuscoguttata* individuals in the Tabuga river show that the number of recaptured individuals increase with sampling days, while the number of captured individuals decrease as sampling days go by (Figure 6). During the demographic study, we captured a total of 97 males and 56 females, and the recapture rates of both males and females was high, being 81.44% and 67.86% respectively (Appendix 2A). Throughout all of our sampling days, we recorded a male biased sex ratio (Figure 7). Additionally, we encountered a higher percentage of Age 2 individuals, both males (51.85%) and females (49.12%), compared to the other age categories (Figure 8). Also, we did not find significant differences between the gender of the captured individuals and their age on the first capture ( $\chi^2=1.31$ ,  $df=3$ ,  $p=0.7275$ ).

The best model to explain the variability of the data of the population of *H. fuscoguttata* in the Tabuga river is  $\Phi(g)p(g)$  (Appendix 3), which indicates that both, survival rate and recapture probability, depend on the sex of the individuals. Using this model, the daily

survival rate was estimated as  $0.96\pm 0.01$  for males and  $0.93\pm 0.02$  for females. Based on these results, we calculated a longevity of 22.6 days for males and 13.03 days for females.

Additionally, the program POPAN, estimated a population size of  $60\pm 6.69$  males and  $30\pm 6.18$  females.

#### *Hetaerina fuscoguttata* in the Buenaventura stream

The capture and recapture curves of individuals of *H. fuscoguttata* in the Buenaventura stream show that in our last sampling day, we did not capture new individuals and that the number of recaptures on this date, was the highest of all sampling days (Figure 9). We captured a total of 47 males and recaptured 37 of them, indicating a male recapture rate of 78.72%. On the other hand, we captured a total of 4 females, and we did not recapture neither of them (Appendix 2B). Consequently, the sex ratio in this population was male biased throughout all of the sampling days. All four of the captured females were Age 3, whereas the majority of captured males (55.50%) were Age 2 at the time of their first capture (Figure 10). Since we did not capture enough females, we were unable to run a Chi-Square to determine differences between the gender of the individuals and the age at the time of their first capture.

We did not include the sex of the individuals in the demographic models due to the low number of encountered females. We found that the best model to explain the variability of the data of the population of *H. fuscoguttata* in the Tabuga river is  $\Phi(\cdot) p(\cdot)$  (Appendix 4), which indicates that neither survival rate nor recapture probability of the individuals depend on the time variable. Using this model, the daily survival rate for the individuals was estimated as  $0.85\pm 0.04$ , which allowed us to calculate a longevity estimate of 6.2 days. However, as an anecdotal comment, when we revisited the Buenaventura stream on October 19<sup>th</sup> 2016, over three months after our visit, we encountered a male *H. fuscoguttata* damselfly

that was marked the 27<sup>th</sup> of June 2016, and whose age at the time of its first capture was Age 2. Using POPAN, we estimated a population size of  $27 \pm 3.66$  individuals.

#### *Hetaerina aurora* in the Moromoro stream

The capture and recapture curves of individuals of *H. aurora* in the Moromoro stream indicate that as the sampling days increase, the number of recaptured individuals increase as well. The number of captured individuals tend to decrease with the sampling days, but there is a slight increase of captured individuals on the last day of sampling (Figure 11). We captured a total of 43 males and 41 females of *H. aurora* in the Moromoro stream, and the recapture indices for both genders was similar, being 58.14% for males and 46.34% for females (Appendix 2C). On most sampling days, we found a male biased sex ratio. However, it is important to note that on two sampling days, we encountered more females than males (Figure 12). Overall, the predominant age of females of their first capture was Age 1 (47% of all captured females), while the predominant age for males was Age 0 (34% of all captured males) (Figure 13). Additionally, we found significant differences between the gender of the captured individuals and the age on their first capture ( $\chi^2 = 14.63$ ,  $df = 3$ ,  $p = 0.0022$ ).

The best model to explain the variability of the data of the population of *H. aurora* in the Moromoro stream is  $\text{Phi}(\cdot) p(g)$  (Appendix 5), which indicates that the survival rate of individuals is independent from gender and time, whereas the recapture probability depends on the gender of the individuals. Using this model, the daily survival rate of the individuals of this population was estimated as  $0.90 \pm 0.02$ , which indicates that the estimated longevity of the individuals of this population is 9.84 days. Additionally, using POPAN, we estimated a population size of  $36 \pm 11.57$  males and  $13 \pm 3.89$  females.

## ***Hetaerina* behavior**

### *Time intervals and damselfly activity*

We found that most individuals of *H. fuscoguttata* in the Tabuga river remained perched as opposed to other activities such as fighting, flying, mating or feeding (Figure 14). The mean number of active individuals was higher between time intervals 3 and 4, which correspond to 9h30 through 10h30. However, we found that the number of active individuals of *H. fuscoguttata* was not significantly different between males and females ( $\chi^2=1.77$ ,  $df=1$ ,  $p=0.1829$ ) and neither between time intervals ( $\chi^2=6.75$ ,  $df=6$ ,  $p=0.3442$ ).

In the Buenaventura stream, the number of active individuals was significantly different between the two species of *Hetaerina* present (*H. fuscoguttata* and *H. aurora*) ( $\chi^2= 23.98$ ,  $df=1$ ,  $p<0.0001$ ), *H. aurora* being more active than *H. fuscoguttata*. Additionally, the number of active individuals was also significantly different between genders ( $\chi^2=31.74$ ,  $df=1$ ,  $p<0.0001$ ), where males were more active than females. However, the number of active individuals of both species was not significantly different between time intervals ( $\chi^2= 7.70$ ,  $df=10$ ,  $p=0.6580$ ) (Figure 15).

In the Moromoro stream, the number of active individuals was significantly different between the three species of *Hetaerina* present (*H. fuscoguttata*, *H. aurora*, *H. caja*) ( $\chi^2=33.62$ ,  $df=2$ ,  $p<0.0001$ ), where *H. aurora* was the most active species. The number of active individuals was also significantly different between genders ( $\chi^2=20.63$ ,  $df=1$ ,  $p<0.0001$ ), where females were more active than males. However, the number of active individuals was not significantly different between time intervals ( $\chi^2=10.05$ ,  $df= 15$ ,  $p=0.8166$ ) (Figure 16).

### *Focal observations*

Our focal observations indicate that *H. fuscoguttata* individuals change their perching position an average of 1.2 times in a 10-minute time interval, while the individuals of the same species in Moromoro change their position an average of 0.5 times (Table 1). While we carried out the focal observations, we did not notice many individuals of *H. fuscoguttata* feeding, flying nor fighting in the Buenaventura and Moromoro streams. Also, the mean values for the frequencies of the activities exhibited by *H. aurora* in the Moromoro stream are close to zero, due to the fact that most individuals remained perched in a given spot throughout the duration of the 10 minute observations.

### *Reproductive behavior*

During our sampling period in the Tabuga river, we recorded one copulation attempt of *H. fuscoguttata*, where the male forced the female to engage in tandem but the female seemed unable to bend her abdomen enough to copulate. After five minutes, the female flew away from the male. During this season, we also recorded one oviposition, where the male grabbed the female, and in tandem, flew above the river. The oviposition consisted on the female repeatedly dipping her abdomen in the water until she was let go by the male. Additionally, we observed one copulation of *H. aurora* in the Moromoro stream. The male forced the female to engage in tandem, then copulated for 30 seconds and still in tandem, the female oviposited for 20 seconds in the water. Afterwards, the female flew erratically away from the area where she presumably deposited the eggs. Additionally, we observed one copulation of *H. caja* in the Moromoro stream. The male grabbed the female while she was flying and in tandem, flew over the stream for 25 seconds until perching over a leaf located 0.7m over the water. The copulation lasted for 3.20 minutes and the pair flew in tandem over the water. We didn't observe the oviposition but we assume the female oviposited alone since a few seconds

after the copulation, we observed the same male fighting against another one on the same location where we recorded the copulation.

### Aerial contests

Males of the three studied *Hetaerina* species exhibited two distinct types flights during aerial contests. We classified the first type of flight as “continued circles”, which consisted of males chasing each other rapidly and smoothly in a circled pattern over the river and in front of their territories. The fight would start when one male intruded another male’s territory and they would chase the other, reverting the roles of the chased individual and the chaser (Figure 17).

The second type of flight was classified as “non-continuous flight” because it involved chases between two males, where their flight was not smooth and resembled fluttering movements (Figure 18). The aerial contests that involved this type of flight did not occur in a circled pattern, but rather horizontally between an area no greater than one meter above the water. First, one male would chase another one and then the roles would reverse and the direction of the flights would change as well.

Additionally, we observed that most of the aerial contests between males of the three species of *Hetaerina* involved a combination of both types of flights. They generally initiated with the continued circles flight and was followed by the non-continuous flight. In all of these aerial contests, it seemed as if both males mimicked each other’s flight movements.

We noticed that the aerial contests between *H. aurora* males differed from those of *H. fuscoguttata*. The *H. aurora* fights involved a non-continuous flight and both males would



chase each other a few centimeters above the river, abruptly ascend over two meters above the water and descend again (Figure 19). This pattern was repeated until one male was displaced from its perching site or when both males returned to their perching site.

Although aerial contests were primarily intraspecific, we recorded interspecific fights as well. In the Buenaventura stream, we observed 19 consecutive fights between a *H. fuscoguttata* male damselfly and a *H. aurora* male damselfly. These fights consisted of non-continuous flights and occurred  $0.96 \pm 0.04$  meters above the stream, in front of both individual's perching sites and had a mean duration of  $0.74 \pm 0.59$  seconds. 18 out of the 19 fights were initiated by the *H. aurora* individual, where the male attempted to displace the other *H. fuscoguttata* male. Another *H. fuscoguttata* male entered the fight and the three individuals engaged in an aerial contest, one meter above the stream. After each encounter, the individuals returned to the same area where they were initially perched.

#### Territorial roles and morphological characters

We ran a series of correlations between the morphological characters of male damselflies of the three species of *Hetaerina*. Although most of them were not significant, we found a positive correlation between Body Length and Wing Length ( $R=0.457$ ,  $p<0.0001$ ), as well as Body Length and Clasper Length ( $R=0.568$ ,  $p<0.0001$ ) (Appendix 6).

We identified the three territorial behavior categories (Territorial, Site Fidelity and Non-Territorial) in the male individuals of the three studied species of *Hetaerina*, and in all three sampled streams. Overall, we did not find significant differences between the morphological characters we measured and the males' territorial role. Specifically, we found that the Body Length of males was significantly different between the Buenaventura and Moromoro

streams ( $\chi^2=130.80$ ,  $df= 2$ ,  $p=0.0001$ ), where the Buenaventura individuals were larger than the ones in Moromoro and Tabuga. However, this characteristic was not different between territorial roles of the three studied populations ( $\chi^2=0.38$ ,  $df= 2$ ,  $p=0.8270$ ). We found that male Wing Length was significantly different between stream sites ( $\chi^2=12.75$ ,  $df= 2$ ,  $p=0.0017$ ), where the Tabuga individuals presented a smaller wing length than the Buenaventura and Moromoro individuals. However, this characteristic was not significantly different between territorial roles ( $\chi^2=1.91$ ,  $df= 2$ ,  $p=0.3848$ ). We also found that the red Wing Spot Length of males was significantly different between stream sites ( $\chi^2=17.31$ ,  $df= 2$ ,  $p=0.0002$ ), with the Moromoro individuals presenting the smaller wing spot length; but this characteristic was not different between territorial roles ( $\chi^2=0.06$ ,  $df= 2$ ,  $p=0.9729$ ). The Thorax Length of males was significantly different between streams ( $\chi^2=7.34$ ,  $df= 2$ ,  $p=0.0255$ ), with the Moromoro individuals presenting a smaller thorax length; but this characteristic was not significantly different between roles ( $\chi^2=0.66$ ,  $df= 2$ ,  $p=0.7176$ ). We did not find differences between Thorax Width of males between stream sites ( $\chi^2=0.05$ ,  $df= 2$ ,  $p=0.9742$ ) nor territorial role ( $\chi^2=1.20$ ,  $df= 2$ ,  $p=0.5478$ ). The Clasper Length of males was different between stream sites ( $\chi^2=92.92$ ,  $df= 2$ ,  $p=0.0001$ ), with the Tabuga individuals presenting smaller claspers than the individuals in Buenaventura and Moromoro. However, this characteristic was not significantly different between territorial roles ( $\chi^2=3.77$ ,  $df= 2$ ,  $p=0.1519$ ). Lastly, we found that the Eye Distance of males was significantly different between stream sites ( $\chi^2=14.64$ ,  $df= 2$ ,  $p=0.0007$ ), with the Tabuga individuals presenting a larger distance, but this characteristic was not significantly different between territorial roles ( $\chi^2=0.07$ ,  $df= 2$ ,  $p=0.9642$ ). In summary, there was not a single morphological character that was different between the territorial roles we identified.

## DISCUSSION

Currently, there are seven described species of *Hetaerina* that have been documented in Ecuador (Garrison 1990). Here, we present the first ecological and behavioral study of three species of this genus in three different riparian lowland ecosystems in Ecuador. We successfully investigated the demography of the three species: *Hetaerina fuscoguttata*, *H. aurora* and *H. caja*, and described both male and female sexual behavior as well as male territorial behavior. Here, we discuss the study's main findings and implications, and propose some ideas for future studies of this genus.

Our demographic study showed that *H. fuscoguttata* was the most abundant species in the Tabuga river and Buenaventura stream, whereas *H. aurora* was the most abundant species in the Moromoro river. Although abundances varied, we found *H. fuscoguttata* in all three sampled stream sites. In all studied populations, we captured more males than females, which resulted generally in male biased sex ratios throughout our sampling dates. The sex ratio of adult damselfly populations tends to be biased due to the behavioral and phenotypic differences between males and females (Corbet & Hoess 1998). In zygopteran populations, males are generally more frequent than females at time of emergence (Corbet & Hoess 1998), yet, this bias is not large enough to explain the sex ratio of adult populations (reviewed by Cordero-Rivera & Stoks in Córdoba-Aguilar 2008). This information of the *Hetaerina* genus is scarce, therefore, we are not certain about the sex ratio at time of emergence of the three species we studied. The population of *H. aurora* was the only one that presented a similar number of males and females, including two sampling days with a female biased sex ratio. We suspect that the number of females might be overestimated due to the similarities between female specimens of the *Hetaerina* genus, since we found all three species in this location (Garrison 1990).

We also found higher recapture rates for males than for females in all studied populations, which could also be explained by behavioral differences between sexes (Garrison & Hafernik 1981). Because females of the three species presented a more cryptic coloration than males, they were harder to capture. This was more evident in the population of *H. fuscoguttata* in the Buenaventura stream, where the complexity of the forest allowed females to occupy higher forest strata, compared to the females of the same species in the Tabuga river and females of *H. aurora* in Moromoro, where they would perch in medium-sized herbaceous riparian vegetation. Interestingly, females of *H. aurora* in the Moromoro stream seemed to perch at a higher level in areas where large trees were available, as opposed to the sugar cane plants, which did not exceed 2 meters in height. This might indicate that females prefer higher perching sites than males, which were generally observed perching no more than 1.5 meters above the streams.

By selecting the best models to explain the variability of our data, we estimated a higher longevity for males of *H. fuscoguttata* in the Tabuga river than females. This population also presented the highest longevity values, compared to the population of *H. fuscoguttata* in the Buenaventura stream and *H. aurora* in the Moromoro stream. Taking into account that we sampled the Tabuga river for more days than the Buenaventura and Moromoro streams, we can infer that the estimations could be more trustworthy as sampling days increase. It has been suggested that CMR studies of calopterygid populations should last a minimum of 45 days for reliable longevity estimates (reviewed by Cordero-Rivera & Stoks in Córdoba-Aguilar 2008). However, due to time constraints, we were not able to sample all three locations for that amount of time. Despite this, we found that all longevity estimates are higher than the average of 7.6 days estimated for zygopterans (Corbet 1999).

Our demographic results indicate that although the number of females might be overestimated or underestimated, the male biased sex ratios we recorded, might explain the territorial behavior of males of the three *Hetaerina* species. It has been described that *Hetaerina* males defend territories to gain access to females, since lek mating systems in this genus have been reported for several species (Grether 1996b, Córdoba-Aguilar et al. 2008). Therefore, males defend their territory to copulate and search for oviposition sites elsewhere after mating (Grether 1996b). Unlike other genera of the Calopterygidae family, there is no pre-copulatory courtship in *Hetaerina* damselflies (reviewed by Córdoba-Aguilar and Cordero-Rivera 2005). We observed one *H. fuscoguttata* male grabbing a female while in the air without a previous courtship. However, we did not record enough data about *Hetaerina* mating behavior during our study, despite the fact that our sampling time surpassed two months in the Manabí and El Oro Provinces altogether. Additionally, during this time, we observed only one copulation of *H. aurora* and one copulation of *H. caja* in the Moromoro stream, as well as a copulation attempt of *H. fuscoguttata* in the Tabuga river. Several authors have reported that *Hetaerina* females deposit their eggs by submerging underwater while the male adopts a guarding posture above the submergence site (e.g. Johnson 1961, Bick & Sulzbach 1966, Grether 1996a, Eberhard 1986). However, during our study, we observed a different type of oviposition of *H. fuscoguttata* in the Tabuga river, which consisted of the female dipping her abdomen repeatedly in the water while in tandem with the male. Nevertheless, these contrasting results do not allow us to generalize about the mating nor oviposition behavior of any of the studied *Hetaerina* species.

As for all territorial calopterygid damselflies, we recorded several aerial contests between territorial males of the three species of *Hetaerina* as a way to defend their territories. As opposed to other species of this genus, we did not observe one way chases between

*Hetaerina* males, as recorded for *H. americana* (Grether 1996b). We found that every aerial contest involved two way chases and mimicry in terms of flight type and direction between the contenders. We identified three types of aerial contests that were common to *H. fuscoguttata*, *H. aurora* and *H. caja*, as well as an aerial contest specific to *H. aurora* males. Additionally, we observed interspecific fights in the Buenaventura and Moromoro streams. It has been reported that male *Hetaerina* damselflies with similar coloration patterns are more likely to engage in interspecific aerial contests than damselflies that exhibit different coloration patterns (Anderson & Grether 2011).

It has been proposed that territorial males are usually larger than non-territorial males (Convey 1989). However, there has not been a consensus between studies of species of the *Hetaerina* genus regarding males' territorial role and their morphological measurements (reviewed by Suhonen et al.2008). For example, in a study of *H. miniata*, territorial males tended to win aerial contests, despite the fact that their body sizes were not different from non-territorial males (Lefevre & Muehter 2010). Also, the body sizes of territorial and non-territorial males of *H. americana* were not significantly different from each other. However, larger territorial males exhibited a larger proportion of fat reserves, which are useful for areal fights in order to defend their territory. In general, a larger body size is advantageous for territorial males because it can increase their fight rates, their fighting abilities and wing pigmentation (Serrano-Meneses et al. 2007). For example, there is a positive correlation between wing spot characters and territory tenure in *H. americana* (Grether 1996b).

However, we did not find significant differences between the territorial roles of males and morphological characteristics such as body length, thorax width, thorax length, eye distance, wing spot length, wing length and clasper length. This could be attributed to the way in which we classified males into territorial roles. We included the category of "Site Fidelity" to

those males who were observed on the same location for more than 2 consecutive days but who were not observed defending their territory. This classification might be problematic because aerial contests might be related to environmental factors, such as solar radiation. Additionally, it has been reported that calopterygid males might switch between territorial roles (Raihani et al. 2008). For example, in Lefevre & Muehter (2010), wandering males of *Hetaerina miniata* occupied the territories of owner males after their removal, indicating that they were not able to secure a territory and therefore, adopted a satellite behavior instead (Lefevre & Muehter 2010).

Despite being conspicuous on many stream ecosystems in Ecuador, the *Hetaerina* genus has not been extensively studied like it has been in other neo-tropical neighboring countries. Still, there are many questions related to the reproductive activity of the studied damselflies, since the data we have collected is scarce, as opposed to other *Hetaerina* studies in the American continent. Future studies should attempt to determine the sex ratio of these species at the time of emergence, as well as female behavior, and explore the possibility that these females might be territorial as well.

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## FIGURES

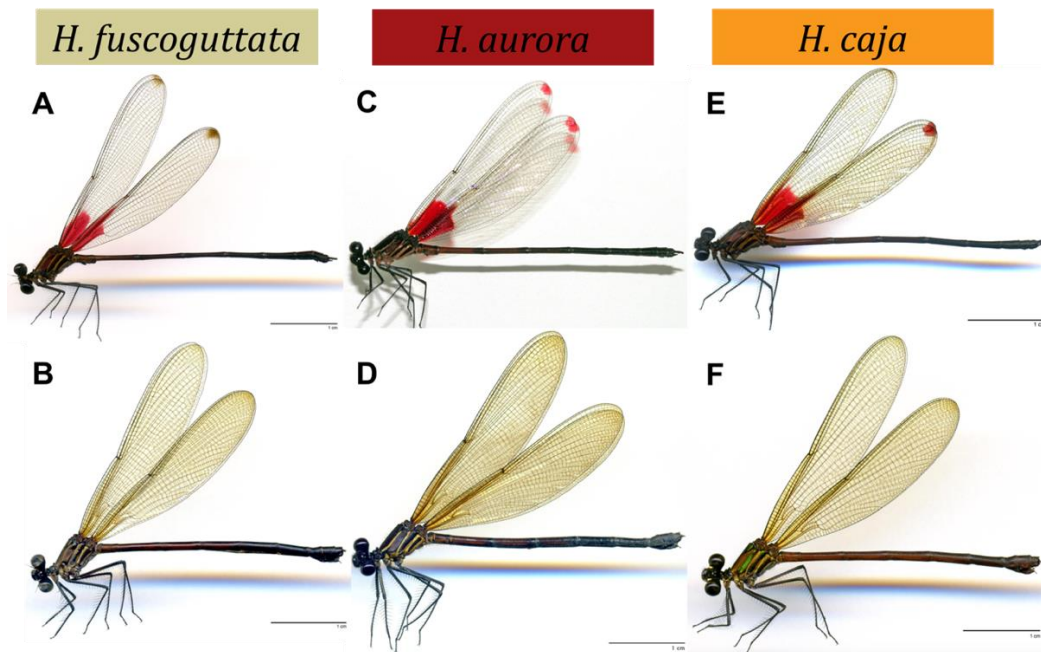
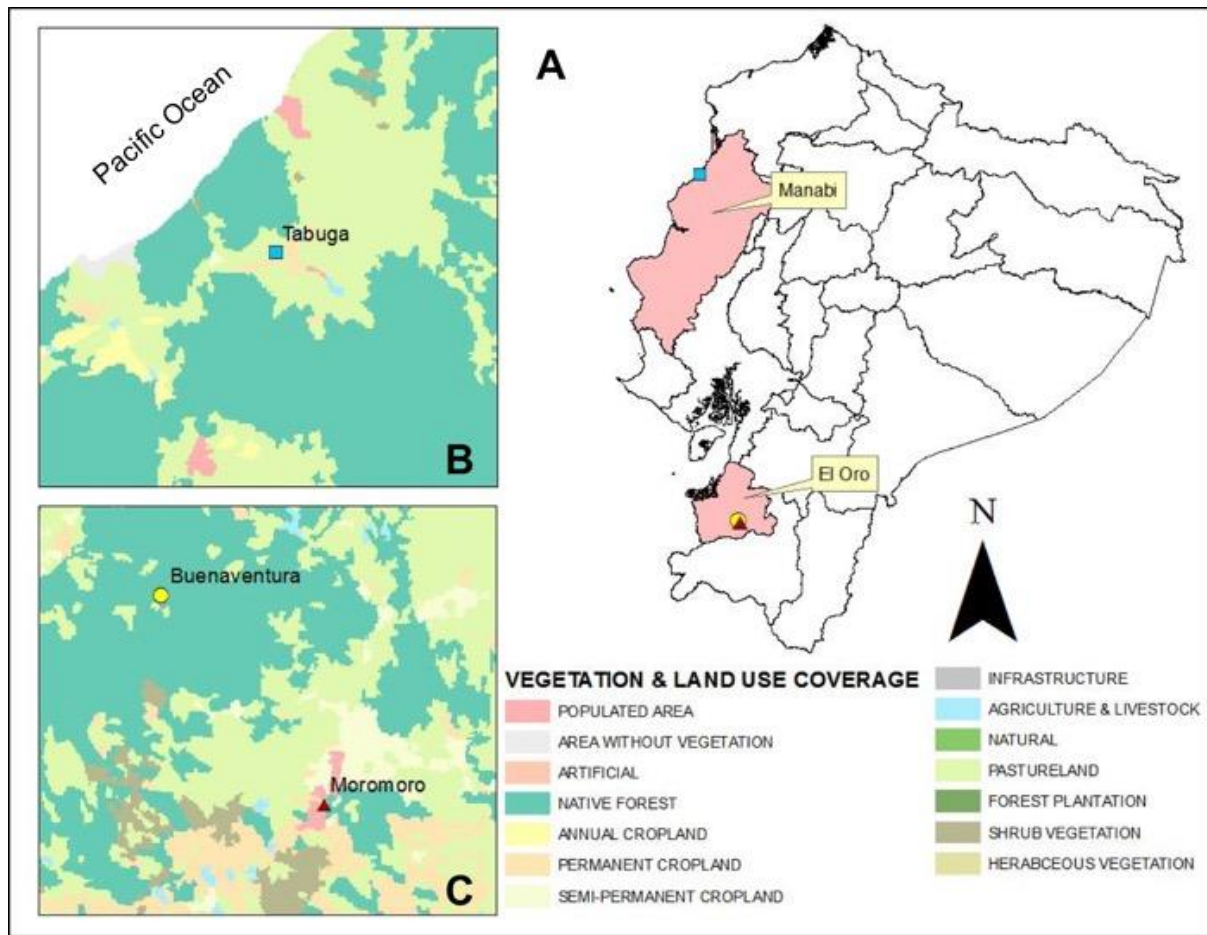
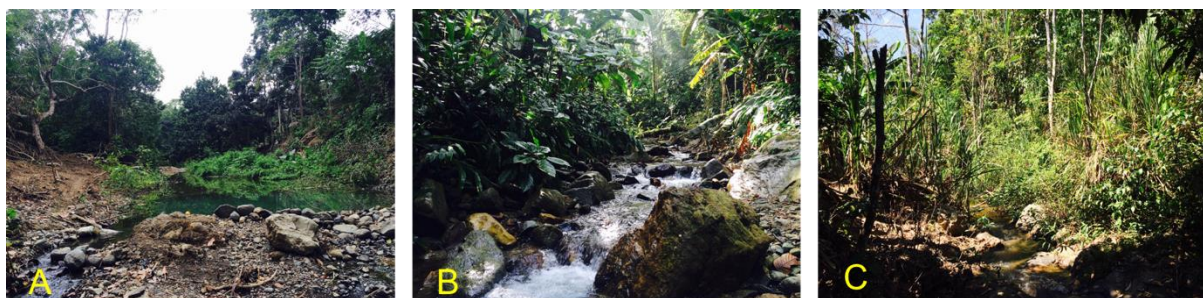


Figure 1. Male and female specimens of: **1A, B** *Hetaerina fuscoguttata*; **1C, D** *H. aurora*; **1E, F** *H. caja*. Images were obtained from the Electronic Field Guide of Dragonflies and Damselflies (Odonata) of Ecuador (Source: Haber & Wagner 2014).



*Figure 2.* Map of the three sampled locations within their respective province in Western Ecuador: **2A)** Political map of Ecuador highlighting the provinces of Manabí and El Oro; **2B)** Vegetation and land use coverage map of the Tabuga area in the province of Manabí; **2C)** Vegetation and land use coverage map of the Buenaventura and Moromoro areas in the province of El Oro. This map was developed using images from Ministerio de Ambiente del Ecuador (SUIA) and stream site coordinates.



*Figure 3.* A view of the three sampled stream ecosystems. **3A)** Tabuga river, Province of Manabí; **3B)** Buenaventura stream, Province of El Oro; **3C)** Moromoro stream, Province of El Oro.



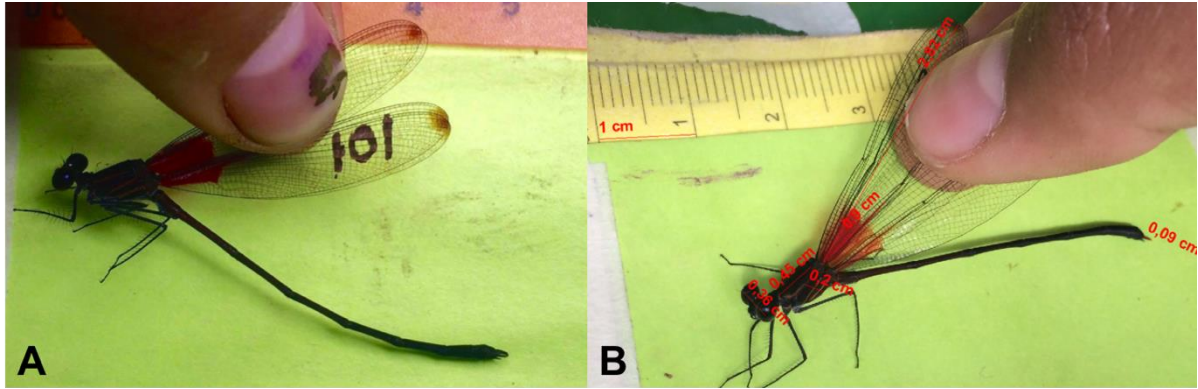


Figure 4. Specimens of *Hetaerina* spp. in which is shown **4A**) the label that we used in the hind wing to identify each individual; **4B**) detail of each measurement done in each individual (body length BL, forewing length WL, thorax length TL, thorax width TW, eye distance ED of males and females, and clasper length CL and wing spot length WSL for males only).

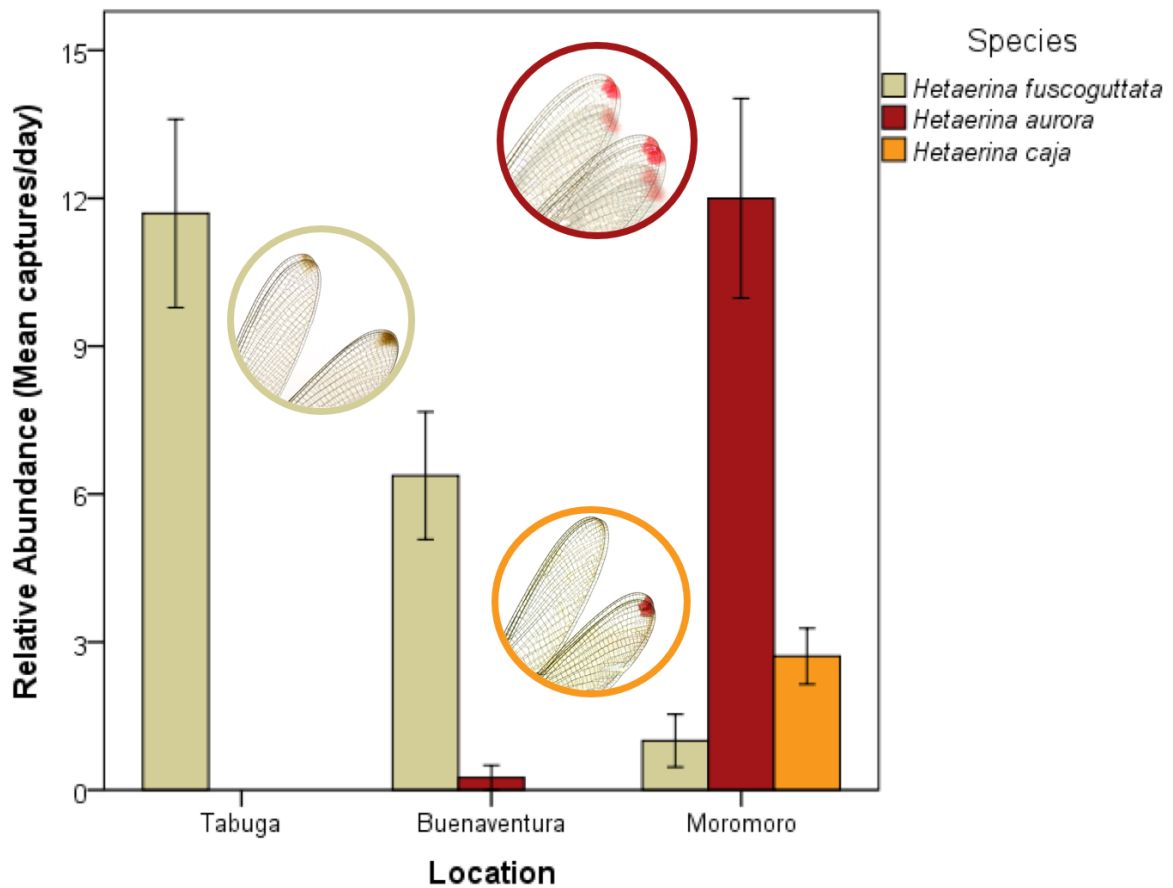


Figure 5. Relative abundance values calculated as the mean number of captures per day of *H. fuscoguttata*, *H. aurora* and *H. caja* in the Tabuga, Buenaventura and Moromoro streams.

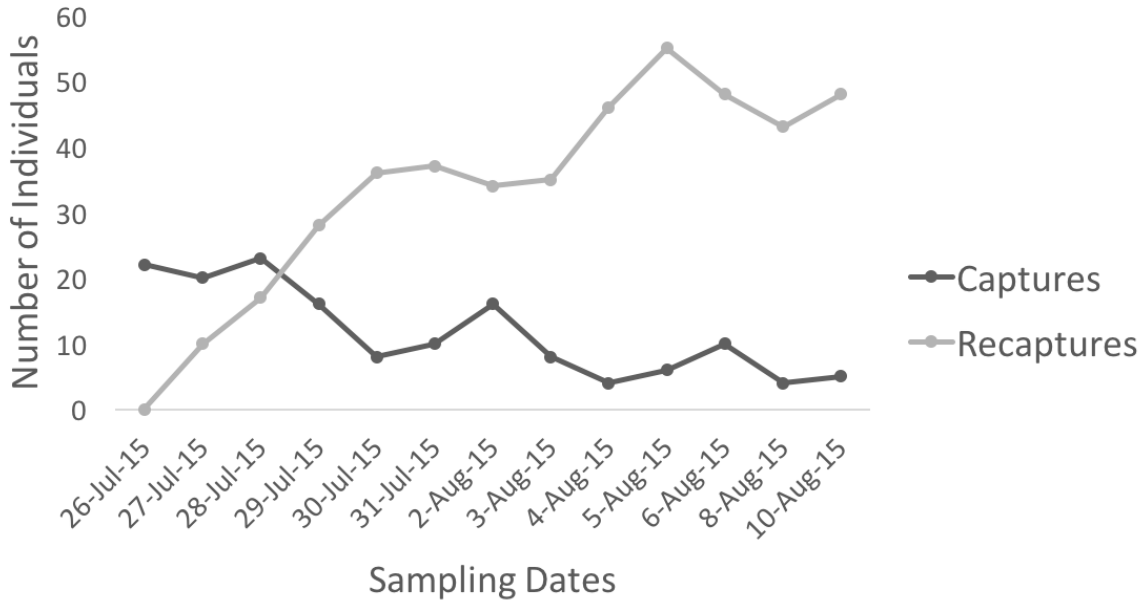


Figure 6. Number of captured (black) and recaptured (gray) individuals of *H. fuscoguttata* through time in the Tabuga River, Province of Manabí, Ecuador

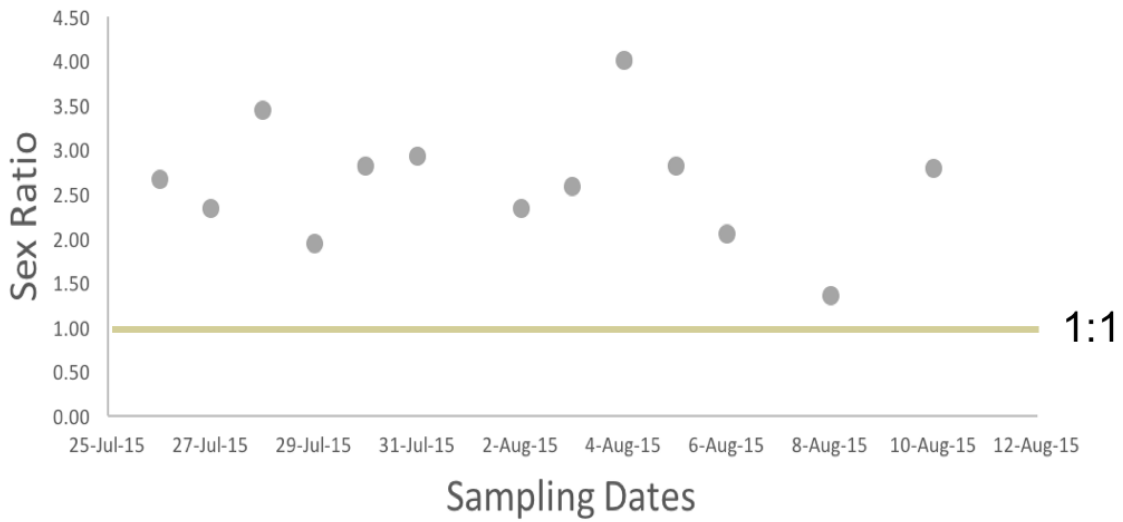


Figure 7. Daily sex ratio (males: females [M:F]) of captured and recaptured individuals of *H. fuscoguttata* in the Tabuga River, Province of Manabí, Ecuador.



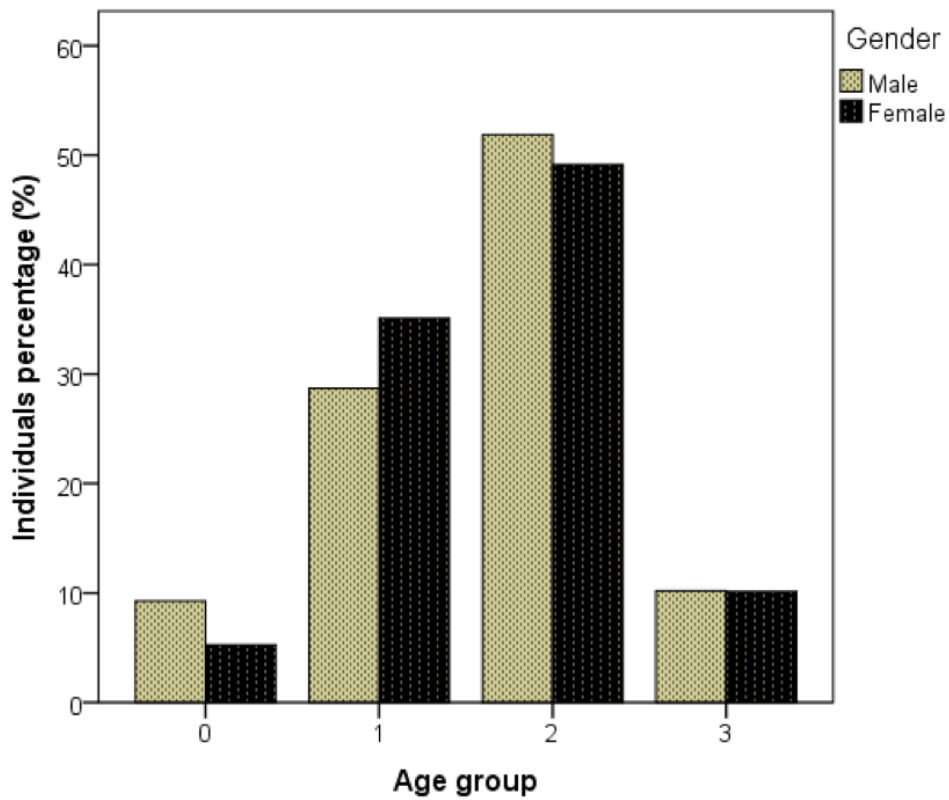


Figure 8. Total percentage of *H. fuscoguttata* males and females and the age category of their first capture in the Tabuga River, Province of Manabí, Ecuador.

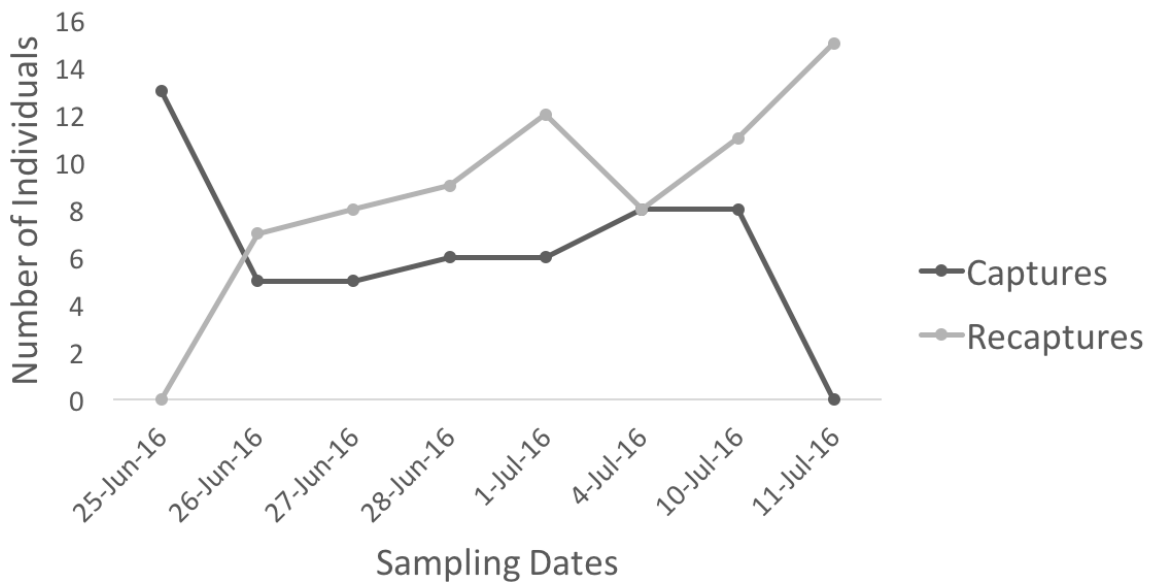


Figure 9. Number of captured (black) and recaptured (grey) individuals of *H. fuscoguttata* through time in the Buenaventura stream, Province of El Oro, Ecuador.

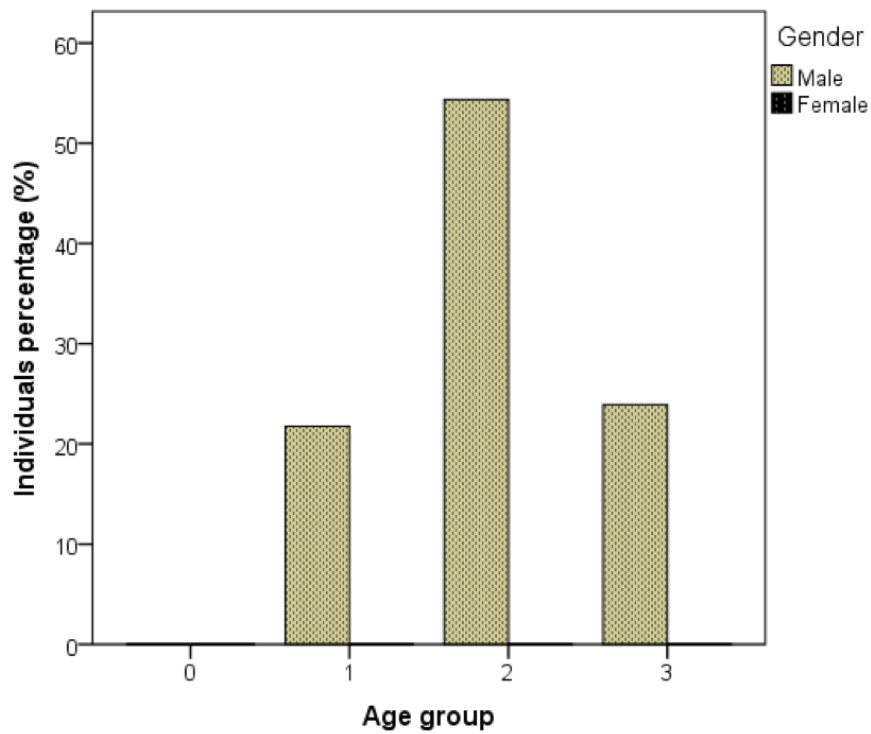


Figure 10. Total percentage of *H. fuscoguttata* males and females and the age category of their first capture in the Buenaventura stream, Province of El Oro, Ecuador.

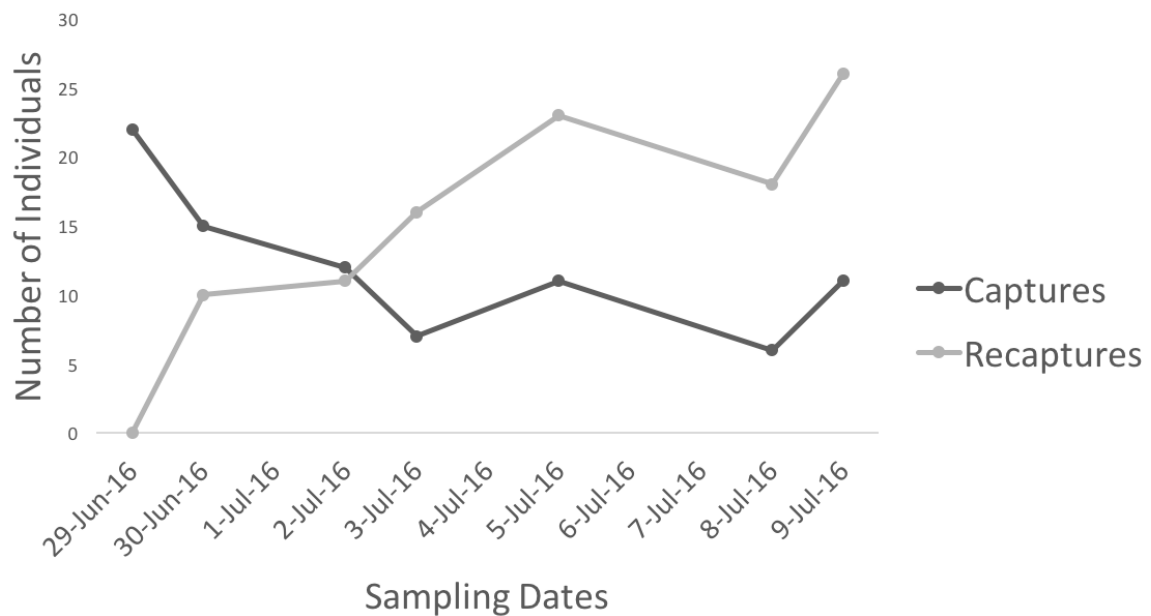


Figure 11. Number of captured (black) and recaptured (gray) individuals of *H. aurora* in the Moromoro stream, Province of El Oro, Ecuador.

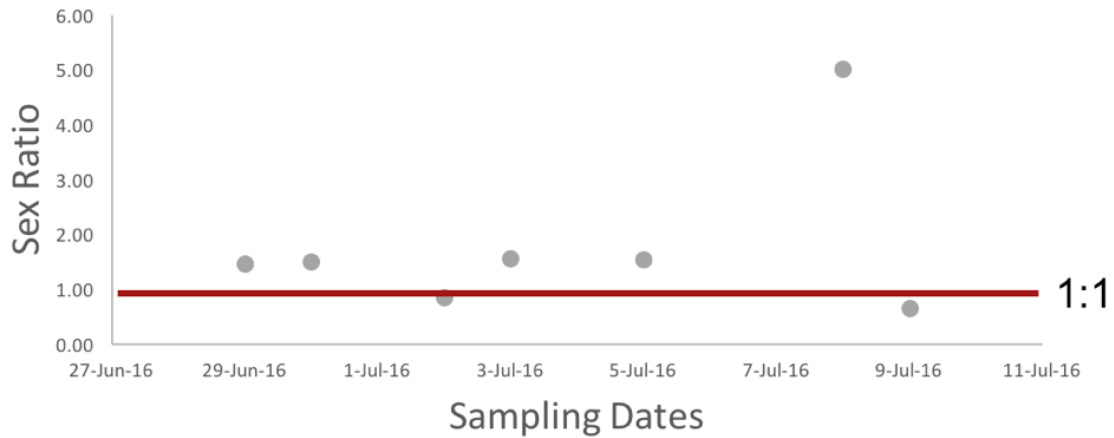


Figure 12. Daily sex ratio (males: females [M:F]) of captured and recaptured individuals of *H. aurora* in the Moromoro stream, Province of El Oro, Ecuador.

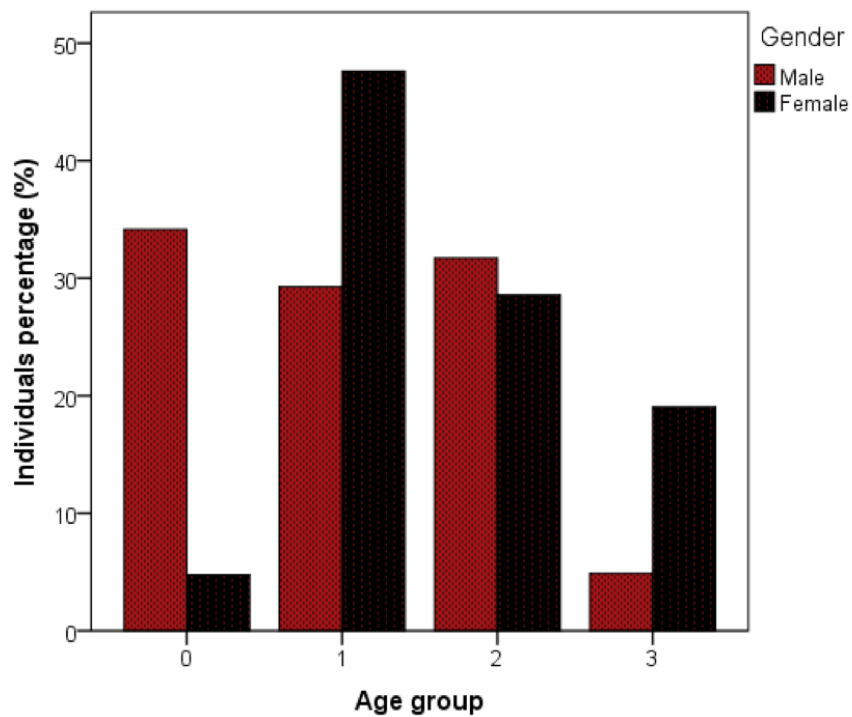


Figure 13. Total percentage of males and females of *H. aurora* and the age category of their first capture in the Moromoro stream, Province of El Oro, Ecuador.

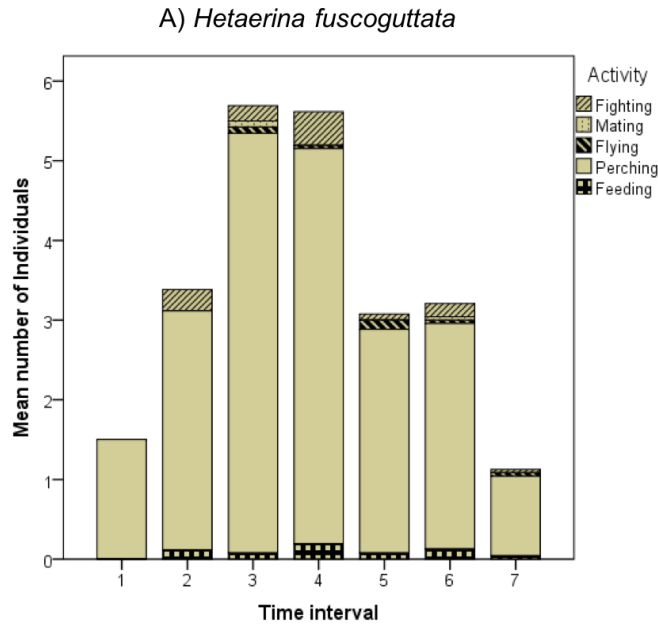


Figure 14. Mean number of *H. fuscoguttata* individuals according to their recorded activity on each time interval in the Tabuga river, Province of Manabí, Ecuador.

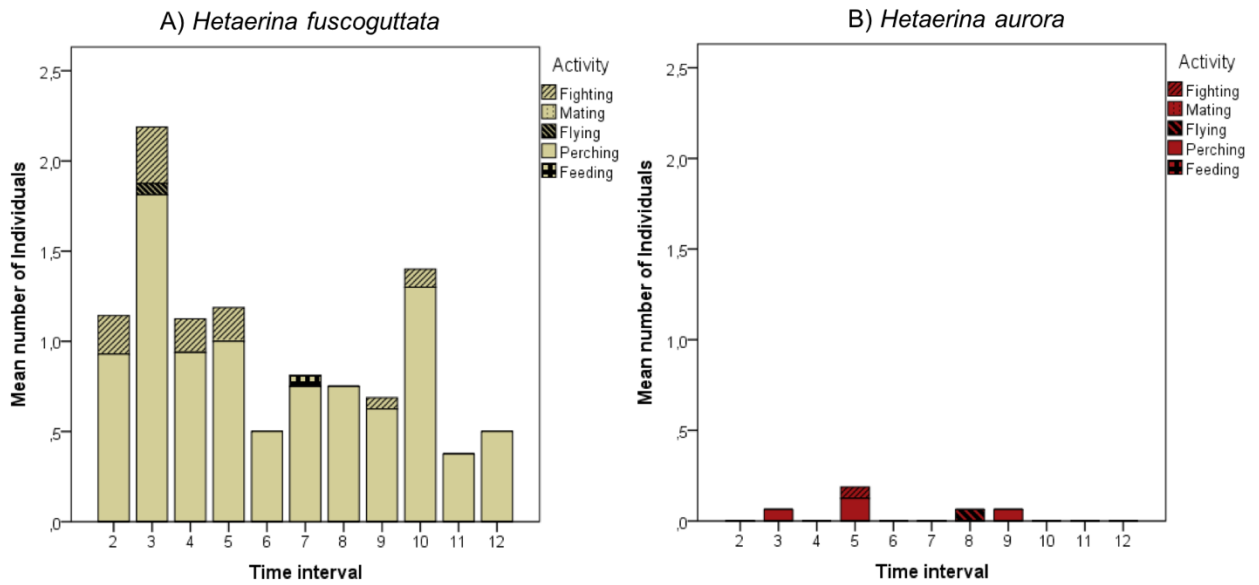


Figure 15. Number of *H. fuscoguttata* and *H. aurora* individuals presenting each observed activity in the Buenaventura stream, Province of El Oro, Ecuador.

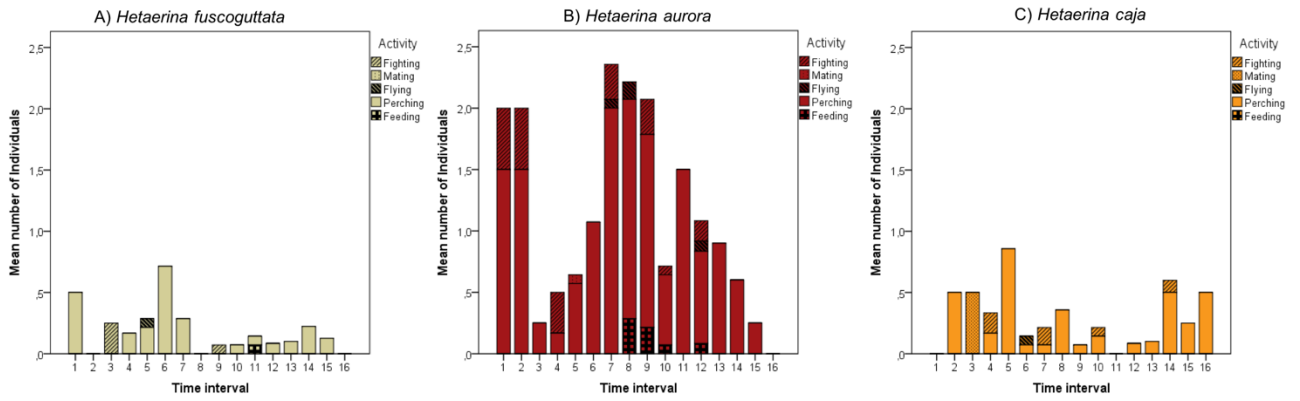


Figure 16. Number of *H. fuscoguttata*, *H. aurora* and *H. caja* individuals presenting each observed activity in the Moromoro stream, Province of El Oro, Ecuador.

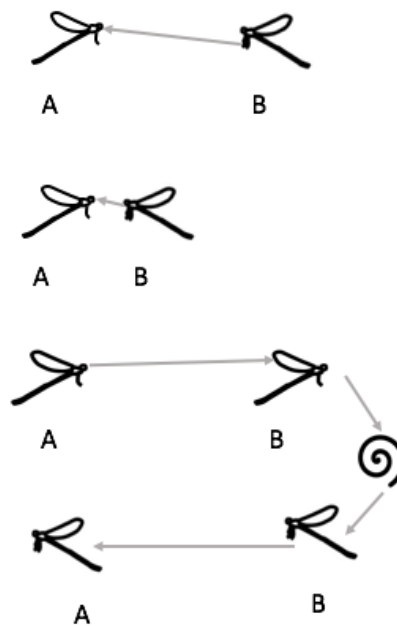
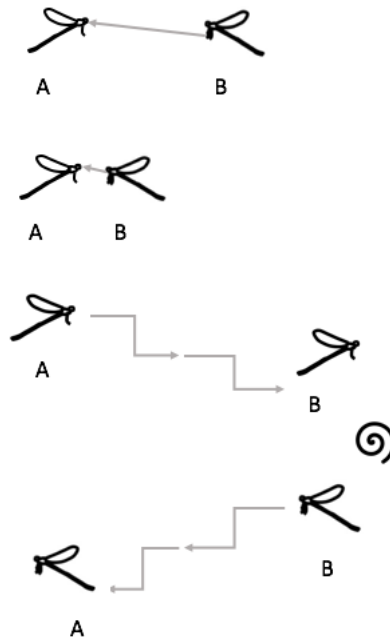
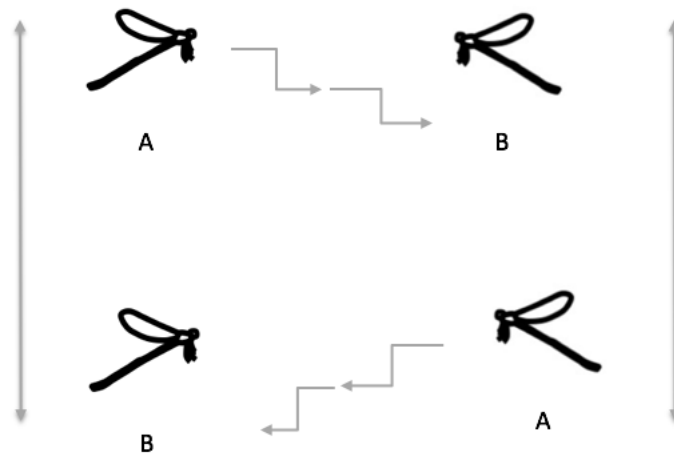


Figure 17. Representation of “continued circles” flight. The type of flight is continuous and the chases occur in a circled pattern. The spiral represents a switch between the male who is chasing and the male who is being chased, as well as a change in the direction of the circle.



*Figure 18.* Representation of “non-continuous flight”. This type of flight is not smooth. The spiral represents a switch between the male who is chasing and the male who is being chased, as well as a change in the direction of both males.



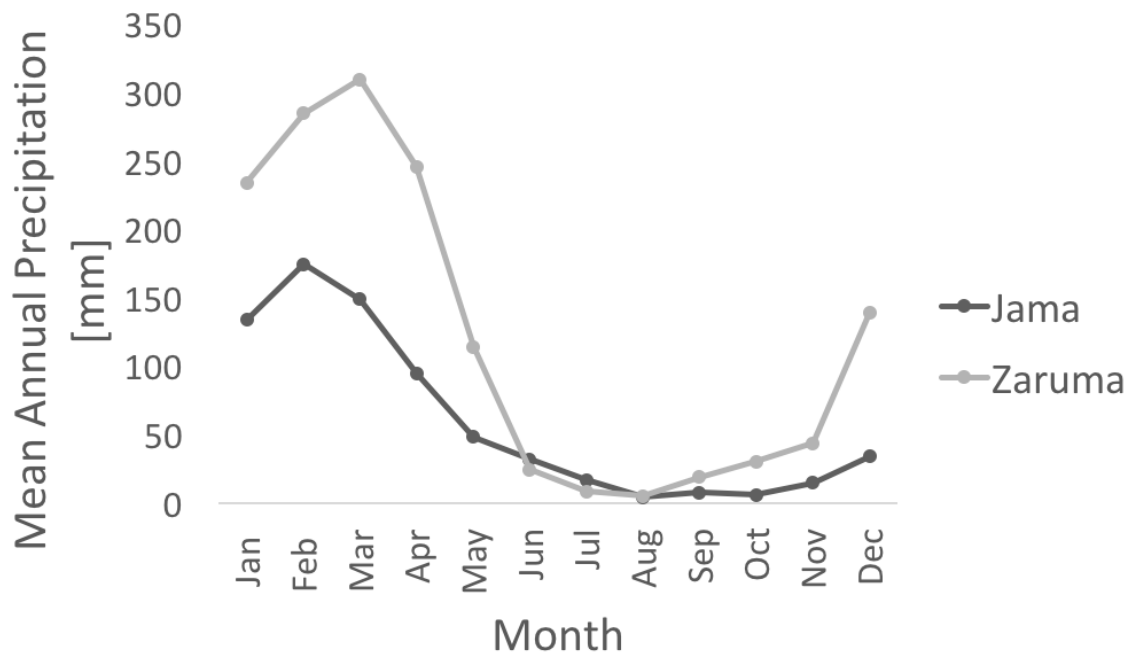
*Figure 19.* Areal contest exhibited by males of *H. aurora*. This type of flight is non-continuous and it consists of both males chasing each other a few centimeters above the stream and abruptly flying over two meters above the water.

## TABLES

Table 1. Mean values for the frequencies of each activity exhibited by *H. fuscoguttata* and *H. aurora* in the Buenaventura and Moromoro streams, Province of El Oro, Ecuador.

	<b>Position Change</b>	<b>Feeding</b>	<b>Flying</b>	<b>Fighting</b>
<i>H. fuscoguttata</i>				
<b>Buenaventura</b>	1.2±1.16	0.46±1.08	0.26±0.57	0
<b>Moromoro</b>	0.5±0.73	0.71±2.05	0	0.21±0.41
<i>H. aurora</i>				
<b>Moromoro</b>	0.41±0.65	0.8±1.52	0.09±0.41	0.14±0.34

## APPENDICES



Appendix 1. Mean annual precipitation values for each month of the year belonging to the INAMHI meteorological stations located in the city of Jama in the province of Manabí (data from 1963 to 2014) and the city of Zaruma in the province of El Oro (data from 1931 to 2015).

Appendix 2. Recapture indices of the populations of *H. fuscoguttata* in the Tabuga river (Province of Manabí) and Buenaventura stream (Province of El Oro), and the population of *H. aurora* in the Moromoro stream (Province of El Oro).

<b>Tabuga river</b>			
<b>A) <i>H. fuscoguttata</i></b>			
	<b>Captures</b>	<b>Recaptures</b>	<b>% Recaptures</b>
<b>Male</b>	97	79	81.44
<b>Female</b>	56	38	67.86
<b>Total</b>	153	117	76.47
<b>Buenaventura stream</b>			
<b>B) <i>H. fuscoguttata</i></b>			
	<b>Captures</b>	<b>Recaptures</b>	<b>% Recaptures</b>
<b>Male</b>	47	37	78.72
<b>Female</b>	4	0	0
<b>Total</b>	51	37	78.72
<b>Moromoro stream</b>			
<b>C) <i>H. aurora</i></b>			
	<b>Captures</b>	<b>Recaptures</b>	<b>% Recaptures</b>
<b>Male</b>	43	25	58.14
<b>Female</b>	41	19	46.34
<b>Total</b>	84	44	52.38



Appendix 3. Model selection for *H. fuscoguttata* in the Tabuga river, Province of Manabí, Ecuador.

<b>Model</b>	<b>QAIC<sub>c</sub></b>	<b>Delta QAIC<sub>c</sub></b>	<b>AIC<sub>c</sub> Weights</b>	<b>Model Likelihood</b>	<b>Num. Par.</b>	<b>QDeviance</b>
{Phi(g) p(g) PIM}	1380.7327	0	0.43744	1	4	838.8111
{Phi(.) p(g) PIM}	1381.3793	0.6466	0.3166	0.7238	3	841.4879
{Phi(g) p(.) PIM}	1382.3553	1.6226	0.19435	0.4443	3	842.4640
{Phi(.) p(.) PIM}	1385.2776	4.5449	0.04508	0.1031	2	847.4088
{Phi(t) p(g) PIM}	1389.7948	9.0621	0.00471	0.0108	14	827.1409
{Phi(g) p(t) PIM}	1392.8632	12.1305	0.00102	0.0023	14	830.2092
{Phi(t) p(.) PIM}	1393.9786	13.2459	0.00058	0.0013	13	833.4337
{Phi(.) p(t) PIM}	1395.9342	15.2015	0.00022	0.0005	13	835.3893
{Phi(g*t) p(g) PIM}	1404.9275	24.1948	0	0	26	816.3175
{Phi(t) p(t) PIM}	1405.5143	24.7816	0	0	23	823.5076
{Phi(g*t) p(.) PIM}	1405.8655	25.1328	0	0	25	819.4653
{Phi(g) p(g*t) PIM}	1406.0199	25.2872	0	0	26	817.4099
{Phi(.) p(g*t) PIM}	1406.4563	25.7236	0	0	25	820.0561
{Phi(g*t) p(t) PIM}	1416.4178	35.6851	0	0	35	807.5216
{Phi(t) p(g*t) PIM}	1416.9209	36.1882	0	0	35	808.0246
{Phi(g*t) p(g*t) PIM}	1432.6469	51.9142	0	0	46	797.94

*Appendix 4* Model selection for *H. fuscoguttata* in the Buenaventura stream, Province of El Oro, Ecuador.

<b>Model</b>	<b>QAIC<sub>c</sub></b>	<b>Delta QAIC<sub>c</sub></b>	<b>AIC<sub>c</sub> Weights</b>	<b>Model Likelihood</b>	<b>Num. Par.</b>	<b>QDeviance</b>
{Phi(.) p(.) PIM}	177.9818	0	0.98893	1	2	70.5188
{Phi(t) p(.) PIM}	188.1852	10.2034	0.00602	0.0061	8	76.3103
{Phi(.) p(t) PIM}	188.5505	10.5687	0.00501	0.0051	8	76.6756
{Phi(t) p(t) PIM}	198.2780	20.2962	0.00004	0	13	73.8450

Appendix 5 Model selection for *H. aurora* in the Moromoro stream, Province of El Oro, Ecuador.

<b>Model</b>	<b>QAIC<sub>c</sub></b>	<b>Delta QAIC<sub>c</sub></b>	<b>AIC<sub>c</sub> Weights</b>	<b>Model Likelihood</b>	<b>Num. Par.</b>	<b>QDeviance</b>
{Phi(.) p(g) PIM}	291.4503	0	0.59446	1	3	114.9318
{Phi(g) p(g) PIM}	293.4396	1.9893	0.21986	0.3698	4	114.8103
{Phi(t) p(g) PIM}	295.2863	3.836	0.08733	0.1469	8	107.9169
{Phi(g) p(.) PIM}	297.0013	5.551	0.03705	0.0623	3	120.4827
{Phi(.) p(.) PIM}	297.5551	6.1048	0.02809	0.0473	2	123.1187
{Phi(.) p(g*t) PIM}	298.3891	6.9388	0.01851	0.0311	13	99.3769
{Phi(g) p(g*t) PIM}	300.2909	8.8406	0.00715	0.012	14	98.8475
{Phi(g) p(t) PIM}	302.8478	11.3975	0.00199	0.0033	8	115.4784
{Phi(t) p(g*t) PIM}	303.0714	11.6211	0.00178	0.003	17	94.1146
{Phi(t) p(.) PIM}	303.3156	11.8653	0.00158	0.0027	7	118.1771
{Phi(.) p(t) PIM}	303.3714	11.9211	0.00153	0.0026	7	118.2329
{Phi(g*t) p(g) PIM}	305.6112	14.1609	0.0005	0.0008	14	104.1677
{Phi(t) p(t) PIM}	308.4662	17.0159	0.00012	0.0002	11	114.2116
{Phi(g*t) p(.) PIM}	310.5303	19.08	0.00004	0.0001	13	111.5181
{Phi(g*t) p(g*t) PIM}	313.5976	22.1473	0.00001	0	22	91.336
{Phi(g*t) p(t) PIM}	317.3847	25.9344	0	0	17	108.4279

Appendix 6 Correlation values of morphological measurements of the *Hetaerina fuscoguttata*, *H. aurora* and *H. caja* in the Tabuga river, Buenaventura stream and Moromoro stream.

		Correlaciones						
		BL	WSL	WL	TL	TW	CL	ED
BL	Correlación de Pearson	1	-,026	,457**	,118	,181*	,568**	-,175*
	Sig. (bilateral)		,747	,000	,140	,023	,000	,028
	N	159	159	128	159	159	154	159
WSL	Correlación de Pearson	-,026	1	,279**	,261**	,132	-,248**	,149
	Sig. (bilateral)	,747		,001	,001	,098	,002	,060
	N	159	159	128	159	159	154	159
WL	Correlación de Pearson	,457**	,279**	1	,286**	,355**	,355**	-,046
	Sig. (bilateral)	,000	,001		,001	,000	,000	,607
	N	128	128	128	128	128	124	128
TL	Correlación de Pearson	,118	,261**	,286**	1	,261**	-,103	,204**
	Sig. (bilateral)	,140	,001	,001		,001	,201	,010
	N	159	159	128	159	159	154	159
TW	Correlación de Pearson	,181*	,132	,355**	,261**	1	,154	,066
	Sig. (bilateral)	,023	,098	,000	,001		,056	,408
	N	159	159	128	159	159	154	159
CL	Correlación de Pearson	,568**	-,248**	,355**	-,103	,154	1	-,199*
	Sig. (bilateral)	,000	,002	,000	,201	,056		,013
	N	154	154	124	154	154	154	154
ED	Correlación de Pearson	-,175*	,149	-,046	,204**	,066	-,199*	1
	Sig. (bilateral)	,028	,060	,607	,010	,408	,013	
	N	159	159	128	159	159	154	159
Role Cat	Correlación de Pearson	-,135	,046	-,052	-,016	,030	-,055	,047
	Sig. (bilateral)	,089	,567	,557	,846	,703	,499	,559
	N	159	159	128	159	159	154	159

\*\* . La correlación es significativa al nivel 0,01 (bilateral).

\* . La correlación es significante al nivel 0,05 (bilateral).