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Strong seasonality and clear choice of resting plant in a Neotropical harvestman (Arachnida: Opiliones)

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Abstract. Preliminary observations suggested that the Neotropical harvestman *Jussara* sp. (Sclerosomatidae, Eupnoi) had a patchy distribution and a marked seasonality, comparable to species in the Northern hemisphere. This would be an unusual pattern, since conditions of temperature and humidity are very different between tropical and temperate environments. Using a mark-recapture method, we investigated the phenology, habitat use and individual movement of *Jussara* sp. in a tropical rainforest in southern Brazil. We found a very marked seasonality in the population of adults, with a positive correlation between temperature, humidity and number of adults found. Adults were found only in the wet and warm months and significantly preferred the plant *Psycothria suterella* (Rubiaceae) as a resting substrate, spending the days motionless on its leaves, often in groups. The same individuals were found for a maximum of three months after their first capture, 30 m from their original site of capture. At night, the harvestmen would descend from the plants, forage and interact with conspecifics on the leaf litter. In this first long term behavioral study with a representative of the suborder Eupnoi in Brazil, we provide quantitative evidence that, despite the milder climate, Neotropical harvestmen may show a seasonality similar to the seasonality shown by related species in temperate regions.

Keywords: Microhabitat selection, phenology, stenochrone, mark-recapture, Sclerosomatidae

Habitat selection is influenced by the quality of resources found and also by the opportunities for survival and reproductive success of a given species (Brown 1969; Schowalter 2012). It is therefore a result of the balance perceived by animals between costs, such as exposure to predators, dehydration, etc., and benefits, such as proximity to potential mates and food abundance (Van Beest et al. 2012). In this way, such balance may be obtained by alternating between different micro-habitats: animals may alternate between open places for foraging and more sheltered areas that offer more protection against predators (Godvik et al. 2009).

Seasonality can also influence the distribution of an animal population, as previously observed in distinct terrestrial invertebrate taxa (Powell & Logan 2005; Yaro et al. 2012; Belozerov 2013). The intensity of seasonality is often related to temperature and humidity (Wolda 1988). In temperate regions, where the climate varies more drastically between seasons, the adults of several invertebrates die when winter approaches, and juveniles or eggs overwinter (Wolda 1988; Belozerov 2013). In tropical areas, in contrast, the overall seasonality is distinctly lower than in temperate regions and most of the tropical species can be found year round in the adult stage (Novotny & Basset 1998), even if variations can be observed between seasons (Gharbi et al. 2013; Checa et al. 2014).

Harvestmen feed on a variety of animal and vegetal matter in addition to fungi (Acosta & Machado 2007). They lay eggs in deep crevices, or on soil, rocks or leaves (Machado & Macias-Ordóñez 2007a). Some species cover the eggs with debris, while others actively guard them (Machado & Macias-Ordóñez 2007a). Harvestmen may shelter in the leaf litter, on vegetation, under rocks and tree trunks and in crevices (Curtis & Machado 2007). Ontogeny is known to affect their spatial distribution: *Phalangium opilio* (Linnaeus 1758) uses leaf litter in its early instars and then moves to higher strata of the vegetation as it matures (Allard & Yeargan 2005). Resting places also often differ from foraging sites. That is the case, for example, of species that forage at night outside the caves where they rest during the day (e.g., Willemart & Gnaspini 2004). Within the suborder Eupnoi, site fidelity and the formation of communal roosts in periods of inactivity are common (Grether & Donaldson 2007; Mukherjee et al. 2010; Wade et al. 2011; Teng et al. 2012; Grether et al. 2014). Adults of Paleartic and Neartic Eupnoi typically live only a few months, and eggs or immatures overwinter, whereas adult Neotropical laniatoreans can live up to four years (Curtis & Machado 2007; Gnaspini 2007).

Preliminary observations suggested that an adult population of the harvestman *Jussara* sp. (Sclerosomatidae, Eupnoi) in southeastern Brazil had an unusually marked seasonality for a tropical species and had a patchy distribution on leaves of shrubs. We therefore investigated seasonal patterns of distribution, microhabitat selection and individual movement in this species.

METHODS

Field observations.—We collected field data in the Parque Estadual Serra da Cantareira, núcleo Engordador, a fragment of tropical Atlantic rain forest north of the city of São Paulo – SP, Brazil (23° 22' 44" S, 46° 31' 38" W). From August 2011 to July 2012, we made 24 field trips. During half of these trips, we searched for juvenile individuals of *Jussara* sp. and during the other half, we marked and recaptured adult individuals (see below). Our main transect was 100 m long and 1 m wide, divided in 50 parts of 2 m each.

The method for monitoring seasonality was as follows: one person (GFP) searched for the harvestmen on every trip, always between 10 am and 5 pm, from the floor up to 2 m on the vegetation, for 3 min for each 2 m of the transect. Whenever a harvestman was found, we stopped the stopwatch

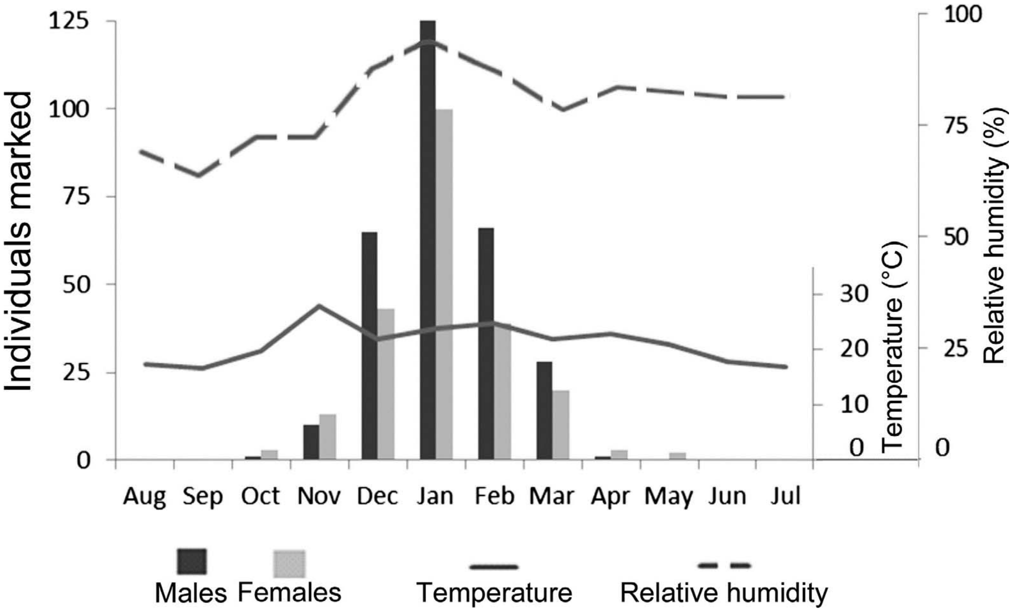

Figure 1.—Temperature, humidity and number of adult males and females captured throughout the year in the Neotropical harvestman *Jussara* sp. (Opiliones, Sclerosomatidae). Spring and summer (wet and warm seasons) are from 1 September 2011 to 28 February 2012.

to take notes and marked the individual. We recorded its number (see below), sex, in which 2 m interval of the transect it was found, whether it was alone or aggregated with others (i.e., three or more individuals with overlapping legs, Machado et al. 2000) and if it was on the superior or inferior surface of the leaf. We also noted whenever an individual shared the same plant with conspecifics, which does not mean they were aggregated since their legs were not necessarily overlapping. We marked the harvestmen only the first time they were found using individual tags glued to their dorsum (cf. Macías-Ordónez 1997; Grether & Donaldson 2007). The tag was a 5 x 4 mm greaseproof paper in which letters and numbers were printed with a monochromatic laser printer. We do not have evidence that these tags affected the behavior or survival of the animals. We started searching for the animals from one end of the transect in one trip and from the opposite end in the following trip. For every trip, we measured temperature and humidity at 1400 h, with a portable digital meteorological station (Instrutemp ITHT2210).

Since only adults of *Jussara* sp. are usually seen on top of the vegetation (G.F. Pagoti, personal observations), we wanted to know where juveniles can be found. For this purpose, we established a second transect, 2 km away from the main transect to avoid disturbance of the studied population of adults, but in a region where these are known to occur. This second transect was divided in 5 equal parts of 20 m, where we looked for juvenile individuals in monthly trips for 12 consecutive months. In each 20 m part, we sieved the leaf litter of a 1 m^2 section 2 m inside the trail border over a white tray. In addition, in each 20 m part we selected two trees with diameters at chest height ranging from 10 to 25 cm and heights ranging from 2 to 5 m to search for juveniles. We had the trees surrounded by a white sheet of 2 x 2 m and shook them vigorously for one minute. We would then collect, preserve in alcohol and identify the harvestmen that fell on the sheet. We monitored the same 10 trees for 12 consecutive months.

Estimation of the available area provided by each plant species.—In order to differentiate substrate preference and substrate availability, we estimated the available area offered by each plant species as substrate for the harvestmen. We collected 5 leaves of 5 different plant individuals in our transect, calculated their area and then their mean area. We counted the number of leaves of 5 individuals and obtained a mean number of leaves of that species. We calculated the area available of each plant species by multiplying the mean area of a leaf by the mean number of leaves per plant multiplied by the number of individuals of that species in the transect.

Laboratory observations.—Here we aimed at understanding whether the animals forage on the vegetation or leaf litter and opportunistically observed egg laying or interactions with conspecifics. We collected 10 individuals of each sex on 10 January 2012. We kept them in a large terrarium (1 x 1 m) with soil and leaf litter brought from the site where we collected the animals. A 10 cm diameter bowl of water in the center of the terrarium provided humidity. The animals were maintained for 10 days in the laboratory, exposed to natural light, but a red light was used at night. We fed the animals with canned dog food on days one and five. Because they would spend the day motionless on leaves, we only made observations at night. Every night we recorded the animals for 3 hr with a Sony HandyCam in nightshot mode, between 8 pm and 1 am.

Data analysis.—We followed Zar (1996) for statistical analyses. We used parametric tests whenever data met assumptions, using SigmaStat software (SYSTAT SOFTWARE INC)) to run the tests. Yates correction was used for χ^2 tests when one of the values was below 5.

RESULTS

Seasonality, microhabitat choice and movements.—There was a clear seasonality, with adults being absent in the colder and drier months and adult females appearing earlier and disappearing later than males (Fig. 1). We marked 296 males

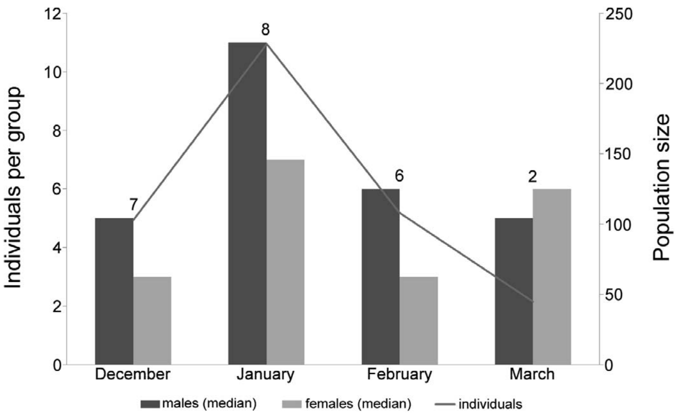

Figure 2.—Number of groups (numbers on top of bars), males and females per group (bars, left axis) and population size (line, right axis) in the months in which groups of the harvestman *Jussara* sp. were found. See text for definition of a "group".

and 223 females and recaptured 22 males and 18 females, representing a 7.7% recapture rate. January was the month with highest number of captures and recaptures. The median distance between captures was 12 m (range = 0–84 m, $n = 22$) for males and 2 m (range = 0–66 m, $n = 18$) for females. There was no significant difference between the sexes (Mann-Whitney test, U = 254.0, $P = 0.085$). Two females were recaptured three months after they were marked, 30 m away from their original location. Two other females and a male were recaptured 2 months after they were marked. Humidity (Spearman correlation: $r_s = 0.859$, $P < 0.0001$, $n = 12$) and temperature (Spearman correlation: $r_s = 0.676$, $P = 0.014$, $n = 12$) were positively correlated to the number of individuals captured. Temperature and humidity were not correlated to one another but the P value was close to significance (Spearman correlation: $r_s = 0.558$, $P = 0.055$, $n = 12$, Fig. 1).

During the day, 98% of the harvestmen were found on plant leaves and 2% were found on rocks or on leaf litter. Significantly more individuals were on the upper surface of the leaves (70%, $n = 508$) than on the lower surface (30%, Chi-square homogeneity test, $\chi^2_1 = 40.9$; $P < 0.001$). A total of 327 individuals (202 males and 125 females) were found in groups of 5 or more individuals on the same plant. The sex-ratio in these groups was 1.6:1 male biased (similar to the population sex ratio of 1.3:1 male biased). These groups were only observed from December to March (Fig. 2), with the maximum number of individuals observed in January (24 and 45 individuals on the same plant). The number of individuals per group positively correlated to the number of individual captures the same month (Pearson correlation: $r = 0.989$, $P = 0.012$, $n = 4$), meaning that the number of individuals in the population affects the number of individuals found within a group. Individuals on the same plant were in aggregations (any group of at least three harvestmen whose legs are overlapping) in 30% of the observations (110 out of 370 individuals).

Out of the 17 species of plants found along the transect, 26% of the plants on top of which we found *Jussara* sp. were *Psychotria suterella* (Rubiaceae) (Fig. 3). However, there were only five individuals of *P. suterella* out of 192 plants in the transect (Chi-square test with Yates correction, $\chi^2_2 = 50.2$, $P < 0.001$, Fig. 4). Within our transect, *P. suterella* occupied an area of approximately 81 m^2, which represents 3% of the available area. Therefore, if we use the area of the leaves instead of the number of individuals, we also get a significant response (Chi-square test with Yates correction, $\chi^2_2 = 391.9$, $P < 0.001$). Sifting leaf litter resulted in finding only three juveniles of the suborder Laniatores, and by shaking trees we only found four immature Eupnoi of another species.

Laboratory observations.—In the laboratory, we only detected nocturnal activity. During the day, when feeding,

Figure 3.—A group of *Jussara* sp. on its preferred plant, *Psycothria suterella* (Rubiaceae). Photo: G.F. Pagoti.

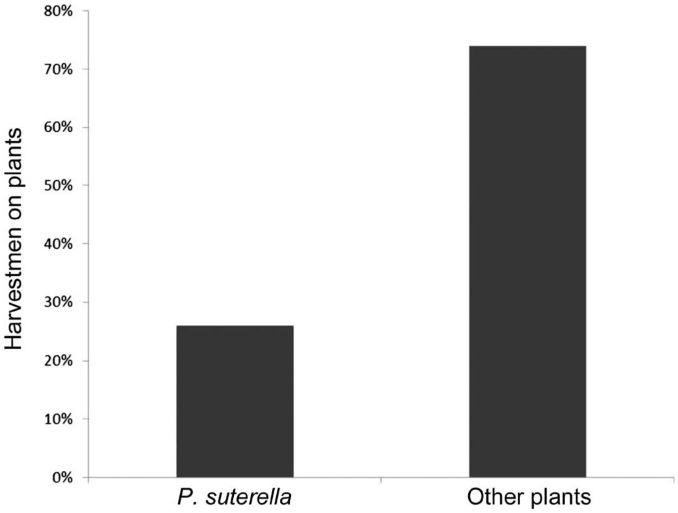

Figure 4.—Proportion of the harvestman *Jussara* sp. found resting on the plant *Psycothria suterella* (which occupies only 3% of the available leaf area of the transect), and on other plant species.

watering and maintenance occurred, we did not detect any activity. After sunset, all the animals descended from the plants and spent the whole night on the floor of the terrarium. We observed 23 copulation attempts, 15 of which were prevented by females by leaning the anterior part of the body against the substrate. We also observed 11 male-male fights. These involved biting the opponents legs, in one case amputating it. We did not observe females ovipositing or any eggs in the substrate.

DISCUSSION

Jussara sp. displayed a marked seasonality, with a high number of adults found in the wet and warm season and none in the dry and cold season. Adults more often shared the same plant with other individuals and would almost always rest on leaves, usually on the upper surface. The sex ratio was male biased and there was a clear preference for the plant *Psychotria suterella* as a resting site. Juveniles were not found on trees or within leaf litter in any month. Reproductive activity, male-male fights and foraging were not observed during the day on plants but were observed at night on the ground (data from laboratory observations).

The marked seasonality in *Jussara* sp. is comparable to that of stenochronous species in the temperate zone (Todd 1949; Jones et al. 2001; Curtis & Machado 2007). The case we describe herein is very unusual, since adults totally disappear in winter, just like some Eupnoi species in the northern hemisphere (Jones et al. 2001; Curtis & Machado 2007). Adult females appear earlier than males, but the latter are more abundant in the peak of the population, from December to January (Fig. 1). Adult females can be observed for a longer period of time, from October to May, whereas males were observed only from November to March. A similar pattern was observed by Tsurusaki (2003) in Eupnoi harvestmen in Asia. The life cycle of *Jussara* sp. may therefore be similar to the life cycles of related species outside the tropics. An alternative hypothesis would be that they migrate to the canopy of trees and live more than a year, but this is unlikely because our recapture data gave us 3 months of maximum adult survival and Eupnoi from the Northern hemisphere typically live only a few months (Gnaspini 2007). We expect that *Jussara* sp. overwinters as eggs and juveniles (see Tsurusaki 2003).

Temperature variation and photoperiod variation probably explains marked seasonality in the northern hemisphere, whereas in the tropics, humidity may be more important (Wolda 1988; Musolin & Saulich 1999). Though we cannot infer a causal relationship, the number of animals we found was positively correlated to both temperature and humidity, and most harvestmen are particularly sensitive to the latter (Santos 2003; Almeida-Neto et al. 2006; Proud et al. 2012).

Juveniles are often hard to find in Neotropical harvestmen (e.g., Burns et al. 2007), and we found none in leaf litter or on vegetation from 0 to 2 m. Tourinho et al. (2014) also seldom found Eupnoi harvestmen in litter. These results contrast with data on sclerosomatids from the Northern Hemisphere, which migrate from leaf litter to the vegetation as they grow (Todd 1949; Edgar 1971; Tsurusaki 2003). In our study, eggs were not found in the field or in captivity. Eggs of laniatorean harvestmen are sometimes covered with soil (Willemart 2001; Zatz et al. 2011) and are hard to find. In Eupnoi, they are usually laid in crevices and are therefore also difficult to see (Machado & Macías-Ordóñez 2007a).

In Neotropical harvestmen of the order Laniatores, a marked seasonality has also been found but in a different fashion. Long-lived adults of *Serracutissoma proximum* (Mello-Leitão 1922) (Gonyleptidae) appear to migrate from the vegetation on river margins to rock crevices and caves in the colder and drier months. This migration greatly influences the population sizes of this species in both environments throughout the year (Buzatto et al. 2007; Chelini et al. 2011). In another long-lived laniatorean, *Mischonyx cuspidatus* (Roewer 1913), the population may increase 300% in wet and warm months (Mestre & Pinto-da Rocha 2004). In other tropical arthropods, adults are typically found in winter even if the population diminishes (e.g., González et al. 2001; Wiwatwitaya & Takeda 2005; Mineo et al. 2010). These phenological data all differ from ours because in these studies adults were always present, even if their population was greatly reduced.

Individuals of *Jussara* sp. often shared the same plant and sometimes were aggregated, which has been suggested to have several advantages. Among them, defense has been suggested to be one of the most important in harvestmen because of dilution and confusion effects, the use of alarm pheromones, and the fact that the contact between legs allows animals to detect group members fleeing (Machado & Macías-Ordóñez 2007b; Chelini et al. 2012). Reproduction has typically not been invoked to ultimately explain why harvestmen aggregate, mainly because they copulate outside aggregations and because they aggregate mostly in the non-reproductive season (Machado & Macías-Ordóñez 2007b; Chelini et al. 2012). However, *Jussara* sp. is found in groups during the reproductive season and may copulate about a meter away from where they rest during the day, which we observed both in the field and in captivity. In this case, staying among conspecifics may help finding a mate when activity starts at night. Harvestmen rely mainly on chemoreception to find resources in general, including shelter, food and mates (Willemart & Chelini 2007; Costa & Willemart 2013; Santos et al. 2013; Fernandes & Willemart 2014). Particularly for Eupnoi harvestmen, detection of conspecifics occurs through contact with chemicals deposited on the substrate or on the animal itself (Donaldson & Grether 2007; Grether & Donaldson 2007; Willemart et al. 2009). That amplifies the importance of staying close to conspecifics for reproductive reasons, as previously suggested (Willemart & Hebets 2012).

The low recapture rate and distance between recaptures suggests that *Jussara* sp. do not always use the same individual plants even if they consistently prefer *P. suterella* as a diurnal resting site. Our results contrast with those of Donaldson & Grether (2007) who found a higher fidelity to the same site, but in a different system where the animals form large aggregations. The several advantages provided by such large aggregations (Machado & Macías-Ordóñez 2007b) probably increase the advantages of returning to the same plant, where other individuals are.

Finally, the disturbance we caused by marking the individuals may also have influenced these results, as also noticed by Grether et al. (2014). In herbivorous insects, preferred plants are often oviposition or feeding sites (Del-Claro & Torenzan-Silingardi 2012). We never found eggs on any plant in our transect and Eupnoi typically lay eggs in crevices on the ground. Feeding in *Jussara* sp. occurred at night on the ground (like in the Neotropical Eupnoi *Prionostemma* sp., Burns et al. 2007; Wade et al. 2011), with prey occasionally being carried to the vegetation after they were captured on leaf litter. *Jussara* sp. was never observed feeding on any part of *P. suterella*. There are no striking morphological differences between *P. suterella* and other available plants. The exact spots where the individuals were found were not more sheltered, shaded or closer to sources of food, water or other resources. The ultimate reasons why *Jussara* sp. picks this plant species are therefore unknown. The laniatorean *Serracutisoma proximum* (Gonyleptidae) also has a preferred plant species for egg laying, but the reasons are also unknown (Buzatto & Machado 2008). Proximally, *Jussara* sp. could be either attracted to physical or chemical characteristics of *P. suterella* (Takemoto et al. 2012; Trigo et al. 2012; Anderson et al. 2013) or to chemicals left by conspecific harvestmen (Donaldson & Grether 2007; Grether & Donaldson 2007; Teng et al. 2012; Willemart & Hebets 2012; Grether et al. 2014). These hypotheses remain to be tested.

In summary, we provided evidence of a strong preference for a specific plant and a highly marked seasonality in a tropical species. Both results are quite unusual and surely deserve further study.

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