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Amblypygi parthenogenesis, embryonic and post-embryonic development: a case study with the Amazonian species *Charinus guto* Giupponi and Miranda, 2016 (Amblypygi: Charinidae)

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ABSTRACT

Parthenogenesis is documented in a few species of Amblypygi, but it is unknown how widespread in the order this reproductive behaviour is, and little has been researched regarding aspects of embryonic and post-embryonic development in the group. Here, we studied the parthenogenetic capacity of an Amazonian whip spider (*Charinus guto*) evaluating the time of egg and embryonic development and inter-moult period. We also provide a review on embryonic and post-embryonic development in Amblypygi, compiling and analysing data from 43 species in three families. Fifty-two females and 42 juveniles of *C. guto* were collected in fragments of a secondary forest in Belém (Brazil); specimens were kept in captivity and observed weekly from 2018 to 2020. Nineteen specimens were collected with and 32 without egg sacs. Fourteen of the non-ovigerous females developed eggs in captivity, six of them moulted (i.e. lost stored sperm from previous contacts with males) before developing an egg sac, proving to be parthenogenetic. The mean time between the first day in captivity and moult was 96 days. In both adults and juveniles, a mean of 147 days passed between first day in captivity and first moult, and 125 days for a second moult. After moulting, a mean of 113 days passed for the females to develop an egg sac; the embryonic development took a mean of 59 days. Juveniles left the mother's abdomen after 10 days of hatching from the egg and the mean number of live free-living protonymphs was five. Other amblypygids, especially charinids, have similar embryonic development and post-embryonic growth and a detailed discussion with all known information for whip spiders is presented. We also demonstrate a positive correlation between clutch size and female size across Amblypygi, in which larger females carry more eggs and have larger offspring regardless of climate and habitat.

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Introduction

Parthenogenesis is a type of asexual reproduction in which genetically identical offspring is produced through unfertilised eggs and is relatively rare compared the sexual reproduction (Lynch 1984; Lourenço 2008; Ross 2010). In Arachnida, parthenogenesis is reported for Amblypygi (Armas 2005; Weygoldt 2005, 2007), Araneae (Camacho 1994; Edwards et al. 2003; Korenko et al. 2009), Scorpiones (Lourenço et al. 2007; Francke 2008; Souza et al. 2016), Opiliones (Burns et al. 2018), Acariformes, and Parasitiformes (Oliver 1971; Freitas et al. 2002; Domes et al. 2007; Heethoff et al. 2011; Maraun et al. 2019). In Amblypygi, 99% of the species reproduce sexually, with males depositing a spermatophore containing a sperm sac that is picked up and stored by the female gonopod. Sperms are kept in a genital atrium for a few weeks and they fertilise eggs secreted by the ovary when passing through the atrium (Weygoldt 2000). When moulting, female amblypygids shed the ectodermal seminal receptacle and genital atria losing all stored sperm (Weygoldt 2000). However, some species of whip spiders produce viable eggs even after moulting, that is, without eggs meeting any male gametes, indicating parthenogenetic capability (Armas 2005; Weygoldt 2005, 2007).

Eggs laid by females (either by sexual or asexual reproduction) are stored inside an egg sac (or brood sac) located under the mother's abdomen (or opisthosoma), which is secreted by the ovaries and oviducts (Weygoldt 2000). The number of eggs varies according to female size, as has been demonstrated in Phrynidae whose carapace length correlates with offspring size (Weygoldt 2000; Armas and Pérez 2001; Torres et al. 2019). After completion of the embryonic period, prenymphae hatch from the egg, leave the egg sac, and climb the mother's opisthosoma to the dorsal side; this marks the beginning of the post-embryonic period. Then, the prenymphae hold to their mother's body with their claws and arolium (or pulvilli) (Wolff et al. 2015), while continuing their development, until moulting to protonymphae, which is the first free-living instar (Weygoldt 2000).

Although important advances on the understanding of courtship and sperm transfer have been made for Charinidae (Weygoldt 1999, 2002a, 2006, 2008), Charontidae (Weygoldt 2002a), Phrynichidae (Weygoldt and Hoffmann 1995; Weygoldt 1999, 2002b, 2002c, 2003, 2008, 2009) and Phrynidae (Peretti 2002; Weygoldt et al. 2010; Seiter et al. 2017), little is known regarding reproductive strategy, generation time, the number of offspring and details on parental care for the majority of whip spider species. The largest amblypygid family, Charinidae, with approximately 95 species, is the only one to produce offspring from unfertilised eggs. So far, two species of *Charinus* Simon, 1892 (Armas 2005; Weygoldt 2005, 2007) and one of *Sarax* Simon, 1892 (Seiter and Wolff 2014) are known to reproduce parthenogenetically (which is 3% of the total number of species of the family).

Charinus acosta (Quintero, 1983) from Cuba is one of the best-studied species of Amblypygi regarding distribution range and reproduction strategies, and only females are known among the more than 150 collected specimens (Quintero 1983; Armas and Ávila Calvo 2000; Armas 2000, 2005; Teruel and Rodríguez-Cabrera 2016). This species can successfully produce egg sacs in captivity after moulting, that is, losing any stored sperm, which demonstrates its ability to reproduce parthenogenetically (Armas 2000, 2005; Weygoldt 2000; Teruel 2011). Therefore, the absence of known males in such a well-sampled species reinforces *C. acosta* is an obligate parthenogenetic species (Armas 2000).

In *Charinus ioanniticus* Kristscher, 1959, from the Eastern Mediterranean, female-only populations are known from the islands of Rhodes and Kos (Greece) and it has been shown it can reproduce parthenogenetically in captivity (Weygoldt 2005, 2007). Nonetheless, males of *C. ioanniticus* have been recorded in populations from Turkey (Kovařík and Vlasta 1996; Weygoldt 2005; Seyyar and Demir 2007), Israel (Rosin and Shulov 1960), and Egypt (El-Hennawy 2002), showing that this species might be facultatively parthenogenetic (Weygoldt 2005; Seiter and Wolff 2014). Other populations of *C. ioanniticus*, such as those in continental Greece (Athens) (Agapakis and Miranda 2019), Italy (Colla et al. 2020), and Jordan (Shakhatreh et al. 2020), still require more studies to verify the exact type of reproduction, however, all known specimens are females. The only *Sarax* species known to reproduce parthenogenetically is *S. buxtoni* Gravely 1915 from Singapore, whose evidence for parthenogenesis came from captivity experiments (Seiter and Wolff 2014). In addition to these species, many other charinids are known from females only (Giupponi and Kury 2002; Miranda and Giupponi 2011; Jocque and Giupponi 2012; Giupponi and Miranda, 2016; Vasconcelos and Ferreira 2016, 2017; Miranda et al. 2016a, 2016b), which indicates that likely more species in the family are parthenogenetic.

Information on reproduction is particularly scarce for Amazonian species of Amblypygi (Weygoldt 1972; Baptista and Giupponi 2002, 2003; Giupponi and Kury 2002; Pinto-da-Rocha et al. 2002; Miranda and Giupponi 2011; Vasconcelos et al. 2013, 2014, 2016; Giupponi et al. 2016; Vasconcelos and Ferreira 2016, 2017; Miranda et al. 2016a). To further push the knowledge on the natural history of Amblypygi, we studied the parthenogenetic capacity of an Amazonian species of whip spider in captivity, *Charinus guto* Giupponi and Miranda, 2016, in which only females are known. We investigated gestational period, duration of maternal care, the time between ecdysis, offspring size, the time between gestations, and seasonality of reproduction for the species. We also tested for a correlation between female size and offspring size (number of eggs and pre- and protonymphae) in Amblypygi to investigate whether animals exposed to different environments (climatic and microhabitat conditions) from around the world exhibit the same maternal-size correlation (Rollinson and Rowe 2016).

Materials and methods

Specimens of *Charinus guto* were collected in fragments of secondary Amazonian rainforest in the Research Campus of the Museu Paraense Emilio Goeldi (MPEG) (1° 27′5.73″ S; 48°26′37.90″ W) and the Zoobotanical Garden Bosque Rodrigues Alves (1° 25′48.67″ S; 48°27′24.71″ W), both in Belém, Pará, Brazil. Specimens were collected through active search under rotting fallen trees, rocks, and remains of building material, such as roof tiles.

The whip spiders were individually kept in identified transparent plastic containers measuring 5 cm (width) x 15 cm (length), containing wet soil and a small piece of tree bark horizontally positioned. Amblypygids were fed, once a week, with terrestrial isopods (adults and juveniles) and termite workers, soldiers, and nymphs (*Nasutitermes* ssp. and *Heterotermes tenuis* (Hagen, 1858)), common prey in the environment in which *C. guto* is found. Specimens were observed once a week from 14 February 2018, to 27 January 2020.

A flowchart to illustrate the specimens included in each analysis were prepared in R using the packages *DiagrammeR* (Iannone 2020) and *ggplot2* (Wickham 2016).

The compilation of offspring size (number of eggs and pre- and protonymphs) in Charinidae, Charontidae, Phrynichidae, and Phrynidae was done by literature search using the keywords eggs, huevos, embriones, preninfas, prenymph, protonymph, and protoninfas (see Table 3). Carapace length was used as a proxy for female size (Weygoldt 2000), and the correlation between length and clutch size was evaluated through R-squared and p values. Data were curated and figures produced using the R packages *dplyr* (Wickham et al., 2021), *ggplot2, ggthemes* (Arnold 2021), *gridExtra* (Auguie 2017), and *tidyr* (Wickham, 2021).

After behavioural studies, individuals were preserved in 70% and 100% ethanol at MPEG (Belém, PA, Brazil) and Museu Nacional do Rio de Janeiro (Rio de Janeiro, RJ, Brazil).

Results

We collected 51 females and 42 juveniles of *Charinus guto* (Figure 1). We found 19 specimens in their natural environment with egg sacs and 32 without a brood sac. Fourteen of the non-ovigerous females developed eggs in captivity; six of them moulted before developing an egg sac, i.e. eliminated any potential sperm stored in the female's gonopod atrium; those six unmated females demonstrated the species is capable of parthenogenesis (Figure 1).

Among the specimens that developed egg sac after moulting (n = 6), the mean time between the first day of captivity and the first moult was 96 days (SD = 21.6). Among all adults and juveniles, a mean of 148 days passed between the first day in captivity and first moult (SD = 29.2; n = 24,) and 111 days from the first to the second moult (SD = 25; n = 8) (Table 1). *Charinus guto* moulted in all months of the year (Figure 2).

After moulting, it took a mean of 113 days (SD = 31.3) for females to develop an egg sac (n = 6) (Figure 3). Females of *C. guto* developed egg sacs in January, February, April, May, September, November, and December (Figure 4, Table 2). The embryonic development (from egg sac to prenymphs on the dorsum of the mother's abdomen) took a mean of 59 days (SD = 18.8; n = 11) (Figure 5), and juveniles left the mother's abdomen after 10 days of hatching from the egg (SD = 0.8; n = 8) (Figure 5).

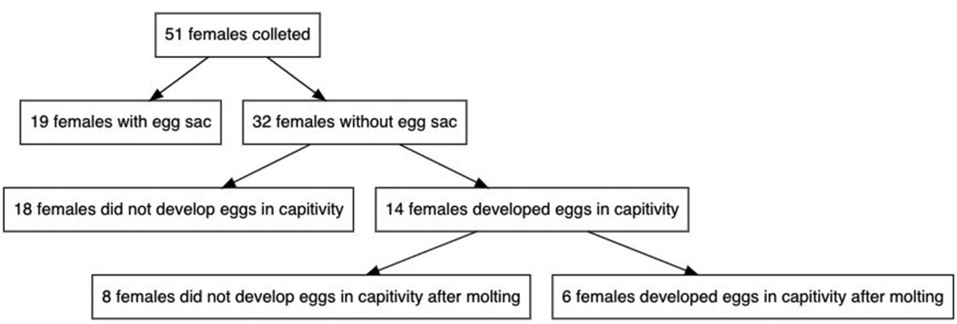

Figure 1. Flowchart illustrating the female specimens of *Charinus guto* Miranda and Giupponi, 2016 used in the study.

Table 1. Summary of development and growth time of *Charinus guto* Giupponi and Miranda, 2016.

Description	Days (mean)	Sample size
Time in captivity until first moult (specimens that developed egg sacs in captivity (left), all other specimens (right))	96/147	6/23
Time between 1st and 2nd moults	125	5
Time from moult to egg sac	113	6
Duration of embryonic development (eggs to protonymphs)	59	11
Time for protonymphs to leave mother's abdomen	10	8

In *Charinus guto*, the mean number of protonymphs that left the mother's opisthosoma was five (SD = 0.4; n = 19) (Table 3). For Amblypygi on average 15 juveniles leave the mother's abdomen (SD = 3.2; n = 14), a mean of 8 for Charinidae (SD = 1.4; n = 8), 28 for Phrynichidae (SD = 12,5; n = 2) and 23 for Phrynidae (SD = 6.6; n = 4). A significant positive correlation was found between the number of offspring and female size, with larger females laying more eggs than smaller females (R-squared: 0.4308, p-value: <0.001; Table 3, Figure 6).

Discussion

Amblypygi is the only order of Arachnida with post-ultimate ecdysis in all known species (Chapin and Hebets 2016). When reproduction is asexual, that is, through parthenogenesis, female whip spiders can yield many offspring throughout their life, since they do not depend on encountering males for mating. For example, Seiter and Wolff (2014), noted that the parthenogenetic species *S. buxtoni* produced egg sacs 4 months after the last set of embryos and only 2 months after the previous eggs hatching.

It is straightforward to assess if an amblypygid is parthenogenetic when specimens are successfully maintained in captivity. Female whip spiders lose any potentially stored

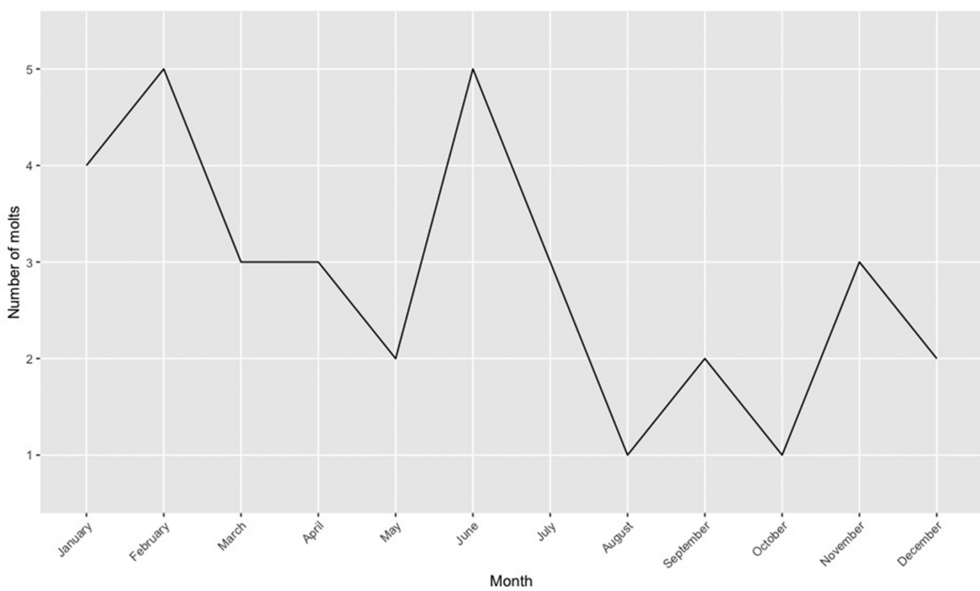

Figure 2. Total number of moults per month of *Charinus guto* Giupponi and Miranda, 2016 in captivity.

Figure 3. Dorsal habitus of *Charinus guto* Miranda and Giupponi, 2016 (upper); retrolateral view of ovigerous female (bottom). Photos: César Favacho.

sperm in the gonopods after moulting and the production of egg sacs after ecdysis is strong evidence of reproduction via non-fertilised egg (Weygoldt 1999; 2000, 2005, 2007; Seiter and Wolff 2014; Chapin and Hebets 2016). Although previous studies have shown

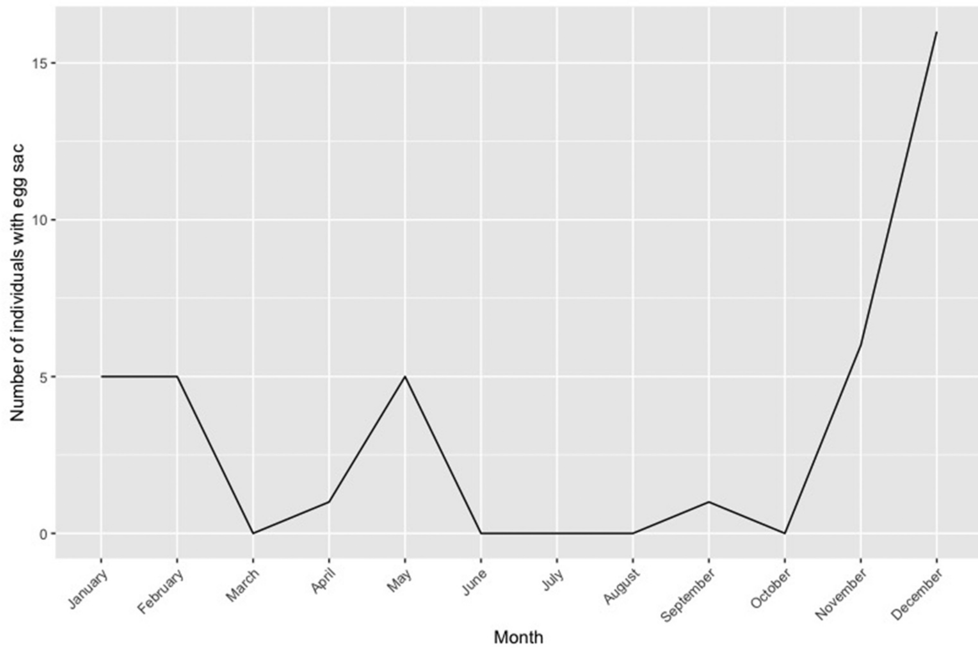

Figure 4. Number of individuals of *Charinus guto* Giupponi and Miranda, 2016 with egg sac per month.

that three species of Amblypygi are parthenogenetic (*C. acosta, C. ioanniticus*, and *S. buxtoni*), how widespread is parthenogenesis in the order and details on the time of gestation, offspring size, and length of inter-moult stages, are still largely unknown (Armas 2000; Weygoldt 2000, 2005; Seiter and Wolff 2014; Chapin and Hebets 2016). Here we provide an overview of the current state of knowledge on these topics, contextualise our results and point future directions for research.

Embryonic and post-embryonic development

The embryonic development (from eggs to prenymphs) of most whip spider species is considered to last about three to three and half months in laboratory conditions (26–28°C) (Weygoldt 2000; Chapin and Hebets 2016). In *C. guto*, the embryonic development took about 2 months (60 days; Table 1). Similarly, the gestation period of *C. acosta* develops for 51–62 days (Armas 2000, 2005), of *Charinus asturius* for 2 months (Pinto-da-Rocha et al. 2002), while *Charinus reddelli* Miranda et al., 2016c and *Charinus israelensis* Miranda et al. 2016

Table 2. Months of year when egg sacs were observed in Charinidae.

Species	Country	J	F	M	A	M	J	J	A	S	O	N	D	Reference
Charinus acosta	Cuba		■	■	■	■	■	■	■					Armas (2005)
Charinus asturius	Brazil	■	■	■							■	■	■	Pinto-da-Rocha et al. (2002)
Charinus ioanniticus	Greece		■	■	■	■								Weygoldt (2005, 2007)
Charinus guto	Brazil		■	■		■				■		■	■	This study
Charinus neocaledonicus	New Caledonia												■	Weygoldt 2006
Sarax buxtoni	SE Asia			■	■		■				■	■	■	Seiter and Wolff (2014)

develop eggs for longer periods, 150 and 90 days respectively (Miranda et al. 2016b, c). The difference in length of gestation between the first three species (*C. acosta, C. asturius*, and *C. guto*) to that observed in *C. reddelli* and *C. israelensis* might relate to differences in habitat. *Charinus acosta, C. asturius*, and *C. guto* inhabit the leaf litter of tropical forests, while the other two species are found inside caves in Belize and Israel, respectively. The strict environmental conditions subterranean environments play over its biota have been demonstrated to drive morphological, physiological, and behavioural adaptations. Examples are loss of pigmentation, reduction of eyes, and elongation of appendages (Mammola et al. 2020). Here, the observed difference of embryonic development in *Charinus*, that is, longer development time in cave species, might also result from adaptation to those constraints, such as food availability (i.e. lower energetic intake by the mothers living in caves compared to epigean females) and lower temperate (i.e. cave species with slower metabolism compared to the non-cave species). However, further research is needed to elucidate the potential drivers of those differences.

Juveniles of *Charinus guto* left the mother's abdomen after about 10 days of hatching from the egg and the mean number of whip spiders that left the abdomen was five (Table 3). For *C. acosta*, the prenymph stage lasted seven days and the offspring varied from four to nine (Armas 2000, 2005). There is no information about the duration of parental care for *C. ioanniticus*; regarding the size of the egg clutch, large females can carry 9–11 eggs, while smaller females carry one, four, or six eggs; after hatching, around 12 prenymphs stays in the mother's abdomen (Weygoldt 2005, 2007). In *C. israelensis*, the offspring stayed in the mother's dorsum for 12 days and the egg sac had between 9 and 30 eggs (Miranda et al. 2016b). In *C. asturius*, the egg sac can contain between 10 and 15 eggs and prenymphs remain on the mother for 14 days (Pinto-da-Rocha et al. 2002). Differences in offspring size might not relate to inherent physiological differences between the species, but due to the size of females when of the reproduction, as discussed below.

It has been noted that smaller females usually have a small brood, while larger females have a larger clutch (Weygoldt 2000; Armas 2005; Torres et al. 2019). This pattern is consistent both intra- and interspecifically in Amblypygi (Table 3, Figure 6). Large charontid, phrynid, and phrynichid species can carry between 50 and 80 eggs, while the maximum number of eggs for adult charinids (in which all species are smaller than in the other families) is 30 (Figure 6). Likewise, the highest number of prenymphs observed in a female's abdomen is 14 for charinids, while phrynichids can carry up to 53, and phrynids 58 (this number is unknown for Charontidae; Table 3, Figure 6). No offspring size difference was observed in species from different climates (e.g. Mediterranean vs tropical) and habitats (e.g. epigean vs hypogean) within individuals of similar size.

Parthenogenesis

We confirmed that *Charinus guto* is parthenogenetic because our results show it can produce viable eggs after moulting and without contact with other individuals, specifically they do not have sperm stored and did not have contact with males and still produced offspring. Additionally, only females of *C. guto* have ever been found in the field, even after intense searches, supporting our captivity experiments of females giving birth to other females.

While it took between 96 and 147 days for *Charinus guto* to moult in captivity (Table 1), *C. acosta* moulted after 31–59 days and *C. ioannticus* after 60–390 days (Armas 2000, 2005;

Table 3. Summary of the clutch size data in Charinidae, Charontidae, Phrynichidae, and Phrynidae. Asterisk denotes species capable of parthenogenesis.

Family/species	Country of observation	Number of eggs	n	Number of protonymphs	n	Reference
Charinidae						
*Charinus acosta**	Cuba	3–9	16	4–9	6	Armas and Ávila Calvo (2000), Armas (2005)
Charinus aguayoi	Puerto Rico	4–7	3	–	–	Armas (2010)
Charinus asturius	Brazil	10–15	2	14	N/A	Pinto-da-Rocha et al. (2002)
Charinus bruneti	Saint Barthélemy	9	1	–	–	Teruel and Questel (2011)
Charinus eleonorae	Brazil	5–15	2	–	–	Baptista and Giupponi (2003)
*Charinus guto**	Brazil	–	–	2–9	19	This study
*Charinus ioanniticus**	Greece	1–13	10	12	N/A	Weygoldt (2005, 2007)
Charinus israelensis	Israel	9–30	–	12	N/A	Miranda et al. (2016b)
Charinus kakum	Ghana	7	1	–	–	Harms (2018)
Charinus longitarsus	Peru	6–8	3	–	–	Armas et al. (2016)
Charinus pardillalensis	Venezuela	–	–	4	1	González-Sponga (1998)
Charinus perezassoi	Puerto Rico	2–7	6	3–7	2	Armas (2010)
Charinus pescotti	Australia	7–16	4	Up to 5	7	Gray and Robinson (1986)
Charinus reddelli	Belize	4–10	N/A			Miranda et al. (2016c)
Charinus sp.	Panama	6–13	2	–	–	Víquez et al. (2012)
Charinus wanlessi	Cuba	5	11	–	–	Armas (2006)
Sarax willeyi	Indonesia	7	1	–	–	Rahmadi and Kojima (2010)
Charontidae						
Charon grayi	Java	~80	1	–	–	Takashima (1950)
Phrynichidae						
Musicodamon atlanteus	Morocco	–	–	15	1	Weygoldt (2002b)
Phrynichus brevispina (as *P. scaber longispina*)	Somalia	20	1	–	–	Delle Cave and Simonetta (1975)
Phrynichus dhofarensis	Oman	~50	–	27–53	6	Weygoldt (2002c)
Phrynidae						
Acanthophrynus coronatus	Mexico	28	1	–	–	Armas et al. (2017)
Paraphrynus cubensis	Cuba	32	1	16–58	1	Armas and Ávila Calvo (2000), Armas (2006, 2013)
Paraphrynus laevifrons	Costa Rica	17–69	N/A	–	–	Víquez (2003)
Paraphrynus maya	Guatemala	13	1	–	–	Armas et al. (2018)
Paraphrynus pococki	Mexico	8	1			Luna et al. (2017)
Paraphrynus robustus	Cuba	51	1	–	–	Quintero (1983)
Paraphrynus williamsi	Mexico	31	1			Armas et al. (2018)
Phrynus alejandroi	Puerto Rico	–	–	5–13	5	Armas and Teruel (2010)
Phrynus barbadensis (as *P. gervaisii*)	Colombia	14–79	–	–	–	Chirivi-Joya and Armas (2012), Torres et al. (2019)
Phrynus barbadensis (as *P. gervaisii*)	Costa Rica	9–52	–	–	–	Víquez (2003)
Phrynus barbadensis (as *P. gervaisii*)	N/A	9–24	N/A	–	–	Quintero (1981)
Phrynus damonidaensis	Cuba	7–50	6	–	–	Quintero (1981)
Phrynus eucharis	Republica Dominicana	5–23	9	–	–	Armas and Pérez (2001)
Phrynus garridoi	Mexico	14	1	–	–	Armas (2006)

(*Continued*)

Table 3. (Continued).

Family/species	Country of observation	Number of eggs	n	Number of protonymphs	n	Reference
Phrynus hispaniolae	Republica Dominicana	4–14	6	–	–	Armas and Pérez (2001)
Phrynus kennidae	Republica Dominicana	11	1	–	–	Armas and Pérez (2001)
Phrynus longipes	Republica Dominicana	10	1	–	–	Armas and Ramírez (1989), Armas and Pérez (2001)
Phrynus maesi	Nicaragua			30	1	Armas (1995)
Phrynus marginemaculatus	Republica Dominicana, Bahamas	9–41	14	–	–	Muma (1967), Browne (1992), Weygoldt (2000), Armas and Pérez (2001), Armas (2014)
Phrynus noeli	Cuba	7	1	–	–	Armas (2006)
Phrynus parvulus	Guatemala	30	2	–	–	Armas et al. (2018)
Phrynus perrii	Mexico	6	1	–	–	Guzmán and Chirivi-Joya (2015)
Phrynus pinarensis	Cuba	76–94	3	–	–	Armas and Ávila Calvo (2000)
Phrynus pseudoparvulus	Costa Rica	36–40	2	–	–	Armas and Víquez (2001)
Phrynus whitei	Costa Rica	22–52	–	–	–	Víquez (2003)
Phrynus whitei	Nicaragua	14–19	3	14	1	Armas and Maes (2000)

Weygoldt 2005). Dissimilarities in intermolt time could be a result of species' specific physiology or captivity conditions (the better the captivity mimics natural conditions, the faster the animal moults). *Charinus guto* moulted throughout the whole year (Figure 4, Table 2). In contrast, *C. acosta* from Cuba was reported to moult between April and October (Armas 2000, 2005), *C. ioanniticus* from the eastern Mediterranean between August and February (Weygoldt 2005, 2008; Agapakis and Miranda 2019), *S. buxtoni* from southeast Asia between January and July (Seiter and Wolff 2014), *Charinus africanus* Hansen, 1921 from western Africa from December to May (Weygoldt 2008) and *Charinus neocaledonicus* Kraepelin, 1895 from New Caledonia moults from March to July (Weygoldt 2006). The lack of marked seasonal variation in growth for *C. guto* is possibly explained by the absence of seasonality in the northern part of the Amazon region, where the species is found (Bush 2017; Amorim et al. 2019; Giupponi et al. 2016.

After ecdysis, it took a mean of 113 days for a female *C. guto* to develop a clutch of eggs (Table 1). In contrast, females of *C. acosta* formed egg sacs between 31 and 88 days after ecdysis or previous oviposition (Armas 2000, 2005). For *C. ioanniticus*, egg sac development takes from 3 to 8 months (Weygoldt 2005). In *S. buxtoni*, a mean of 3 months is needed for a female to produce an egg sac after moulting; it has also been observed for this species that younger specimens (second generation 'virgins') take longer to produce egg sacs, going through two ecdyses before having offspring (Seiter and Wolff 2014).

Although *C. guto* did not have seasonal reproduction, egg-laying in other non-parthenogenetic species in the genus is seasonal (Table 2). For example, *C. asturius* Pinto-da-Rocha, Machado and Weygoldt, 2002 from Ilhabela, Brazil, develops egg sacs during the wet-warm season, from October to March (Pinto-da-Rocha et al. 2002); and females of *C. neocaledonicus* Simon, 1895 from Southern Province of Grande Terre, New Caledonia, were observed with egg sacs in December (Weygoldt 2006). Seasonality is also observed among amblypygids with parthenogenesis, such as *C. acosta* from Cuba, in which ovigerous females in captivity are common from March to August, while in the natural environment they were observed in June–August, the warm and humid months (Armas 2000, 2005).

Figure 5. Female of *Charinus guto* Giupponi and Miranda, 2016 with protonymphs on the abdomen's dorsum (upper); juveniles after leaving the mother's body (bottom). Photos: César Favacho and Vanessa Vidal.

A population of *C. ioanniticus* from the Island of Rhodes, Greece, develops egg clutch from February–June, apparently always moulting between gestations (Weygoldt 2005, 2007). An apparent lack of seasonality was also observed in *S. buxtoni*, which lays eggs in April, June, October–December (Table 2).

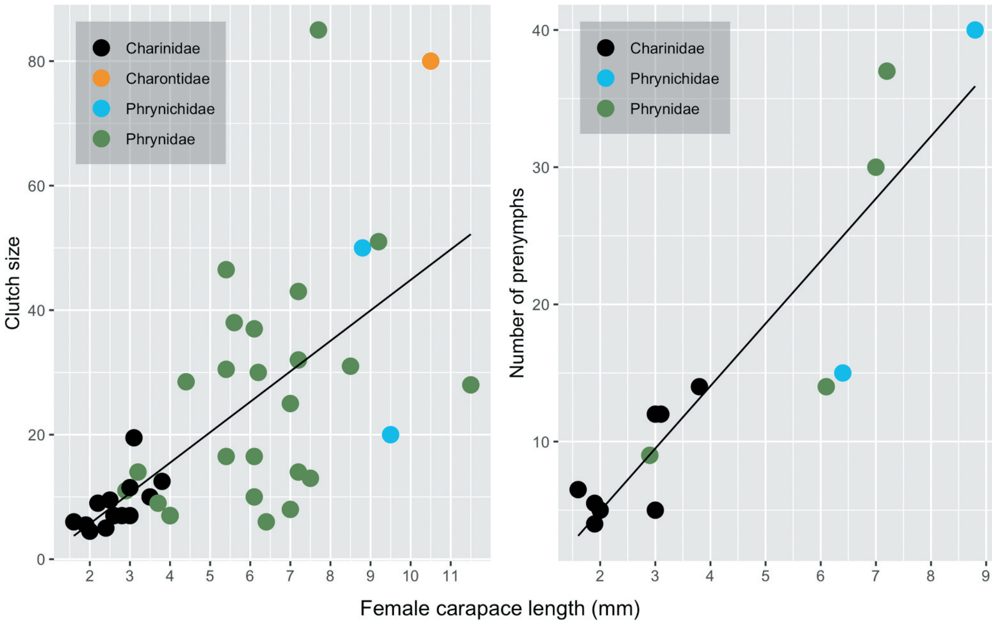

Figure 6. Graphs showing the correlation between clutch size (number eggs; left) and number of prenymphs (right) against female carapace length for 43 Amblypygi species in four families. Details on the values are listed in Table 3.

Further studies are still necessary to unveil details on the reproduction strategies, embryonic and post-embryonic development of other Amblypygi species, enabling an evolutionary perspective on reproduction in the order. In addition, research is needed on the type of parthenogenesis (e.g. arrhenotoky, thelytoky) amblypygids goes through to elucidate the genetics of whip spider's asexual reproduction.

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