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Daily abundance at the breeding site and reproductive behavior of *Polythore gigantea* (Odonata: Polythoridae)

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Abstract. Daily abundance at the breeding site and reproductive behavior of *Polythore gigantea* (Selys, 1853) are described in different localities of Antioquia, Colombia. Observations were done between March and June 2009 from 08:00 to 16:00 h. The highest reproductive activity (i.e. maximal abundance of individuals at the breeding site) was observed between 11:06 and 12:12 h. Oviposition lasted 10 min on average. During courtship, the male exhibited rhythmical movements by opening and closing the wings rapidly, getting closer to the female and holding her in tandem. During oviposition, the female inserts the eggs inside wet trunks and little twigs in the surrounding vegetation under the close surveillance of the male. Males exhibit territorial behavior and conspecific aggression to defend the territory. Factors such as vegetation cover, might influence the time of the day in which oviposition occurs. This study provides, for the first time, information on the reproductive behavior of *P. gigantea*.

Key words. Dragonfly, damselfly, Zygoptera, Colombia, Antioquia

Introduction

The reproductive behavior of Odonata is widely known (e.g., Corbet 1980, 1999). However, information on Neotropical species is still incipient, especially in countries like Colombia, where studies are scarce and many habi-

tats and their species disappear before they can be studied, as a consequence of the high level of nature degradation generated by human activities.

Damselflies of the Polythoridae family are generally found in forested areas, where they prefer narrow first order streams in rainforest (Sánchez & Realpe 2010). Males of some species remain in the same territory for several days, actively defending the location where mating and oviposition occurs (Fraser & Herman 1993). Polythorids perch horizontally with their wings closed, on the tips of branches or thin trunks near the water (Fraser & Herman 1993; Pritchard 1996). *Polythore gigantea* (Selys, 1853) inhabits riparian areas of lotic ecosystems, characterized by abundant and diverse vegetation with high accumulation of litter in the water, which generates specific microclimatic conditions for oviposition, larval growth, and development (Altamiranda & Ortega 2012). *Polythore gigantea* is distributed in Colombia, Ecuador, and northern Peru at elevations between 467 and 2,200 m a.s.l. (e.g., Bick & Bick 1985).

Mark-recapture methods have been widely used in demographic and behaviorial studies on odonates (De Marco et al. 2008). However, information about population attributes using mark-recapture methods is scarce for Neotropical species (Garrison & González-Soriano 1988; Hamilton & Montgomerie 1989; Palacino-Rodríguez et al. 2011; Alves-Martins et al. 2012), and even fewer for this region are the studies including information on the species reproductive behavior using these methods (e.g., Loiola & De Marco 2011).

The objective of this study was to evaluate, at the breeding site: (i) the daily abundance of individuals and (ii) the type and frequency of the reproductive behavior of *P. gigantea*.

Materials and methods

Study sites

The study was carried out at four streams in the metropolitan area of Valle de Aburrá, Antioquia, Colombia (Fig. 1). The percentage canopy cover indicates the amount of light penetrating the canopy in each zone, which was measured with a densitometer.

La Doctora: 06°07'N, 75°36'W, elevation 1,759 m a.s.l., Sabaneta municipality. Canopy cover 40–69 %, dominant vegetation on the bank consisted of grass patches like *Brachiaria* (Trin.) Griseb. in Ledeb, 1853; *Pinus patula* (Schl. et Cham) (Pinaceae) and *Pteridium* (L.) Kuhn (Dennstaedtiaceae).

La Romera: 06°08'N, 75°36'W, elevation 1,930 m a.s.l., Sabaneta municipality. Canopy cover 40–69 %, dominant vegetation on the bank consisted of *Bambusa* Schreb (Poaceae), *Pteridium* (L.) Kuhn (Dennstaedtiaceae) and *Polytrichum* Hedw. (Polytrichaceae).

La Miel: 06°08'N, 75°34'W, elevation 1,987 m a.s.l., Envigado municipality. Canopy cover 10–39 %, with predominance of secondary forest and farming areas subjected to logging and burning.

La Catedral: 06°10'N, 75°35'W, elevation 1,720 m a.s.l., Envigado municipality. Canopy coverage of 70–100 % with abundant *Pteridium* (L.) Kuhn (Dennstaedtiaceae) and *Polytrichum* Hedw. (Polytrichaceae).

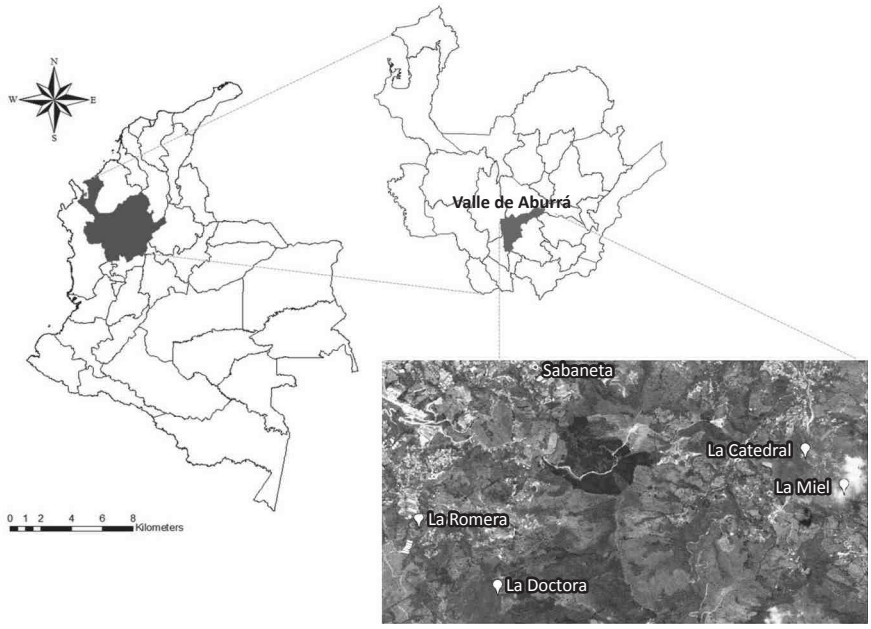

Figure 1. Map of the Antioquia Department, with the localities in Valle de Aburrá where field work of this study on *Polythore gigantea* was conducted, and its situation within Colombia.

Marking, observations and daily abundance

Monitoring the reproductive behavior of *Polythore gigantea* was conducted during the rainy season between March and June 2009. At each study site, adults were collected with an entomological net along a transect of 200 m parallel to the stream shorelines. Each individual was carefully marked with a unique number on one wing using a red fine point marker with indelible ink Sharpie®. Altogether 454 individuals were marked. A total of 180 h were used for observation, recording data on five sessions in 45 h per stream.

Each territory was defined following Kaufmann (1983) as the part of the study area, in which the male remained for long periods of time and where he exhibited agonistic interactions with conspecifics. In each territory, the number of males and females and the vegetation cover percentage were recorded. To delimit each territory, the boundaries were recognized by distinguishable rocks and vegetation characteristics.

The observations followed the focal animal temporal sampling technique (Altmann 1974). Each observation session was from 08:00 to 17:00 h COT (UTC-5), divided into periods of 15 minutes, in which the sequence and changes in behavior were observed and recorded. After 15 minutes we began recording a different marked animal. The observations were classified in the following categories: 1) perch, 2) territorial dispute, 3) courtship, 4) oviposition, 5) partner surveillance (i.e. non-contact guarding). A matrix of the observations in each stream included date and time, code number of the animal and sex of each individual.

Our study was limited to the rainy season because adults congregate near the stream at this time of the year. We limited our study to breeding sites because it was difficult to find individuals elsewhere.

Data analysis

Contingency tables (Pearson chi-square tests) were used to compare the resighting probability of marked individuals, with the resighting probability for the rest of the individuals of the population as follow: (i) males and females in the study, (ii) males and females by locality, and (iii) only males

in all localities or only females in all localities. Recapture rate was analyzed using Chi² tests with Statistica 8.0 software (www.statsoft.com). In order to establish the highest reproductive activity of the species in each locality, a circular analysis of daily abundance at the breeding site was done, obtaining a maximum activity vector for each sex and for both sexes in each stream using the software Oriana 3.0 (RockWare, Inc.).

Results

Mark-Recapture

No significant difference between sexes was found in the recapture rate of the 454 marked individuals of *Polythore gigantea* at each locality, or by sex comparing all localities (Tab. 1). A higher number of males (548) than females (360) were found. 39 % of the males and 29 % of the females were recaptured only once, 15 % of the males and 11 % of the females were recaptured twice, and 3 % of the males and 3 % of the females were recaptured at least three times.

Daily abundance

The daily abundance peak for *P. gigantea* occurred between 11:06 and 12:12 h (Fig. 2, Tab. 2). Females showed the highest daily reproductive activity (number of individuals at the breeding site) between 11:01 and 12:07 h, while males showed a reproductive activity peak between 11:19 and 12:15 h, time at which the sun beams fall more directly over the study area.

Territorial behavior

The territorial behavior in males of *P. gigantea* includes constant searching for potentially receptive females and, after mating, patrolling over oviposition sites. The patrolled territories are usually located in shaded areas with a high volume of leaf litter in the water. On some occasions, three or more males simultaneously tried to enter a guarded territory.

Courtship, mating, oviposition and male guarding

Information on courtship, mating and oviposition was obtained from six matings, while territorial behavior was observed in 20 males. The number

Table 1. Number of individuals of *Polythore gigantea* marked and recaptured in some lotic systems of Valle de Aburrá, Antioquia, Colombia. n − individuals marked; RC − individuals recaptured; M* − Males, comparing all localities; F* − Females, comparing all localities. *P*-values are from Chi² tests.

Analysis	Sex	n	RC	Probability of resighting	*P*	M*	F*
General	Male	274	115	0.42	0.65	0.49	0.56
	Female	180	73	0.41			
La Doctora	Male	83	35	0.42	0.78		
	Female	63	28	0.44			
La Romera	Male	65	27	0,42	0.51		
	Female	35	11	0.31			
La Miel	Male	46	18	0.39	0.91		
	Female	41	17	0.41			
La Catedral	Male	80	35	0.44	0.73		
	Female	41	17	0.41			

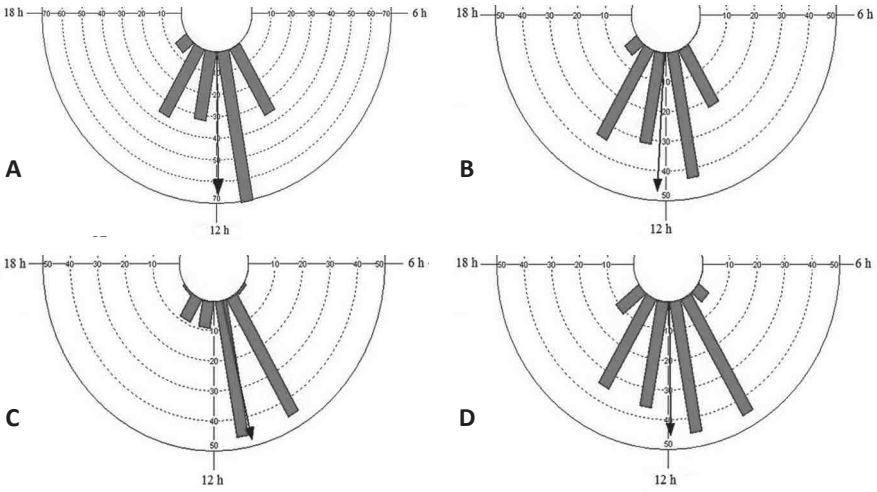

Figure 2. Daily abundance of *Polythore gigantea* individuals of both sexes in some lotic systems of Valle de Aburrá, Antioquia, Colombia. (A) La Doctora, (B) La Romera, (C) La Miel, (D) La Catedral. The arrow indicates the mean abundance vector. The bars indicate the number of individuals; the sum of these values is specified in Table 2.

Table 2. Maximum daily activity period of *Polythore gigantea* in some lotic systems of Valle de Aburrá, Antioquia, Colombia.

	Maximum daily activity period [h, time zone UTC-5]		
Stream	Both sexes	Male	Female
La Doctora	11:58 a.m	11:51 a.m	12:03 p.m
La Romera	12:12 p.m	12:15 p.m	12:07 p.m
La Miel	11:06 a.m	11:19 a.m	11:01 a.m
La Catedral	11:56 a.m	11:53 a.m	11:57 a.m

Table 3. Number of observations of reproductive or territorial behavior of *Polythore gigantea* in some lotic systems of Valle de Aburrá, Antioquia, Colombia.

Stream	Courtship	Mating	Oviposition	Average time of oviposition [min]	Territoriality
La Doctora	3	3	3	9.6	4
La Romera					8
La Catedral	2	2	2	9.8	5
La Miel	1	1	1	10.5	3

of observations for each category is indicated in Table 3. The reproductive behavior observed between 10:28 and 12:00 h included the male arrival and location near streamside vegetation. Courtship began with rapid rhythmical movements in which the male opened and closed the wings and approached and held the female in tandem. Then, the female bent the abdomen inwards and the wheel was completed. Copulation lasted about 10 minutes (n = 6, mean = 9.8, SE = 1.1844). Once the mating was finished, the female flew towards the stream bank to lay eggs in wet trunks and little twigs. During oviposition the males guarded the females without physical contact.

A tandem between conspecific males was recorded at La Doctora stream on 25-iv-2009 at 11:49 h. A non-marked male approached a marked male and executed the courtship, the first holding the second by the prothorax with his cerci and trying to bend its abdomen inwards. The held male did not try to bend its abdomen, as a female would typically do. After a few minutes

without succeed in mating, the marked male was released and both males flew away from the stream.

Discussion

Rehn (2003) found a phylogenetic relationship between Polythoridae and Calopterygidae families, although with a low support value. Recently Dijkstra et al. (2014) proposed that some Megapodagrionidae might be more closely related to Polythoridae than to Calopterygidae. However, the same authors state that there is no strong evidence on the evolutionary relationships between the Calopterygoidea families with certainty. As a result, we have compared *Polythore gigantea* behavior with the information from other Polythoridae species and other zygopterans including Calopterygidae and Megapodagrionidae.

Daily abundance

In order to identify the activity peak of a species, Lambret & Stoquert (2011) suggested two relevant aspects: First, the possibility for the investigator to measure the intensity of the activity, and second, the importance of knowing what is meant by "activity". What is commonly called activity in odonatological studies (reviewed by Lambret & Stoquert 2011) is actually the number of individuals present in the breeding site at a given time (e.g., De Marco & Resende 2002; Lambret & Stoquert 2011). This definition of activity mainly focuses on observing reproductive behavior in these sites.

Our analyses indicate that individuals show a peak of reproductive activity earlier (Fig. 2) in La Miel stream. This might be caused by the reduced vegetation cover (10-39 %) which might facilitate the passage of sunlight, generating a higher temperature closer to the water in the morning. Our results are consistent with those of Fraser & Herman (1993), and Loiola & De Marco (2011) who found that the abundance peak for other Polythoridae species such as *Cora notoxantha* Ris, 1918, *C. obscura* Ris, 1918, *C. semiopaca* Selys, 1878, and *Heteragrion consors* Hagen, 1862 occurs between 10:30 and 12:30 h with a peak of reproductive and territorial behavior between 10:00 and 12:00 h. After this reproductive activity peak, the number of observations declines as both males and females fly to the canopy. These

authors also point out that on cold days the individuals are scarce because they perch high in the vegetation.

Territorial behavior

Similar to *Polythore procera* (Selys, 1869) and other Polythoridae species (Sánchez & Realpe 2010), *P. gigantea* males exhibit a strong affiliation to the territory. González-Soriano & Verdugo (1984) described *Cora marina* Selys, 1869 males as »totally territorial«, because three of the five studied males kept in the same territory. For *Cora* species studied by Fraser & Herman (1993), males are extremely territorial of sites preferred by females for oviposition. The simultaneous presence of several males in a territory is not common and the duration of territorial disputes is variable.

A high number of males in the territories suggest there are more males than available territories (Ortega 1992; Peixoto & De Marco 2009). This is likely to generate higher energy expenditure during mate searching as a consequence of the increase in the amount of territorial clashes (Peixoto & De Marco 2009). One of the hypotheses used by Fraser & Herman (1993) to explain this is that females are not attracted evenly to the oviposition sites, which provokes that non-resident males try to win attractive territories, especially those to which females usually come.

Another possible explanation for the high concentration of territorial males in this area is that favourable environmental conditions provide several ovipositon sites, generating a lek system (Ide & Kondoh 2000) that attracts a great number of females.

The high concentration of *P. gigantea* males contrasts with the low frequency (20 events) of observed tandem and oviposition events, possibly because of the high energy cost of territoriality, which generates physical wear in males, and increases mortality due to, for example, a higher risk of being predated (Briffa & Sneddon 2007; Bergman et al. 2010). As a result, organisms only exhibit territoriality if its benefits (e.g., mating opportunities) are greater than its costs (Bergman et al. 2010). Territoriality is highest when few females are available in the territories, forcing males to

defend places with the best resources (Suhonen et al. 2008). However, the study sites were in altered ecosystems where forest is only found around the stream; this condition could be the cause of such concentrations of males (C.A. Bota-Sierra pers. comm.).

Courtship, mating, oviposition and male guarding

The presence of leaf litter and woody debris in the oviposition sites was similar to that found for other Polythoridae species (Fraser & Herman 1993; Resende & De Marco 2010). *Polythore gigantea* has a variable sex ratio at the breeding site, which chiefly is due to the fact that males congregate at the stream waiting for females whereas females only appear for oviposition. Other factors that might influence the proportion of both sexes in these populations are differences in the survival of males and females due to the parasite load (e.g., eugregarines), variation in the climatic conditions in the season in which the investigation was done (Palacino-Rodríguez et al. 2011), scarce nutritional reserves in recently emerged individuals (Marden 1989) and differential intensity in the predation by vertebrates like birds (Corbet 1999).

Our results regarding mating duration (10 min) are consistent with those for *Chalcopteryx rutilans* Rambur, 1842 (Resende & De Marco 2010). The frequency of observation of tandems and oviposition was low (Tab. 3), which might be caused by several reasons. First, there might be many reproductive events during the year but none coincided with the months of the study. Second, one main reproductive event takes place during the year and this did not coincide with the study either. Altamiranda & Ortega (2012) indicate that adult life span is 20 days, which is relatively short. This statement allows rejecting these two hypotheses. Third, mating is taking place elsewhere in the ecosystem or in locations difficult to access by the observers such as elevated twigs in the vegetation.

Cora species males aggressively defend their territories but, unlike *P. gigantea*, their reproductive behavior does not include courtship (except for *C. marina*) or oviposition guarding (Fraser & Herman 1993; Pritchard 1996). According to Fraser & Herman (1993) males of several species of

Cora cannot locate females during oviposition due to their camouflage: the movements of females do not stimulate a response in the male. Courtship behavior in *P. gigantea* leads us to infer that *P. gigantea* females are clearly detected by males and are not camouflaged. Thus, several males might be stimulated to mate when they perceive the oviposition movements. Also, prolonged territorial disputes lead to missed mating opportunities (Marden & Waage 1990) reducing reproductive success (Stoks 2000). This might explain why males of Polythoridae species, such as *C. rutilans* and *P. gigantea*, have a ritualized territory defense to counteract the reduced number of females.

Mating duration in *P. gigantea* is longer than that reported for *Calopteryx xanthostoma* (Charpentier, 1825) (58 s; Cordero 1989), *C. haemorrhoidalis* (Vander Linden, 1825) (14.2 s; Cordero 1989), *C. virgo* (Linnaeus, 1758) (58 s; Cordero 1989), *H. consors* (5.2 min; Loiola & De Marco 2011), and *Neoneura bilinearis* Selys, 1860 (4 min; Osorio 2008). However, it did not exceed the mating duration reported for *C. marina* (56.8 min; Gonzalez & Verdugo 1984), *Ischnura graellsii* (Rambur, 1842) (1-5 h; Cordero 1990), *Chloroneura quadrimaculata* (Rambur, 1842) (20.33 min; Srivastava & Babu 1985) or for *P. capillaris* (Rambur, 1842) (53.41 min; Trapero et al. 2005). This implies that sperm competition is more intense in *P. gigantea* than in the species that spend less time mating but less intense than in the others. One could also expect oviposition guarding to be longer in those species which have longer mating times. In the case of *P. gigantea*, male vigilance during oviposition was always evident, behavior that might or might not be present in *C. rutilans* but definitely is not present in all other species of *Cora*. De Marmels (1982) and Loiola & De Marco (2011) reported that oviposition in *Euthore f. fasciata* (Hagen, 1853) and *Heteragrion consors* (Hagen in Selys, 1862) was also completed in the company of a male. Male surveillance during oviposition reduces the chances of male access to new partners (Alcock 1982), but guarding might increase reproductive success of the male if the guarded females lays more eggs fertilized by that male than unguarded ones, especially in species where males have the ability to remove previously deposited sperm (Waage 1979).

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