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BIOLOGICAL SCIENCES

Population dynamics and reproductive phenology of a harvestman in a tidal freshwater wetland

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Abstract: There is a great amount of ecological information for terrestrial arthropods in several types of habitats, but few studies have focused on populations living in tidal freshwater wetlands. During a two-year field survey, we studied the temporal dynamics of the harvestman *Discocyrtus prospicuus* inhabiting a freshwater wetland exposed to predictable tides and unpredictable floods. We also explored the effects of temperature, precipitation, and tide level on the population dynamics and reproductive phenology. Our findings are markedly different from those reported in other harvestman species living in different habitats and also from conspecific populations living in the mainland. Adults, subadults, and juveniles remain active throughout the year, and a long breeding season was observed. However, the number of adults, subadults, juveniles, and egg clutches showed clear variations over the year without a consistent seasonal pattern. Contrary to the general pattern in harvestmen, no climatic variables were significant predictors of abundance fluctuations. We discuss the potential masking effect of unpredictable flood events, obscuring the relationship between abundance and abiotic factors. In addition, given that climatic conditions seem to favor harvestmen activity throughout the year, we also hypothesized that abundance variations could be driven mainly by biotic rather than by abiotic interactions.

Key words: Abiotic factors, breeding season, phenology, sex-ratio, unpredictable floods.

INTRODUCTION

Temperature and precipitation are key factors influencing the spatial and temporal distribution of terrestrial arthropods (Chown & Nicolson 2004). These two abiotic factors are also considered the most critical determinants of the distribution, habitat use, and richness of species belonging to the order Opiliones, commonly known as harvestmen or daddy long-legs. Harvestman species are usually absent at the lower ends of temperature and precipitation ranges but are diverse and abundant in places with moderate to high temperature and precipitation (reviewed by Curtis & Machado 2007). In a study conducted along three elevational gradients in the Brazilian Atlantic Forest, both species density and specimen abundance of litter-dwelling harvestmen were positively correlated with temperature and humidity (Almeida-Neto et al. 2006). Lack of spiracular control, low osmotic hemolymph concentration, and a high surface/volume ratio may explain why harvestmen occur mainly in damp and shaded areas (Santos 2007). Temperature and precipitation are also important determinants of harvestmen phenology, influencing embryonic, and post-embryonic development, as well as adult activity (Belozerov 2012). A recent comparative study, including more than 100 harvestman species belonging to all living suborders and distributed worldwide, has shown that the length of the breeding season is primarily influenced by the number of warm months. Precipitation plays a significant, but secondary role in modulating the period devoted to reproduction (Machado et al. 2016).

The role of other abiotic factors on the ecology and phenology of harvestman species is far less studied. For European trogulids (Dyspnoi), for instance, species occurrence is correlated with soils derived from limestone, which are rich in calcium carbonates (Hillyard & Sankey 1989). Given that representatives of this family feed exclusively on snails, organisms that require calcium carbonate to build their shells, the distribution of trogulids may actually reflect the distribution of their prey (Curtis & Machado 2007). In central Amazonia, reproduction and early development of two species of litter-dwelling harvestmen (Laniatores) occur on tree trunks while the forest is flooded. After the water recedes, development to adulthood proceeds on the forest floor before the individuals retreat once more up into the trees (Friebe & Adis 1983). Thus, for species living in places subject to seasonal flooding, habitat use, population dynamics, and reproductive phenology may be adjusted to annual hydrological regimes.

The harvestman *Discocyrtus prospicuus* (Holmberg 1876) (Laniatores: Gonyleptidae) is found primarily in shady forests of temperate environments in central and northern regions from Argentina and Uruguay (Acosta & Guerrero 2011). Some populations inhabit a tidal freshwater wetland in Argentina (the Lower Delta region), a region without a dry season and hot summer (Peel et al. 2007). The hydrological regime is mainly affected by lunar tides, but also by unpredictable floods produced by south to southeastern winds (Kandus & Malvárez 2004). When the tide level is high, the Lower Delta islands are not flooded. However, the soil is drenched, which may have either positive or negative effects on ground-dweller arthropods (e.g. Anderson & Smith 2000, Antvogel and Bonn 2001, Vannier 1983, Verhoef 1977). To date, there are no field surveys of harvestmen inhabiting tidal freshwater wetlands, and the only information available about the phenology of *D. prospicuus* is limited to a few *ad libitum* observations of continental populations from Uruguay (Stanley 2011, Toscano-Gadea 2011). Therefore, the species is an exciting study system to investigate how species adjust the timing of life-cycle events when faced with different environmental parameters (e.g. hydrological regime). Here we describe the temporal dynamics of the harvestman *D. prospicuus* inhabiting a Lower Delta island during a two-year field survey. In addition, we investigate whether variation in temperature, precipitation, and tide level influence the population dynamics and reproductive phenology in this island population.

MATERIALS AND METHODS

Study area

We conducted this study in one of the Lower Delta islands of the Paraná River (34°22’55”S, 58°34’38”W; ~8 m above sea level) in the northeastern part of the Buenos Aires province, Argentina. This region is a tidal freshwater wetland with a temperate climate: mean annual temperature of 16.7 °C (min.–max. = 6–30 °C) and mean annual rainfall of 1,073 mm, without marked monthly variation in precipitation levels (Kandus & Malvárez 2004; Fig. 1). The island lies in the downstream sector of the Lower Delta region, which is dominated by predictable tides and unpredictable floods produced by south to southeastern winds (Kandus & Malvárez 2004). Winds can raise the water level up to 2.5 m above the average level, and floods may last from several hours to a few days (Kandus et al. 2006). The flooding period depends, among other things, on the topography because the island has an elongated shape with levees surrounding their perimeter and a depressed central portion that accumulates water (Fig. 2). Because the study island shows a high degree of anthropization, we selected a slightly tree-covered area of 2,500 m^2 located 40–120 m inland from the stream coast as the sampling area. This site is only occasionally flooded and has moderate draining efficiency (Fig. 2). Moreover, the site has numerous fallen logs that can be used by individuals of *D. prospicuus* as diurnal shelter and/or oviposition sites.

Fieldwork

As unpredictable floods change the location and number of fallen logs that can be inspected, we were unable to mark and track marked logs to be used as sampling units throughout the entire fieldwork. Thus, the sampling method was based on examining all fallen logs found within the sampling area (2,500 m^2). The sampling area was inspected each month from August 2012 to July 2014, totaling two years of samples. The survey began regularly at 10:00 AM, and it usually lasted from 3 to 3.5 hours, during which we carefully inspected all fallen logs in the sampling area. From each log, we recorded the number and sex of adults and subadults, the number of juveniles, and the number of egg clutches. We visited the study site once a month, and each monthly sampling lasted one day. Given that the harvestmen we found each month were not collected or individually marked, the same individual could be counted in different samplings during the study period.

Adult harvestmen can be easily distinguished from subadults because the later do not have complete tarsal segmentation. Moreover, males and females of *D. prospicuus* can be easily distinguished because males have conspicuous

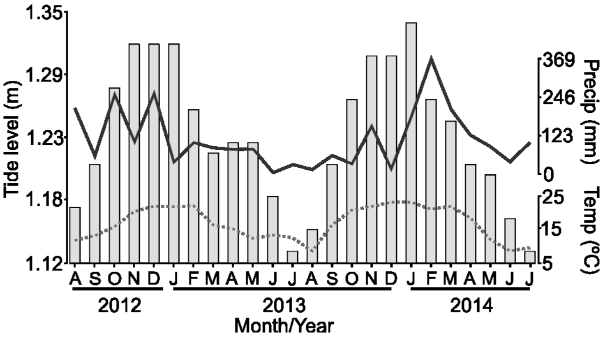

Figure 1. Monthly climatic data recorded during two years of monthly samples in a tidal freshwater wetland from Argentina. Temp: average of the mean daily temperature (dotted line); Precip: cumulative precipitation (solid line); Tide level: average of the daily highest tide (bars).

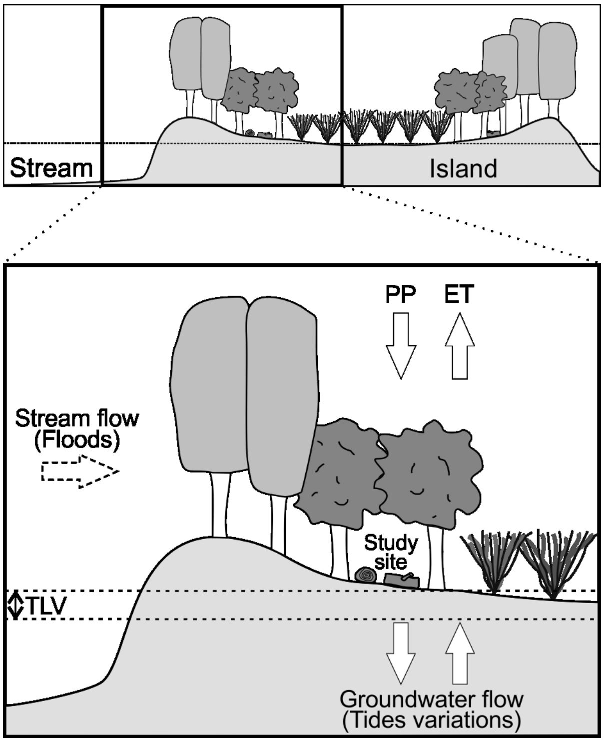

Figure 2. Schematic representation of the island topography showing the study area, the principal water inputs, and tide level variations (TLV). Figure adapted from Kandus & Malvárez (2004) and Batzer & Boix (2016).

spines on the coxa and femur of the fourth pair of legs (Ringuelet 1959). Subadult males can be distinguished from fifth instar juveniles because the former already have incipient armature on the coxa and femur of the fourth pair of legs. Subadult females can be distinguished from fifth instar juveniles by differences in body size. According to measures we took from individuals collected during preliminary surveys, the dorsal scute length of subadult females is always larger than 3.4 mm. Thus, all non-adult individuals without any signal of leg armature and smaller than 3.4 mm were classified as juveniles. Finally, females of the population studied here do not lay isolated eggs, as previously recorded for *D. prospicuus* populations in the mainland (Canals 1936). Instead, the eggs are laid in small clutches, and females were seen resting over the eggs (P. P. Iglesias and M. O. Pereyra, unpublished data). Therefore, it was easy to locate and record the presence of egg clutches under the fallen logs during the study period.

Voucher specimens were deposited in the Arachnological collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” – CONICET, Buenos Aires, Argentina (MACN-Ar 40300).

Climatic data

Temperature and precipitation data were obtained from the Meteorological Station “Delta del Paraná” (Instituto Nacional de Tecnología Agropecuaria, INTA), located 35 km from the study site. Tide records for San Fernando Port were obtained from Servicio de Hidrografía Naval, Ministerio de Defensa de la República, Argentina. Monthly data are based on average daily temperature, cumulative precipitation, and the average of the daily highest tide (Fig. 1).

Statistical analyses

To compare the number of males and females (subadults and adults) recorded in the sampling area at each month, we used a generalized linear model (GLM) with a binomial distribution of errors. If mean monthly sex ratio (number males/ number of females) estimated by the model was higher than one and the 95% confidence interval (CI) did not cross one, we considered the sex ratio male-biased. In turn, if the mean monthly sex ratio estimated by the model was lower than one, and the 95% CI did not cross one, we considered the sex ratio female-biased.

To evaluate the effect of temperature, precipitation, and tide level (predictor variables) on the number of adults, subadults, juveniles, and egg clutches (response variables), we used generalized least square (GLS) models. Although the typical analysis for count data is a GLM with Poisson distribution of errors and log link function, our response variables were temporally auto-correlated, and the assumption of independence was not met. Therefore, we chose to pursue a more complex but appropriate model framework. To account for the auto-correlation effect, a temporal correlation structure (auto-regressive model of order 1:AR-1) was included in GLS analyses. The correlation structure considers that the farther away two data points are separated in time, the lower their correlation is (Zuur et al. 2009). We assessed multi-collinearity between the predictor variables by means of variance inflation factors (VIFs) using the *vif* function from the *car* package (Fox et al. 2007). The VIFs of each variable were in the range of 1.00 to 1.05, which indicates low levels of multi-collinearity (following Dormann et al. 2013 and Esposito Vinzi et al. 2010). The predictor variables were fitted as residuals obtained from a linear regression against day length to remove the seasonal trend (Rivrud et al. 2010). They were centered and standardized to make the coefficients of the models comparable (Schielzeth 2010). The variables number of clutches, subadults, and juveniles were square-root transformed to meet statistical criteria of normality. The list of candidate models included a complete model containing only the additive effect of the three predictor variables and all combinations of simpler models, including the null model. We choose the most plausible model selecting the one with the lowest AICc, which is the Akaike's information criterion (AIC) for small samples (Bolker 2008, Symonds & Moussalli 2011). The most parsimonious model was the one with the lowest AICc value, & all models with ΔAICc < 2 were considered as equally parsimonious (Burnham & Anderson 2003). Variables were considered important if their model-averaged 95% confidence intervals did not overlap zero.

All the statistical analyses were run in the software R version 3.5.1 (R Core Team 2015) using the packages nlme (Pinheiro et al. 2014) and MuMIn (Barton 2015).

RESULTS

Phenology

Adults of *D. prospicuus* were recorded throughout the year, but we found a decrease in the number of individuals during the austral late spring-early summer period (Fig. 3a). The lowest number of individuals was recorded in December 2013. We recorded juveniles during all months and subadults during all months except August 2012 and November 2013. The number

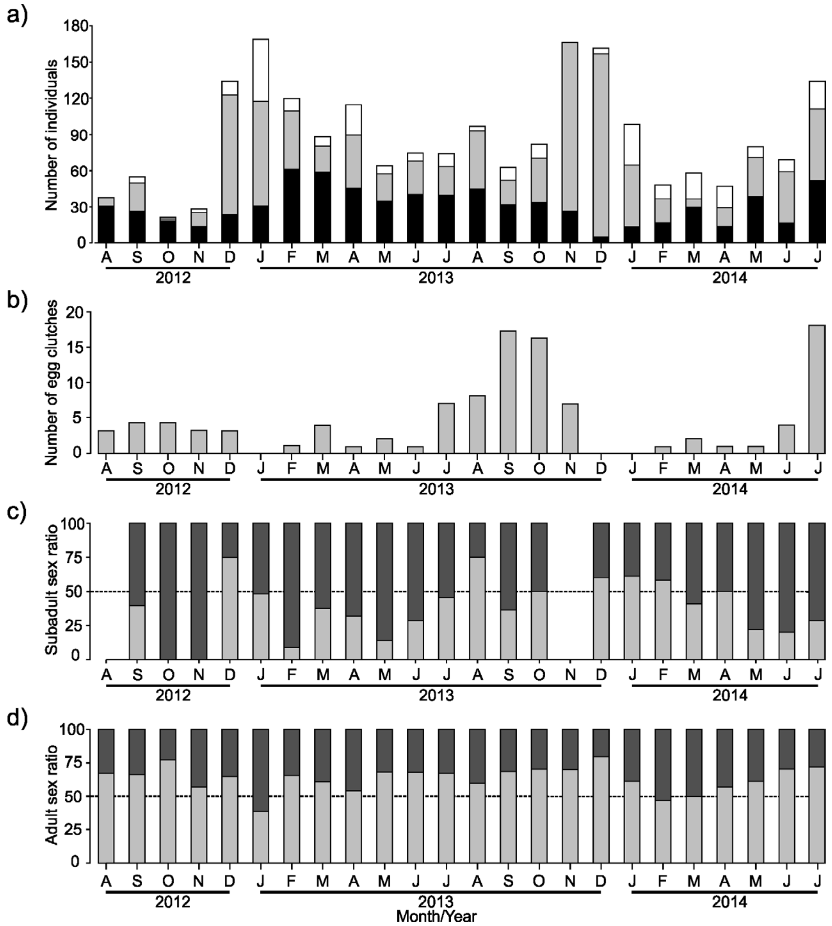

Figure 3. Population dynamics and reproductive phenology of the harvestman *Discocyrtus prospicuus* in a tidal freshwater wetland from Argentina. (**a**) Monthly numbers of adults (black), subadults (white), and juveniles (gray). (**b**) Monthly numbers of egg clutches found in each month. (**c**) Monthly sex-ratio of subadults (males = dark grey; females = light grey). (**d**) Monthly sex-ratio of adults (males = dark grey; females = light grey).

of juveniles showed a peak in December 2012–January 2013 and November–December 2013 (Fig. 3a). The number of subadults, in turn, showed a peak in January, both in 2013 and 2014 (Fig. 3a). Egg clutches were found throughout the year, except in January and December 2013, and January 2014 (Fig. 3b). There were peaks in the number of egg clutches in September–October 2013 and July 2014 (Fig. 3b). In general, subadult sex ratio was male-biased (estimate = 1.34; 95% CI = 1.07–1.69, Fig. 3c). However, adult sex ratio was female-biased (estimate = 0.57; 95% CI = 0.49–0.66, Fig. 3d). From the 24 months of samplings, in only two we found more adult males than adult females (Fig. 3d).

Effects of abiotic factors

The environmental variables included in this study had little effect on monthly variations in population composition (Table I). The best-ranked model to describe monthly variations in the number of adults included temperature, precipitation, and tide level (Table I). In contrast, the null model was the best ranked model to describe monthly variations in the abundance of subadults, juveniles, and egg clutches (Table I). Although one or more predictor variables were included in the other models with ΔAICc < 2 for the four response variables (Table I), no predictor variables were considered important when coefficients were model-averaged, with all 95% confidence intervals overlapping zero (Table II).

DISCUSSION

Seasonal variations in population size seem to be the rule among harvestmen, and this pattern has already been described for several species living in both temperate and tropical regions (Curtis & Machado 2007). The harvestman *D. prospicuus* was no exception, and the number of adults, subadults, and juveniles showed clear variations throughout the year (Fig. 3a). However, contrary to other species, in which the peak in the number of adults occurs during spring and summer (e.g. Acosta et al. 1995, Gnaspini 1996, Mestre & Pinto-da-Rocha 2004), the population dynamics of *D. prospicuus* does not follow a consistent seasonal pattern. In 2013, the peak in the number of adults occurred in late summer (February–March), but the number of adults recorded during this same period in 2014 was very low when compared with the beginning of the winter (July). The lack of clear seasonal fluctuation in the abundance of adults may be related to the unpredictability of wetlands, which are affected by occasional floods. In our study site, floods produced by south to southeastern winds may disturb the habitat, especially the fallen logs used as shelter and oviposition site by individuals of *D. prospicuus*. Floods may also kill some individuals that are unable to disperse to a non-flooded area (Klimeš 2002). Thus, unpredictable floods may induce equally unpredictable variations in population dynamics of *D. prospicuus* living in tidal wetlands. This scenario is very different from seasonal flooding in the Amazon forest, where both population dynamics and reproductive phenology are adjusted to predictable variations in the water levels (Friebe & Adis 1983).

No seasonal interruption in the reproductive activity of *D. prospicuus* was detected (Fig. 3b). The length of the breeding season in harvestmen is primarily influenced by the number of months with a mean temperature above 5 °C; whereas precipitation has a secondary, but still important effect (Machado et al. 2016). In our study site, the mean monthly temperature is always above 5 °C, and precipitation is not markedly seasonal.Thus, both temperature and precipitation (Fig 1).

Table I. Best models to predict the number of adults, subadults, juveniles, and egg clutches of the harvestman *Discocyrtus prospicuus* in a tidal freshwater wetland from Argentina.

Predictor variables	K	AICc	ΔAICc	w
Number of adults (males and females)				
Temperature + Precipitation + Tide level	6	189.7	0.00	0.241
Temperature + Tide level	5	190.0	0.29	0.208
Precipitation + Tide level	5	190.2	0.56	0.182
Tide level	4	190.9	1.19	0.133
Temperature + Precipitation	5	191.8	2.09	0.085
Temperature	4	192.5	2.78	0.060
Precipitation	4	192.6	2.90	0.057
Null model	3	193.6	3.88	0.035
Number of subadults (males and females)				
Null model	3	97.7	0.00	0.382
Precipitation	4	98.8	1.06	0.225
Temperature	4	99.5	1.77	0.157
Tide level	4	100.8	3.07	0.082
Temperature + Precipitation	5	101.2	3.44	0.068
Precipitation + Tide level	5	102.3	4.54	0.040
Temperature + Tide level	5	102.6	4.84	0.034
Temperature + Precipitation + Tide level	6	104.8	7.07	0.011
Number of juveniles				
Null model	3	114.6	0.00	0.260
Temperature	4	115.1	0.45	0.207
Precipitation	4	115.6	0.94	0.163
Tide level	4	116.3	1.66	0.113
Temperature + Precipitation	5	116.3	1.72	0.110
Temperature + Tide level	5	117.5	2.85	0.063
Precipitation + Tide level	5	117.6	3.02	0.058
Temperature + Precipitation + Tide level	6	119.2	4.57	0.027
Number of egg clutches				
Null model	3	77.4	0.00	0.501
Tide level	4	79.3	1.94	0.190
Precipitation	4	79.9	2.47	0.146
Temperature	4	81.2	3.86	0.073
Precipitation + Tide level	5	82.1	4.71	0.048
Temperature + Tide level	5	83.6	6.22	0.022
Temperature + Precipitation	5	84.2	6.79	0.017
Temperature + Precipitation + Tide level	6	86.8	9.44	0.004

K is the number of parameters in the model, AICc is the Akaike's information criterion for small samples, ΔAICc is the difference between the AICc value of the model and the best-ranked model, and *w* is the weight of the model. When model averaged, 95% confidence intervals overlap with zero for all variables (see Table II).

Table II. **Coefficients of the predictor variables based on model average. The full list of models for each response variable is presented in Table I. When the 95% confidence interval does not cross zero, the coefficient is highlighted in bold.**

Response variable	Coefficient (95% confidence interval)			
	Intercept	Temperature	Precipitation	Tide level
Number of adults	**31.92** (21.02, 42.82)	0.53 (-5.49, 7.30)	-1.03 (-4.37, 6.44)	-3.84 (-9.86, 2.18)
Number of subadults	**3.12** (2.17, 4.07)	0.42 (-0.32, 1.16)	-0.52 (-1.18, 0.13)	—
Number of juveniles	**5.93** (3.74, 8.12)	-0.72 (-1.78, 0.32)	-0.61 (-1.54, 0.31)	-0.44 (-1.48, 0.60)
Number of egg clutches	**1.86** (0.79, 2.92)	—	—	-0.32 (-0.77,0.12)

conditions seem to favor reproductive activity throughout the year. However, in a continental population from Uruguay facing similar climatic conditions (i.e. seasonal variation in temperature and precipitation), the breeding season of *D. prospicuus* is restricted to the wettest and warmest months, from October to March (Toscano-Gadea 2011). Therefore, the interpopulation difference in the length of breeding season cannot be explained by these two abiotic factors. We argue that high soil moisture throughout the year, as occurs in coastal wetlands around the world (Tiner 2018), could explain this difference. Given that harvestman eggs are sensitive to dehydration (Belozerov 2012), high soil moisture may favor no interruption in the reproductive activity of *D. prospicuus* in tidal wetlands. The length of the breeding season is important because it influences the synchrony of female reproduction and the intensity of male-male competition for mates (Emlen & Oring 1977). At the interspecific level, short breeding seasons in harvestmen are associated with scramble competition polygyny mating system and low sexual dimorphism related to male weaponry (Machado et al. 2016). At the intraspecific level, however, we have limited data on how the type of mating system and the magnitude of sexual dimorphism vary between populations (e.g. Burns & Tsurusaki 2016). Therefore, *D. prospicuus* may be a good study species to explore this question.

Although we do not have quantitative data on sexual differences in survival or movement during development for any harvestman species, the data gathered here show that subadult sex ratio was male-biased (Fig. 3c). This finding suggests that male survival during juvenile stages may be higher than female survival or that females tend to disperse to other areas before reaching adulthood. However, the sex ratio was female-biased after individuals reach adulthood (Fig. 3d), which contrasts with other species of Laniatores studied (e.g. Ferreira et al. 2009, Gnaspini 1996, Mestre & Pinto-da-Rocha 2004, Pinto-da-Rocha 1996a,b). Since surrounding areas in the island exhibit a high degree of landscape anthropization (where we never found *D. prospicuus* individuals) or are depressed areas that accumulate water, the hypothesis of an active dispersion strategy can be rejected. Nevertheless, a passive dispersal could take place since this species can survive long-distance raft dispersal during flooding events (Guerrero et al. 2017)

Most harvestmen species belonging to the suborder Laniatores occur in a diversity of habitats where population dynamics seems to be affected mainly by temperature and/or precipitation (Acosta et al. 1995, Gnaspini 1996, Mestre & Pinto-da-Rocha 2004). Contrary to this general pattern, none of the studied variables was a strong predictor of individual abundance in this island population. Unpredictable variations in population density due to flooding events may obscure the relationship between abundance fluctuations and abiotic factors. However, given that fluctuations in temperature and soil moisture seems to be small enough to favor harvestmen activity throughout the year, abundance variations could be also driven by biotic rather than by abiotic interactions. Harvestmen predators and/or food availability may play an important role in the regulation of population density (Batzer & Boix 2016). As in the case of European trogulids, whose distribution reflects the distribution of their prey (Curtis & Machado 2007), abundance variations of *D. prospicuus* may be reflecting prey abundance fluctuations over the year. The match-mismatch hypothesis postulates that those individuals that best match their phenology with resource phenology have the highest fitness (Cushing 1990). Given that offspring diets vary throughout ontogeny, several prey phenologies must be considered. Fluctuations on ground-dwelling invertebrates, such as small arthropods and earthworms, may decrease or increase food availability to adults and subadults (e.g. Vannier 1983, Kizilkaya et al. 2011). However, given body size constraint, fluctuations in the abundance of micro-arthropods may increase or decrease food supply to juveniles. Harvestman eggs are highly sensitive to fungal infection (Cokendolpher & Mitov 2007), and fungi also show a well-marked periodicity throughout the year (Gulis et al. 2006). Temporal changes in vegetation and soil properties may increase the availability and diversity of suitable microhabitats for both prey and predators (De Szalay & Resh 2000). Also, although we focused on monthly variations of the daily highest tide, changes in water-level fluctuations can occur over varying time scales—from hourly to decadal (Cooper & Uzarski 2016). It has been shown that regular water-mixing action helps to distribute nutrients and other dissolved materials that could affect ground-dwelling invertebrates (Cooper & Uzarski 2016). For instance, micro-arthropods usually respond to waterlogging performing vertical migrations in the soil (Eisenbeis & Wichard 2012). Despite their importance for management and conservation issues, the complex ecology of wetland invertebrates is still poorly known (Batzer & Boix 2016). In line with this, the predators or the preys of *D. prospicuus* in natural conditions in this area are also unknown.

There is a great amount of ecological information for terrestrial arthropods in several types of environments, but few studies have focused on populations living in tidal freshwater wetlands. Our findings indicate that the population dynamics and reproductive phenology of the harvestman *D. prospicuus* in a tidal freshwater wetland are markedly different from other harvestman species living in other types of habitats. In forests, grasslands, and even caves, water is a limiting factor, so that abundance, individual activity, and the reproductive period are positively related to rainfall (Curtis & Machado 2007). In wetlands, constant high moisture coupled with mild temperatures probably allows individuals of

D. prospicuus to remain active throughout the entire year and to have a more extended breeding season than conspecific populations living in drier habitats in the mainland. In the future, it would be interesting to study populations of *D. prospicuus* living in different habitat types to better understand how local ecological conditions shape interpopulation variations in ecological, behavioral, and life-history traits.

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P.P.I. and M.O.P conceived of the study and carried out the fieldwork. P.P.I. performed the analyses and wrote the original draft of the manuscript. M.O.P. provided critical comments on the manuscript. All authors approved the final version of the manuscript for submission.