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Artículos

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Aspectos de la historia natural de *Phrynus barbadensis* (Pocock, 1893) (Amblypygi: Phrynidae)

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Abstract: Information on preys and predators of the amblypygids is scarce, largely disperse and sometimes overlooked by the arachnologist. *Phrynus barbadensis* is a Neotropical whip spider widely distributed, but its natural history is poorly known. The main purpose of this contribution deals with preys, predators, reproductive effort and microhabitat preferences of *P. barbadensis* in a Colombian locality. Field work was carried out by two researchers during four expeditions of six days each, between June and November 2017. Two observed cases of intragremial predation concerned to the spitting spider *Scytodes longipes* Lucas (Araneae: Scytodidae) and the giant whip spider *Heterophrynus caribensis* Armas, Torres-Contreras & Álvarez (Phrynidae: Heterophryninae). A new case of a mollusk as prey of whip spiders is also recorded. The number of embryos *per* batch in *P. barbadensis* was 14-79 (n = 27, mean = 40, standard error = 3.83), having a positive correlation with the female size. This species was highly associated to fallen trunks and rocks, but poorly to the litter and rocky walls ($\chi 2 = 16.26$, $P < 0.001$); with respect to the substrate temperature, it showed a positive association. The cannibalism and necrophagy among the whip spiders are briefly commented, and updated lists of the known preys and predators of the amblypygids are also provided.

Keywords: Ecology, *Heterophrynus* , necrophagy, *Scytodes* , South America.

Resumen: La información sobre las presas y los depredadores de los amblipígidos es escasa, en gran parte dispersa y, a veces, olvidada por el aracnólogo. *Phrynus barbadensis* es una araña látigo neotropical ampliamente distribuida, pero su historia natural es poco conocida. El objetivo principal de esta contribución se refiere a las presas, los depredadores, el esfuerzo reproductivo y las preferencias de microhábitats de *P. barbadensis* en una localidad colombiana. Dos investigadores llevaron a cabo el trabajo de campo durante cuatro expediciones de seis días cada una, entre junio y noviembre de 2017. Dos casos observados de depredación intragremial se relacionaron con la araña *Scytodes longipes* Lucas (Araneae: Scytodidae) y la araña látigo gigante *Heterophrynus caribensis* Armas, Torres-Contreras & Álvarez (Phrynidae: Heterophryninae). También se registra un nuevo caso de un molusco como presa de las arañas látigo. El número de embriones por lote en P. *barbadensis* fue 14-79 (n = 27, promedio = 40, error estándar = 3,83), teniendo una correlación positiva con el tamaño de la hembra. Esta especie estuvo altamente asociada a troncos caídos y rocas, pero pobremente a la hojarasca y las paredes rocosas ($\chi 2 = 16,26$; $P < 0,001$); con respecto a la temperatura del sustrato, mostró una asociación positiva. El canibalismo y la necrofagia entre las arañas látigo son brevemente comentadas, y también se proporcionan listas actualizadas de las presas y depredadores conocidos de los amblipígidos.

Palabras clave: Ecología, Heterophrynus , necrofagia, Scytodes , Sudamérica.

INTRODUCTION

Amblypygi is a moderately diverse order of arachnids distributed in most tropical and subtropical terrestrial ecosystems. They have dorso-ventrally flattened bodies, raptorial pedipalps, and first pair of elongate legs, mainly of sensorial function (Weygoldt, 2000; Chapin & Hebets, 2016). To date, there are approximately 200 extant named species, which are included in 17 genera and 4 families (Maquart & Réveillion, 2016). Nevertheless, data on its natural enemies and preys is poorly documented (Weygoldt, 2000, Armas et al., 2013, Gonçalves-Souza et al., 2014; Torres-Contreras et al., 2015; Chapin &Hebets, 2016; Prous et al., 2017). Most of its known predators are scorpions and other whip spiders (intraguild competition and cannibalism), whereas the only true spider (Araneae) recorded as its predator is an undetermined Lycosidae (Chapin, 2011).

Under particular conditions, intraguild predation, including cannibalism, might play an important role in the trophic structure of those ecosystems in which the whip spiders are abundant (Chapin & Hebets, 2016). Although field studies on this ecological aspect have not been conducted, sporadic observations seem to reinforce this hypothesis, but this does not constitute a high criterion.

Amblypygids, also known as whip spiders or tailless whipscorpions, are generalist that include several insects in their diet, mainly Orthoptera, Lepidoptera, and Dictyoptera (Chapin & Hebets, 2016), but also other preys, as freshwater shrimps, terrestrial mollusks, schizomids, scorpions, harvestmen, spiders, millipedes, centipedes, frogs and lizards, have been recorded. Owen & Cokendolpher (2006) reported a hummingbird (Apodiformes: Trochilidae) predated by the West Indian *Phrynus longipes* Pocock, but as it is unknown how the whip spider obtained that prey; necrophagy cannot be disregarded, because previous cases of this behavior have been observed in the group (Peck, 1974; Armas & Abreu-Collado, 1999; García-Rivera et al., 2009; Prous et al., 2017).

Phrynus barbadensis is a phrynid species well represented in the Colombian Caribbean (Chiriví-Joya & Armas, 2012). In recent years, some aspects of its natural history have been documented (Chiriví-Joya & Armas, 2012; Torres-Contreras et al., 2015). In the present contribution, additional preys and predators of this whip spider are documented, as well as data on its habitat preferences and reproductive biology.

MATERIAL AND METHODS

Study site

The field work was conducted in Montes de María (09° 31' N; 75° 20' W - 250 m a.s.l.), Colosó municipality, Sucre department, Colombia. This is

a tropical dry forest, in a mountainous landscape with primary forest and several springs. The annual mean temperature is 26.8 °C, the precipitation varies between 1000 and 1200 mm and the relative humidity is 77% (Aguilera, 2005).

Sampling

The field work was carried out between 19:00 and 23:00 h by two researchers, during four expeditions of six days each, from June to November, 2017. To determine the reproductive effort, 27 ovigerous females of *P. barbadensis* were collected. Four microhabitats (rocks, fallen trunks, crevices in rocky walls, and litter) were manually examined randomly searching for whip spiders. The sampling effort were distributed evenly with 20 minutes for each microhabitat. Temperature of the substratum was assessed by means a Thermoworks 24-inch waterproof digital thermometer.

All the specimens were preserved in ethanol 75%. Voucher specimens are deposited in the Zoological Museum of the University of Sucre, Colombia (MZUSU) with the collection number MZUSU-I00001, MZUSU-I00002, MZUSU-I00003, MZUSU-I00004, MZUSU-I00005. The specimens were collected within the framework permission for the collection of specimens of wild species of biological diversity for the purpose of scientific research granted by the National Environmental License Authority (ANLA) to the University of Sucre.

Statistical analyses

Carapace length was used as a measure of size of specimens and, a correlation analysis of Spearman was applied by means of the software PAST version 3.14 (Hammer et al., 2001).

To determine microhabitat preference, an analysis of binary logistic regression was applied in function of the substratum temperature, by means of the software SPSS version 22 for Windows (IBM, Armonk, NY, USA). A test of homogeneity (X^2) was applied to reject the null hypothesis of similar preference of microhabitat by this species, assuming that all the microhabitats had the same probability of being occupied.

RESULTS

Predation by Scytodes longipes (Fig. 1a, Table I)

On Oct 18th, 2017, a spitting spider *Scytodes longipes* (Araneae: Scytodidae) was found underneath a rock feeding on the whip spider *P. barbadensis*. The spider was an adult female (total length: 9.95 mm, prosoma length: 4.15 mm). The whip spider was an adult female (total length: 9.42 mm, carapace length: 3.64 mm). At the moment of the

observation, the whip spider was entangled in the web and wrapped by silk on the pedipalps and prosoma, and the spider begun to feed on it.

Fig. 1

Feed interaction in *Phrynus barbadensis*. a, predatation by *Scytodes longipes* and b, by *Heterophrynus caribensis*. c, eating a gastropod mollusc (Ampullaridae)

Photos by Richard A. Torres

Predator	Prey	References
Vertebrates		
Varanus salvator (Laurenti) (Reptilia: Varanidae)	*Catageus dammermani* Roewer (Charontidae)	Dammerman (1948)
Solenodon cubanus Peters, 1861 (Mammalia: Soricomorpha)	*Paraphrynus robustus* (Phrynidae)	Armas (1987: 1)
Lophostoma silvicolum d'Orbigny, 1836 (Chiroptera: Phyllostomidae)	Unidentified Phryninae [possibly *P. barbadensis* and/or *Paraphrynus laevifrons* (Pocock, 1894)]	Humphrey *et al.* (1983: 287)
Invertebrates		
Scytodes longipes Lucas, 1844 (Araneae: Scytodidae)	*Phrynus barbadensis*	**This paper**
Unidentified Lycosidae (Araneae)	*Heterophrynus batesii* (Butler, 1873) (Phrynidae)	Chapin (2011: 3)
Heterophrynus guacharo Armas, 2015	*Heterophrynus guacharo* (cited as *H. cervinus* Pocock, 1894)	Morales-Álvarez & González (1986: 73)
Heterophrynus caribensis Armas, Torres-Contreras & Álvarez, 2015	*Phrynus barbadensis*	**This paper**
Phrynus barbadensis	*Phrynus barbadensis*	Torres-Contreras *et al.* (2015)
Phrynus longipes (Pocock, 1893)	*Phrynus hispaniolae* Armas & Pérez, 2001 (cited as *Ph. levii*?)	Armas & Ramirez (1989: 3)
Alayotityus sierramaestrae Armas, 1973 (Scorpiones: Buthidae)	*Phrynus damonidaensis* Quintero, 1981	Armas *et al.* (2013)
Heteroctenus junceus (Herbst, 1800) (Scorpiones: Buthidae)	*Phrynus pinarensis* Franganillo, 1930	Teruel & Toledo (2014)
Centruroides edwardsii (Gervais, 1843) [cited as *C. margaritatus* (Gervais, 1841)] (Scorpiones: Buthidae)	*Phrynus whitei* Gervais, 1842	Armas (1995: 2)
Unidentified scorpion (Arachnida: Scorpiones)	*Phrynus pseudoparvulus* Armas & Víquez, 2001 (cited as *Phrynus parvulus* Pocock, 1902)	E. Gering in Hebets (2002: 289)

Table I

Known predators of the amblypygids

Modified from Chapin & Hebets (2016). Field observations only.

Predation by Heterophrynus caribensis (Fig. 1b, Table I)

On Aug 26th, 2017, an adult female of H. caribensis (total length: 21.8 mm, carapace median length: 4.8 mm) was found on a rock eating a female *P. barbadensis* (total length: 15 mm, carapace median length: 2.6 mm). At the time of the observation, the predator strongly held the whole body of the prey while consuming its opisthosoma. The individual of *P. barbadensis* was still fresh from an ecdysis.

Predation on a gastropod mollusk (Fig. 1c, Table II)

On Sept 11th, 2017, an adult female of *P. barbadensis* (total length 15.59 mm, carapace median length 5.21 mm) was found under a stone eating a gastropod mollusk. At that moment, the amblypygid grasped with

its pedipalps and chelicerae the soft corporal mass of the mollusk. The shell was empty, with a small rupture in its aperture. Measurements (in millimeters) of the shell were as follows: total length: 6.83, width: 4.64, aperture: 2.59 x 1.94.

Prey	Predator	References
Vertebrates		
Eleutherodactylus coqui Thomas (Anura: Eleutherodactylidae)	*Phrynus longipes* (Pocock)	Formanowicz *et al*. (1981); Pfeiffe (1996: 266); Stewart & Woolbright (1996: 308)
Eleutherodactylus richmondi Stejneger	*Phrynus longipes*	Stewart & Woolbright (1996: table 8.7)
Eleutherodactylus sp.	*Phrynus* sp. (seemingly *Ph. pinarensis* Franganillo)	Schwartz (1958: 42)
Eleutherodactylus sp.	*Phrynus* sp.	Thomas in Stewart & Woolbright (1996: 308)
Pristimantis achatinus (Boulenger) (Anura: Craugastoridae)	*Heterophrynus armiger* Pocock, 1902	Wizen & Aznar (2016)
Anolis crysolepis Duméril & Bibron (Reptilia: Dactyloidae)	*Heterophrynus longicornis* (Butler)	Kok (1998)
Anolis stratulus Cope (Reptilia: Dactyloidae)	*Phrynus longipes*	Reagan (1996: 343, fig. 14.3); Thomas & Kessler (1996: 355)
Anolis sp.	*Phrynus longipes*	Armas & Abreu-Collado (1999)
Orthorhyncus cristatus (Linn.) (Apodiformes: Trochilidae)	*Phrynus longipes*	Owen & Cokendolpher (2006), although does not determined whether it was a predation event or necrophagy.
Invertebrates		
Undetermined mollusks (Mollusca)	*Heterophrynus guacharo* (cited as *H. cervinus*)	Morales-Álvarez & González (1986: 73)
Undetermined Ampullaridae (Mollusca: Gastropoda)	*Phrynus barbadensis*	**This paper**
Macrobrachium sp. (Decapoda: Palaemonidae)	*Heterophrynus cheiracanthus* (Gervais)	Ladle & Velander (2003)
Undetermined isopods (Isopoda: Oniscidea)	*Heterophrynus guacharo* (cited as *H. cervinus*); *Charinus israelensis*; *Charinus ioanniticus* (Kritscher)	Morales-Álvarez & González (1986: 73); Miranda *et al*. (2016: 12); G. Wizen (pers. com., December 13th, 2017)
Undetermined centipede (Chilopoda: Scolopendromorpha)	*Phrynus longipes*	Armas & Ramirez (1989: 3)
Undetermined millipedes (Diplopoda)	*Phrynus pseudoparvulus*	Hebets (2002: 289)
Stenochrus portoricensis Chamberlin (Schizomida: Hubbardiidae)	*Phrynus marginemaculatus* C. L. Koch	Armas (1989)
Centruroides gracilis (Latreille) (Scorpiones: Buthidae)	*Paraphrynus cubensis* Quintero	Forcelledo & Armas (2014)
Undetermined opilions (Arachnida: Opiliones)	*P. pseudoparvulus*	Hebets (2002: 289)

Table II

Known preys of the amblypygids

Field observations only. Amblypygid-amblypygid predation is herein excluded (see Table I).

Prey	Predator	References
Nephila sp. (Araneae: Nephilidae)	*Heterophrynus batesii*	Chapin (2011: 3, as orbweaving spider); Chapin & Hebets (2016: Table 2, fig. 3b) identified it as *Nephila* sp.
Loxosceles sp. (Araneae: Sicariidae)	*Charinus israelensis*	Miranda *et al*. (2016: 12)
Undetermined spiders (Arachnida: Araneae)	*P. pseudoparvulus*	Hebets (2002: 289)
Undetermined Psocoptera (Insecta)	*Charinus israelensis*	Miranda *et al*. (2016: 12)
Diestrammena sp. (Orthoptera: Rhaphidophoridae)	*Sarax yayukae* Rahmadi, Harvey & Kojima, 2010 (Charinidae)	Rahmadi *et al*. (2010: 9)
Amphiacusta sp. (cited as a cricket) (Orthoptera: Gryllidae)	*Phrynus longipes*	Armas (2010: 59, fig. 3 C)
Phalangopsis sp. (Orthoptera: Phalangopsidae)	*Heterophrynus longicornis*	Prous *et al*. (2017: 366-367, fig. 2A)
Undetermined crickets and katydids (Insecta: Orthoptera)	*Phrynus pseudoparvulus*; *P. longipes*; *Heterophrynus guacharo*	Hebets (2002: 289), Armas & Víquez (2001: 14); Peck (1974: 19, as *Tarantula fuscimana*); Morales-Álvarez & González (1986: 73)
Aspiduchus cavernicola (Rehn) (Dictyoptera: Blaberidae)	*Phrynus longipes*	Moyá-Guzmán (2009: 74)
Undetermined cockroaches (Insecta: Dictyoptera)	*P. pseudoparvulus*; *Heterophrynus guacharo*	Hebets (2002: 289); Morales-Álvarez & González (1986: 73)
Undetermined termites (Insecta: Isoptera)	*Charinus tomasmicheli* Armas, (Charinidae)	Rodríguez-Cabrera & Teruel (2016: 69)
Undetermined moths, noctuids, sphyngids (Insecta: Lepidoptera)	*Heterophrynus batesii* (Butler); *H. longicornis*; *P. pseudoparvulus*	Beck & Görke (1974); Carvalho *et al*. (2012: 1267); Hebets (2002: 289)
Undetermined Dolichopodidae (Insecta: Diptera)	*Phrynus longipes*	Moyá-Guzmán (2009: 74)

Table II (cont.)
Known preys of the amblypygids
Field observations only. Amblypygid-amblypygid predation is herein excluded (see Table I)

Reproductive effort

The number of embryos per batch varied between 14 and 79 (n= 27, mean =40, standard error= 3.83), having a positive correlation with the female size: $R^2 = 0.881$, $P < 0.001$ (Fig. 2a).

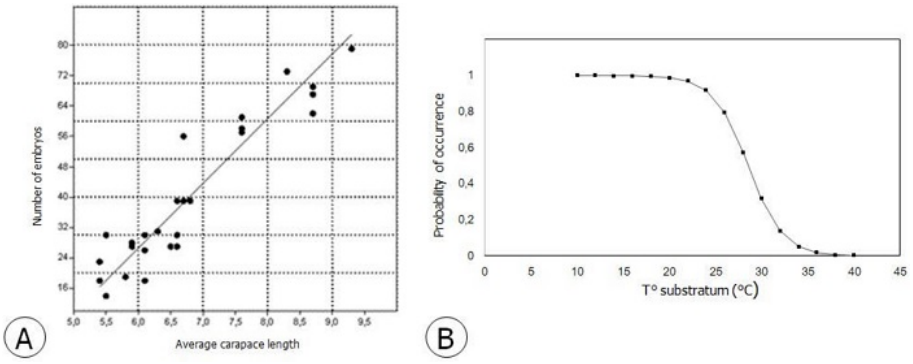

Fig. 2

a) Positive correlation between the carapace median length and the clutch size. b) Model of microhabitat selection of *Phrynus barbadensis* in a Colombian locality, based on substrate temperature.

Microhabitat preference

Phrynus barbadensis was highly associated to fallen trunks (n = 17) and rocks (n = 15), but poorly represented in litter (n = 2) and rocky walls (n = 1) ($\chi 2$ = 16.26, df: 3, P < 0.001). With respect to the substrate temperature, *P. barbadensis* showed a positive association (Fig. 2b) (substratum temperature: coefficient B = -0.528, standard error = 0.166, P < 0.001; Constant: coefficient B = 15.077, standard error = 4.803, P < 0.001).

DISCUSSION

Predators

Of the recorded cases of whip spider predation (Table I), three concern to cannibalism (Morales-Álvarez & González, 1986; Torres-Contreras et al., 2015), two events involve other whip spider species (Armas & Ramirez, 1989; this paper), and six concern predation by spiders and scorpions (Armas, 1995; Gering in Hebets, 2002; Chapin, 2011; Armas et al., 2013; Teruel & Toledo, 2014; this paper). Among vertebrates, Weygoldt (2000) indicated that large lizards, shrews, hedgehogs and mongooses are potential predators of whip spiders, but actually few cases have been recorded, mainly involving mammals and lizards (Dammerman, 1948; Armas, 1987; Stewart & Woolbright, 1996; Reid, 1997). As a whole, those cases refer to nine whip spider species (approximately 5% of the total), mostly belonging to Neotropical taxa of the genera *Phrynus* Lamarck (six species), *Heterophrynus* Pocock (two species) and *Paraphrynus* Moreno (one species), showing a clear panorama of the scarcity of the studies on this matter. Chapin & Hebets (2016: Table 3) erroneously included the small Puerto Rican frogs *Eleutherodactylus coqui* and *E. richmondi* as predating on *P. longipes*, but

actually, the frogs were predated by the whip spiders (Formanowicz et al., 1981; Stewart & Woolbright, 1996).

Two cases of cannibalism in *Heterophrynus guacharo* Armas, were reported by Morales-Álvarez & González (1986), but they did not provide additional details. A similar situation occurs with the intraguild predations recorded by Armas (1995), Gering (in Hebets, 2002) and Chapin (2011). Based on the exiguous available data (Armas & Ramirez, 1989; Armas et al., 2013; Teruel & Toledo, 2014; this paper), only two preliminary conclusions may be addressed: (1) size differences determine amblypygid-amblypygid and other arachnid-amblypygid predation, being the larger individuals the predators; (2) as in other arthropods, the ecdysis and its immediately posterior process of sclerotization represent a hard phase in which the whip spiders are dramatically exposed to predators. Those conclusions are congruent with some results obtained by Polis (1981) and Polis & McCormick (1981) in several North American scorpions.

Certainly, intraguild predation and cannibalism offer remarkable opportunities to understand the dynamic relationships within an ecosystem. Nevertheless, as already pointed out, most existing information on whip spider's predators result of opportunistic field observations, and quantitative assessments of their role as protagonist in the ecosystem trophic structures are lacking (Chapin & Hebets, 2016).

Preys

Amblypygids are generalist pantropical arachnids, seemingly opportunistic (Chapin & Hebets, 2016), but it is obvious that our present knowledge on its preys is meager. Remarkable or curious field observations on the natural history are sometimes totally or partially omitted, mainly because the principal interest had been focused on the taxonomy. In the future, as a result of more detailed researches, perhaps some food items of the amblypygid diet might be not as uncommon as considered at this moment.

A single observation has been recorded for the following whip spider preys: centipedes, scorpions, short-tailed whip scorpions, termites and dipterans (Table II); nevertheless, several amblypygid species utilize termite nests as shelters and potentially as food source too (Weygoldt, 2000; Carvalho et al., 2011, 2012; Réveillion & Maquart, 2015; Chapin & Hebets, 2016). Shrimps, millipedes, harvestmen and Psocoptera are known as regularly predated by one species each [according with Gil Wizen (pers. com., Nov 27th, 2017), Psocoptera are 1-2 mm long and preyed upon by the juvenile *Charinus israelensis* Miranda, Aharons, Gavish-Regev, Giupponi & Wizen, 2016, wandering in the bat guano, which they utilize as a hiding spot].

Crickets and cockroaches seem to be frequently predated by several amblypygid species, largely in caves, whereas moths have been reported as recurrent preys of two Neotropical Phrynidae (Beck & Görke, 1974; Hebets, 2002). Spiders are mentioned as predated by three amblypygid

species, but in the case of *C. israelensis*, only the immature individuals of *Loxosceles* spp. were consumed (G. Wizen, pers. com., Nov 27th, 2017). Terrestrial isopods are recorded as eaten by three species (Table II), but *C. israelensis* was observed that predated on a small-sized isopod species (up to 7 mm in length) in all parts of the cave, mainly on the vertical walls; also, a single adult *C. israelensis* eaten on a larger isopod (15 mm in length), that seemingly entered the cave from the outside (G. Wizen, pers. com., Nov 27th, 2017).

Mollusks have been recorded as predated by vinegaroons (Armas & Milera, 1989; Armas et al., 1989), harvestmen (Andre & Lamy, 1941), and spiders (Andre & Lamy, 1941; Fernández & Berovides, 1996), but rarely by scorpions (Lamoral, 1971; Alayón-García & Armas, 2010), and whip spiders. This is the second record of a mollusk as part of the diet of a whip spider (Table II)

Frogs and lizards seem to be trapped by largest amblypygids only (Table II). An interesting attempt of predation and active shunning of a dendrobatid poison frog by the Costa Rican *Phrynus pseudoparvulus* was recorded by Hovey et al. (2016).

With respect to the necrophagy, Peck (1974) reported it for *P. longipes* (that he identified as *Tarantula fuscimana*) from Aguas Buenas Cave, Puerto Rico, but this interesting record has been overlooked by posterior researchers, excepting Moyá-Guzmán (2009). Armas & Abreu-Collado (1999) mentioned for the same species a similar case observed in a Hispaniolan cave [it was mentioned with some doubt by Armas & Pérez-Gonzalez (2001) and Armas (2006)]. A few years later, García-Rivera et al. (2009) recorded three specimens of the Cuban large amblypygid *Paraphrynus robustus* Franganillo, eating on two dead bats, and recently, Prous et al. (2017) reported bat necrophagy by the large South American amblypygid *Heterophrynus longicornis* Butler. Now, it is out of any doubt that necrophagy might be a frequent behavior in natural populations of some whip spiders.

Reproductive effort

Chiriví-Joya & Armas (2012) mentioned a Colombian female of *P. barbadensis* (carapace median length 7.3 mm) that carried 27 embryos, similar to what was found in this work. For this species, Quintero (1981) recorded 9 to 24 eggs or embryos *per* batch, but its correlation with any morphometric variable was not explored. Positive correlation of the clutch size and the female length was also found by Weygoldt (2000) and Armas & Pérez-González (2001) in three Caribbean *Phrynus* species, although a linear relationship is not always present (Weygoldt, 2000).

Microhabitat preference

High association of *P. barbadensis* with decaying trunks and rocks seems to be in correspondence with the usually humid and temperate condition

of these microhabitats, excellent food source, availability of daytime shelters and appropriate places for reproduction. Although cannibalism occurs (Torres-Contreras et al., 2015), it is common to find several individuals in the same decaying trunk, usually interacting with each other.

Microhabitats as vertical structures (trees and rocky walls) are infrequently used by *P. barbadensis*, mainly because these sites are mostly occupied by *H. caribensis*, a potential predator.

Some species of the genus *Phrynus* are usually associated with large trees bearing buttresses (Hebets, 2002; Bloch & Weiss, 2002), but they are the biggest amblypygids in those places. Large South American species of the genus *Heterophrynus* also occur in similar microhabitats (Weygoldt, 1977; Dias & Machado, 2006; Chapin, 2014).

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