Journal of Natural History

ISSN: 0022-2933 (Print) 1464-5262 (Online) Journal homepage: https://www.tandfonline.com/loi/tnah20

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To cite this article: German Antonio Villanueva-Bonilla, Suyen Safuan-Naide & João Vasconcellos-Neto (2018) Population dynamics and phenology of two congeneric and sympatric lynx spiders *Peucetia rubrolineata* Keyserling, 1877 and *Peucetia flava* Keyserling, 1877 (Oxyopidae), Journal of Natural History, 52:5-6, 361-376, DOI: 10.1080/00222933.2018.1433339

To link to this article: https://doi.org/10.1080/00222933.2018.1433339

JOURNAL OF NATURAL HISTORY, 2018
VOL. 52, NOS. 5–6, 361–376
https://doi.org/10.1080/00222933.2018.1433339

Population dynamics and phenology of two congeneric and sympatric lynx spiders *Peucetia rubrolineata* Keyserling, 1877 and *Peucetia flava* Keyserling, 1877 (Oxyopidae)

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Numerous phenological studies on spiders belonging to the families Oxyopidae, Thomisidae, Lycosidae, Selenopidae (e.g. *Selenops cocheleti*) and Salticidae (e.g. *Psecas chapoda* and *Psecas viridipurpureus*) have been conducted in the neotropical region. However, studies that simultaneously compare population dynamics and age structure in populations of sympatric species are limited, especially in Oxyopidae. The population dynamics and phenology of two congeneric lynx spider (*Peucetia rubrolineata* and *Peucetia flava*) were examined in southeastern Brazil. Several characteristics of the age structure were compared between the two spider species. The variation in the total abundance of individuals and age structure and their relationship with climatic variables were similar between the two spiders. Adults of these spiders were present mainly in spring, indicating an annual reproductive cycle and a 'stenochronous spring' phenological pattern. The recruitment of spiders occurred in summer for *P. rubrolineata* and *P. flava*, followed by successive phenological peaks at all stages of development. Rainfall and temperature had a positive correlation to population flux in the two spider species studied. Despite the significant climatic effects observed in the Serra do Japi, the phenological pattern of the population in this study was not always repeated in other species of spiders (e.g. *Selenops cocheleti*).

ARTICLE HISTORY
Received 18 April 2017
Accepted 22 January 2018
Online 12 February 2018

KEYWORDS
Age structures; Atlantic forest; seasonal patterns; Serra do Japi

Introduction

Population dynamics can be defined as the change in the number of individuals within a population in space and over time, and the understanding of the mechanisms that influence this change (Solomon 1980; Vargas and Rodriguez 2008). Several studies indicate that climatic factors, habitat structure and predation have the greatest influence on the stability of populations. In some species of birds, for example, changes in climate may have effects on reproductive success and adult survival (Wolf et al. 2009; Sandvik et al. 2012). In the tundra ecosystem, rodents are affected more by their habitat structure (configuration of willow bushes) than by climatic factors (Henden et al. 2011). Habitat also seems to be the most influential component in shaping the colonization and

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establishment of amphibians, and influences the increase or decrease in the number individuals within the population (Blaustein et al. 2011). On the other hand, predation was the primary cause of reduction of high densities of an aphid (*Macrosiphum euphorbiae* Thomas) that attacks greenhouse-grown roses (*Rosa hybrida* L.) by the predatory ladybird beetle *Harmonia axyridis* Pallas (Snyder et al. 2004). In the same way, predation was the principal mechanism of the decrease of the wooland caribou population in British Columbia, Canada (Wittmer et al. 2005).

In spiders, the availability and diversity of prey have been described as the critical factors driving population fluctuation (Turnbull 1966; Wise 1993). However, in wandering spiders, environmental factors have been shown to have a more considerable influence on the abundance of individuals than prey availability (Conley 1985; Rana et al. 2016; Villanueva-Bonilla and Vasconcellos-Neto 2016). For example, climatic variables can also affect the growth and development cycle of individuals (Vlijm and Kessler-Geschiere 1967) by altering the reproductive period (Rossa-Feres et al. 2000). Higher rainfall also is correlated with increased production of vegetative branches in the plant *Trichogoniopsis adenantha* (Asteraceae). Such dense branching consequently serves to attract herbivorous insects, which in turn leads to an increase in the population of the spider *Misumenops argenteus* Mello-Leitão, 1929 (Thomisidae) (Romero and Vasconcellos-Neto 2003). Habitat structure also plays an important role in regulating populations. A study on the Salticidae *Psecas chapoda* Peckham and Peckham, 1894 concluded that the flowering pattern and architecture of the plant *Bromelia balansae* (Bromeliaceae) influenced the population dynamics of the spider (Romero and Vasconcellos-Neto 2005a). In another example, the populations of *Ctenus amphora* Mello-Leitão, 1930 and *Ctenus villasboasi* Mello-Leitão, 1949 (Ctenidae) in fragmented habitats within the central Amazon region have been shown to be significantly smaller than what is observed in the continuous forest habitat (Rego et al. 2007).

The phenology of an organism is understood as the temporal variations in the life cycle of the individual (Menzel 2002; Romero and Vasconcellos-Neto 2003), and serves as an important aspect to understanding the population dynamics of a species (Wolda 1988). In spiders, the term phenology has been applied commonly to the study of variations in the age structure of populations (Romero and Vasconcellos-Neto 2003; Villanueva-Bonilla and Vasconcellos-Neto 2016) and to describe the life cycle of individuals (Nieto-Castañeda et al. 2012). Tretzel (1954) and Paquin and Dupérré (2001) argue that spiders may have four phenological patterns based on the reproductive period of the population as determined by the peak abundance of adult males. For example, the spider *Selenops cocheleti* Simon, 1880 (Selenopidae), which is commonly associated with trunks containing loose bark, presents a stenochronic summer phenological pattern – that is, the species has only one reproductive cycle throughout the year and adult males are present in greater abundance in summer (Villanueva-Bonilla and Vasconcellos-Neto 2016). Spiders can adjust their phenological patterns according to climatic conditions (Wise 1984). A study conducted on the west coast of Europe on three species of Lycosidae concluded that climate change and habitat were important factors in the phenological pattern observed in the populations. As such, the spider *Pardosa monticola* Clerck, 1757 presented a eurichronic pattern (several reproductive periods in a year), while *Pardosa nigriceps* Thorell, 1856 presented a diplochronic pattern (two reproductive periods in the year) and *Pardosa pullata* Clerck, 1757 a stenochronic pattern (a single reproductive period in the year) (Vlijm and Kessler-Geschiere 1967). Given these observations, in this paper the term phenology refers to temporal variation in the population structure and its phenological pattern to a better understanding of the dynamic of these populations (Romero and Vasconcellos-Neto 2005a).

Numerous phenological studies on spiders belonging to families Oxyopidae (e.g. *Peucetia viridans*, Arango et al. 2000; *Peucetia flava*, Morais-Filho & Romero 2009), Thomisidae (e.g. *Misumenops argenteus*, Romero & Vasconcellos-Neto 2003), Lycosidae (González et al. 2014), Selenopidae (e.g. *Selenops cocheleti*, Villanueva-Bonilla & Vasconcellos-Neto 2016) and Salticidae (e.g. *Psecas chapoda* and *Psecas viridipurpureus* Simon, 1901, Rossa-Feres et al. 2000; Romero and Vasconcellos-Neto 2005a) have been conducted in the neotropical region, where the reproductive period of a population can vary from once in a year to populations where recruitment of individuals is constant and overlapping generations are observed (e.g. Romero and Vasconcellos-Neto 2005a; Ferreira et al. 2009). However, studies that simultaneously compare population dynamics and age structures in sympatric species populations are limited, especially in Oxyopidae. The Oxyopidae comprises 455 species within nine genera reported to date (World Spider Catalog 2017). They are non-weaver spiders associated with vegetation (Romero and Vasconcellos-Neto 2007; Vasconcellos-Neto et al. 2007; Morais-Filho and Romero 2009). The genus *Peucetia* is cosmopolitan and comprises 47 species, mostly occurring in tropical regions (Santos and Brescovit 2003; World Spider Catalog 2017). Most population studies were conducted on *Peucetia viridans* (e.g. Turner 1979; Randall 1982; Fink 1986; Nyffeler et al. 1987, 1992; Arango et al. 2000; Vasconcellos-Neto et al. 2007), with very little known about the population dynamics of other species of the genus *Peucetia*.

In southeastern Brazil, the congeneric spiders *Peucetia rubrolineata* Keyserling, 1877 and *Peucetia flava* Keyserling, 1877 are found almost exclusively associated with the plant *T. adenantha* (DC) (Asteraceae) (Vasconcellos-Neto and Romero 2012). Both species of spiders persist throughout the year although with different abundances depending on the weather and season. Studies comparing the age structure, population flux and other aspects of these sympatric congeneric species are almost non-existent. Only one study focused on the *P. flava* species inhabiting the *Rhyncanthera dichotoma* (Melastomataceae) plant; this study revealed that the ecosystem (marsh), climatic conditions and availability of prey varied reflecting the ecosystem studied (Morais-Filho and Romero 2009). Knowledge of population fluctuation as well as changes in age structure over time will help, for example, in the understanding of how sympatric congeneric species could persist and coexist if we expect strong competition by resources.

The objective of the present study was to: (1) describe the population dynamics of the two sympatric species *P. rubrolineata* and *P. flava*, and (2) to test the influence of climatic variables (temperature and precipitation) on the spider population dynamics.

Materials and methods

Study area

The Serra do Japi is located between -23.231598 S and -46.936784 W, west of the Atlantic Plateau between the municipalities of Jundiaí, Itupeva, Cabreúva, Pirapora do Bom Jesus and Cajamar in the state of São Paulo, Brazil. Most of which is covered by seasonal mesophyll forest canopy. This area has an altitude ranging from 700 m to 1300 m above mean sea level. In the Serra do Japi the climate is stable with average monthly temperatures varying from 13.5°C in July to 20.3°C in January, with a rainy season in summer (December–March) and dry in winter (June–August) (Pinto 1992). The study was conducted from July 2013 to December 2015. Days of low precipitation and high temperature were recorded in 2014 (Figure 1).

Population dynamics of Peucetia rubrolineata *and* Peucetia flava

To determine variations in the number of individuals of *P. rubrolineata*, we sampled 100 plants of *T. adenantha* (Asteraceae) grown in a shaded area every month over the 2-year study period. The same procedure was followed to determine the variations in the number of individuals of *P. flava*. Given that the *P. flava* spider was rare and observed more in the sunny areas, our sample unit size was modified to 200 plants grown in an open area. Observations were collected along several tracks in areas located between altitudes of 950 and 1100 m. For each inspected plant, we recorded the numbers of individual spiders as well as their stage of development and sex as adults. Later, circular statistics analysis was performed using the Rayleigh uniformity test to verify the population abundance peaks for the two species of spiders once the circular normality of the data was verified (Morellato et al. 2010).

Phenology

In the field, we tried to identify different size classes as an approach to different instars of *Peucetia* spiders. We identified eight size classes and photographed them with a scale in mm (Figure 2). These size classes were used in the categorization of the age structure of these spiders in the monthly counts. Size differentiation was based on the size of the cephalothorax and the femur of the first pair of legs of each individual observed in the field. We used these characteristics because they are quite distinct among instars. In the field, we used printed photographs of the different sizes classes for classification of the individuals observed. Later, to illustrate the age structure of the two populations of *Peucetia*, we grouped the spiders' instars into five categories as described by Romero

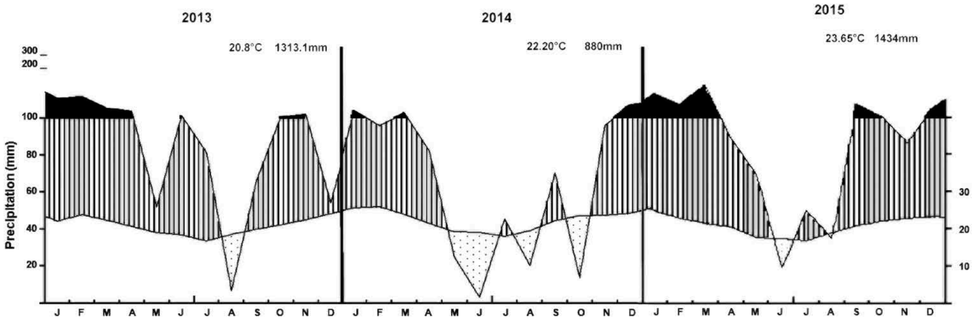

Figure 1. Climatic diagram of the Serra do Japi, SP, Brazil, based on the climatic data collected from the Jundiaí experimental station. Areas in black indicate very humid periods. Areas with vertical lines indicate humid periods. Dotted areas indicate dry periods.

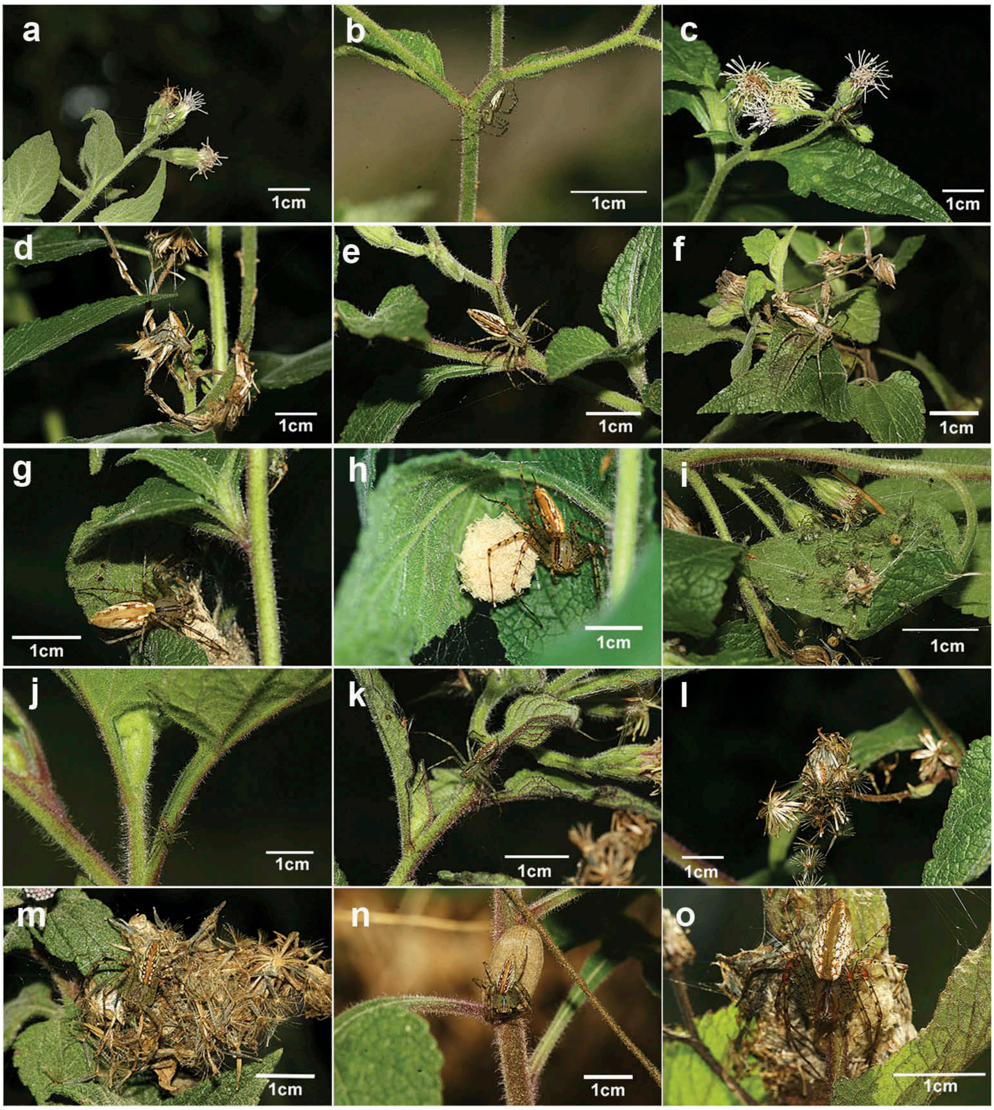

Figure 2. Instars of *Peucetia rubrolineata* (a–h) and *Peucetia flava* (i–o) (Oxyopidae) recorded in the *Trichogoniopsis adenantha* (Asteraceae) plant in the Serra do Japi, SP, Brazil. (a, i) second instar; (b, j) third instar; (c, k) fourth instar; (d, l) fifth instar; (e, m) sixth instar; (f, n) seventh instar (subadult); (g, h, n) eighth instar (adult).

and Vasconcellos-Neto (2005a): Newly emerged (spiderling spiders = second instar); Young spiders (third and fourth); Juveniles (fifth and sixth instar), males and females subadults (seventh instar) and adult males and females (eighth instar).

Synchrony between events

To verify whether the variations in the number of individuals of *P. rubrolineata* and *P. flava* were related to the macro-climate pattern of Serra do Japi (variations in precipitation and temperature), we employed the Spearman correlation test after testing for normality of the data using the Shapiro–Wilk test. To test whether events occurred synchronously, we applied correlation tests with temporal lags of up to 3 months (see Sokal and Rohlf 1994; Zar 1998; Romero and Vasconcellos-Neto 2003). Precipitation and temperature data were obtained from the Jundiaí Experimental Station (ETECJ), which is located approximately 8 km from the study area. Temperature data were adjusted to the study area by subtracting 0.6°C per 100 m elevation (Whiteman 2000).

Results

Population dynamics

The population fluctuation over the course of this study was similar in the two species of spiders (Figure 3), differing only in their densities on the plant. The mean number of individuals per month of *Peucetia rubrolineata* was 24.2 ± 18.13, ranging from 61 individuals in January 2015 to zero individuals recorded in September 2013. During the period of high spider abundance at the 100 plants sampled, only 44 (44%) plants had at least one spider and at times the same plant contained up to four spiders. On the other hand, for *P. flava*, the average number of spiders per month was 20.93 ± 12.38, ranging from 41 individuals in June 2014 to 4 individuals in September of the same year. During the period of high spider abundance, of the 200 plants sampled only 29 (15.5%) had at least one spider and at times the same plant contained up to six spiders. The distribution of the two species was uneven throughout the year with a peak in abundance in March for *P. rubrolineata* (Rayleigh Test: $z = 67.46$; $p = < 0.0001$; Tables 1 and 2; Figure 4) and in April for *P. flava* (Rayleigh Test: $z = 23.02$; $p = < 0.0001$; Tables 1 and 2; Figure 4). The two populations had an increase in the number of individuals at the beginning of summer (moist season) but their population declined by mid-autumn (Figure 3).

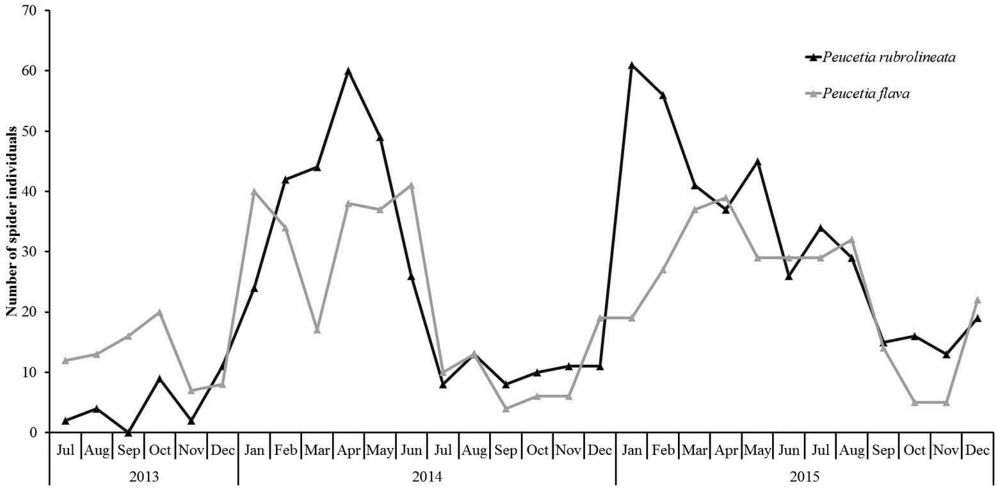

Figure 3. Population fluctuation of *Peucetia rubrolineata* and *Peucetia flava* (Oxyopidae) in 100 and 200 plants, respectively, of *Trichogoniopsis adenantha* (Asteraceae).

Table 1. Circular statistics applied to the phenology of different age groups of the spiders *Peucetia rubrolineata* and *Peucetia flava* (Oxyopidae) in Serra do Japi, SP, Brazil.

	Total	Spiderling	Young	Juvenile	Subadult	Adult
Peucetia rubrolineata						
Number of records	726	24	269	312	58	63
Mean vector (μ)	85.369°	3.33°	46.364°	135.892°	216.71°	305.387°
Month	March	January	February	May	August	November
95% confidence interval (−/+) for μ	75.933°	352.945°	40.992°	129.635°	200.397°	295.486°
	94.805°	13.714°	51.737°	142.149°	233.022°	315.287°
Period of duration (confidence interval)	17 March to 6 April	20 December to 14 of January	10 February to 21 February	12 May to 23 May	21 July to 23 August	25 October to 14 November
Mean vector's length (*r*)	0,305	0,902	0,732	0,63	0,577	0,779
Rayleigh's test	67,469	19,536	144,056	123,912	19,29	38,189
Rayleigh 's test (*p*)	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Peucetia flava						
Number of records	628	22	193	267	46	98
Mean vector (μ)	115.464°	354.133°	50.654°	146.077°	215.726°	287.562°
Month	April	December	February	May	August	October
95% confidence interval (−/+) for μ	99.064°	341.479°	42.649°	139.301°	201.615°	276.412°
	131.864°	6.787°	58.659°	152.854°	229.838°	298.713°
Period of duration (confidence interval)	10 April to 13 May	10 Dezember to 7 January	12 February to 1 March	22 May to 4 June	23 July to 20 August	6 October to 28 October
Mean vector's length (*r*)	0,191	0,869	0,627	0,629	0,696	0,631
Rayleigh's test	23	16,613	75,964	105,757	22,261	38,994
Rayleigh's test (*p*)	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**

Values of *p* in bold type indicate statistically significant differences.

Table 2. Spearman's correlation coefficient between the abundance of *Peucetia rubrolineata* and *Peucetia flava* with environmental factors (rainfall and temperature), with up to 3 months of time lag on the dependent variable. Serra do Japi, SP, Brazil.

	Time-lag (months)	*R*	*p* (value)
Raifall vs abundance of *P. rubrolineata*	0	0.287	0.1738
	1	0.584	0.0034
	2	**0.635**	**0.0015**
	3	0.460	0.0361
Temperature vs abundance of *P. rubrolineata*	0	0.346	0.0974
	1	0.647	0.0008
	2	**0.832**	**0.0001**
	3	0.806	0.0001
Rainfall vs abundance of *P. flava*	0	0.119	0.5795
	1	0.337	0.1161
	2	0.504	0.0167
	3	**0.829**	**0.0001**
Temperature vs abundance of *P. flava*	0	0.007	0.9742
	1	0.309	0.1504
	2	0.582	0.0044
	3	**0.689**	**0.0005**

Values in bold type indicate significant differences.

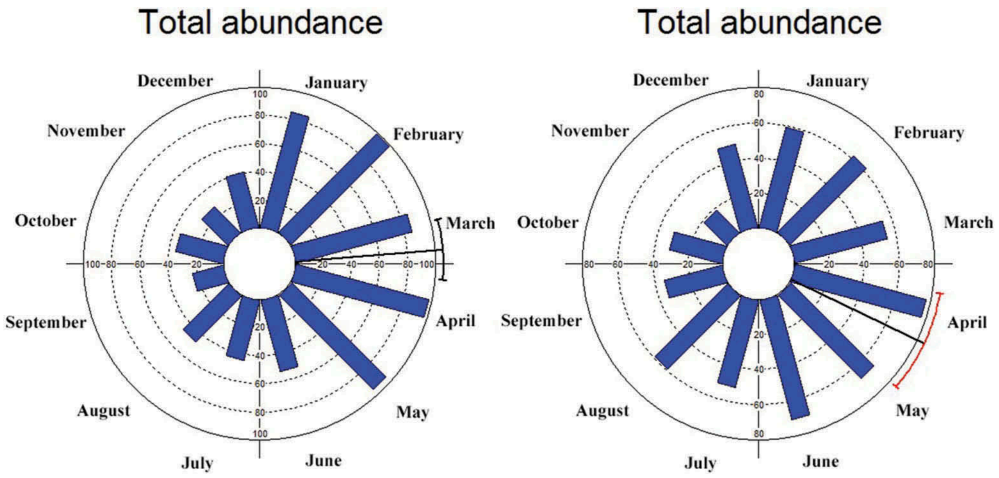

Figure 4. Circular histogram of the abundance of the two spider populations: right, *Peucetia rubrolineata*; left, *Peucetia flava*, from July 2013 to December 2015 in Serra do Japi, SP, Brazil. The black line outside the circle indicates the average angle or direction of the data. The transverse line on the outside of the circle indicates the 95% confidence interval.

Phenology

The phenological pattern of the two species was similar as they had similar distribution in age structure over the study period. The similarity is revealed by the peak of adult abundance (breeding period) in spring followed by the deposition of the egg-sacs, the emergence of spiderlings in summer, young and juveniles in late summer and autumn, and subadults in winter. This cycle repeated with the appearance of adult individuals in the following spring (Figures 5 and 6).

All age classes of both spider species showed marked peaks of abundance during different months of the year. The peaks for the same age class were observed during the

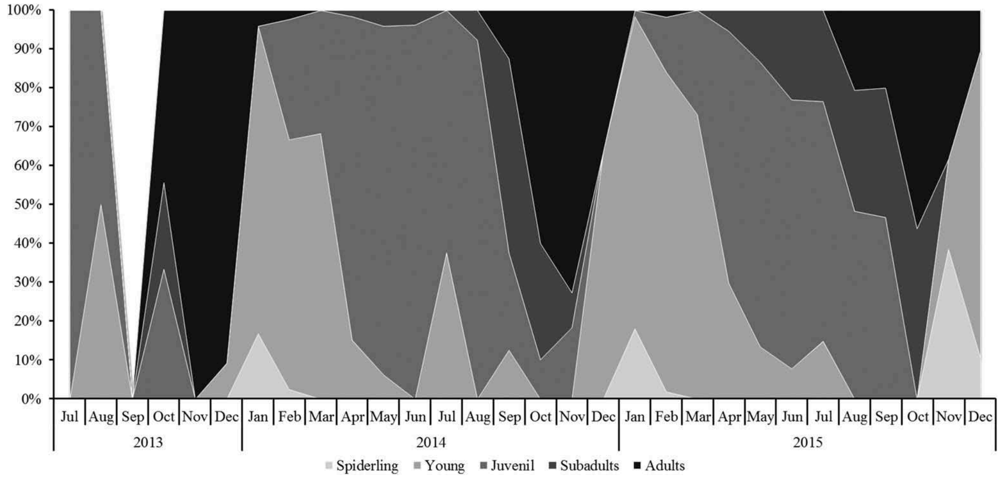

Figure 5. Phenogram of the population of *Peucetia rubrolineata* (Oxyopidae) on *Trichogoniopsis adenantha* (Asteraceae, *n* = 100) between July 2013 and December 2015, Serra do Japi, SP, Brazil.

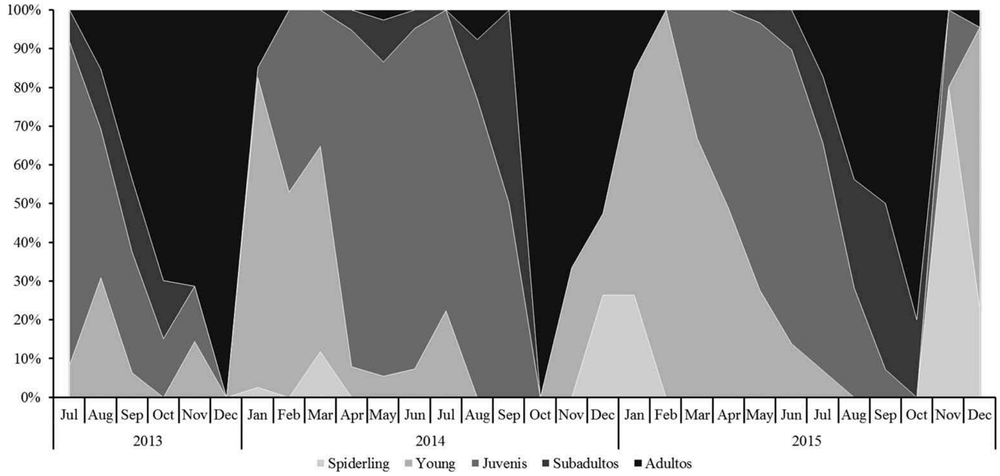

Figure 6. Phenogram of the population of *Peucetia flava* (Oxyopidae) on plants of *Trichogoniopsis adenantha* (Asteraceae, *n* = 200) between July 2013 and December 2015, Serra do Japi, SP, Brazil.

same season (Figures 7 and 8; Table 1). These data indicate that the life cycles of these two species do not differ significantly.

The two populations showed a stenochronic phenological pattern in spring, i.e. was typically a single reproductive period season each year, occurring in the spring. This is shown by the marked peak in adult reproductive period in both species of spiders during spring (Figures 7 and 8; Table 1). However, data reveal that even though their reproductive periods were not synchronized, there was considerable overlap between them. In *P. rubrolineata* the reproductive period occurred during November, while the reproductive period of *P. flava* began a month earlier in October.

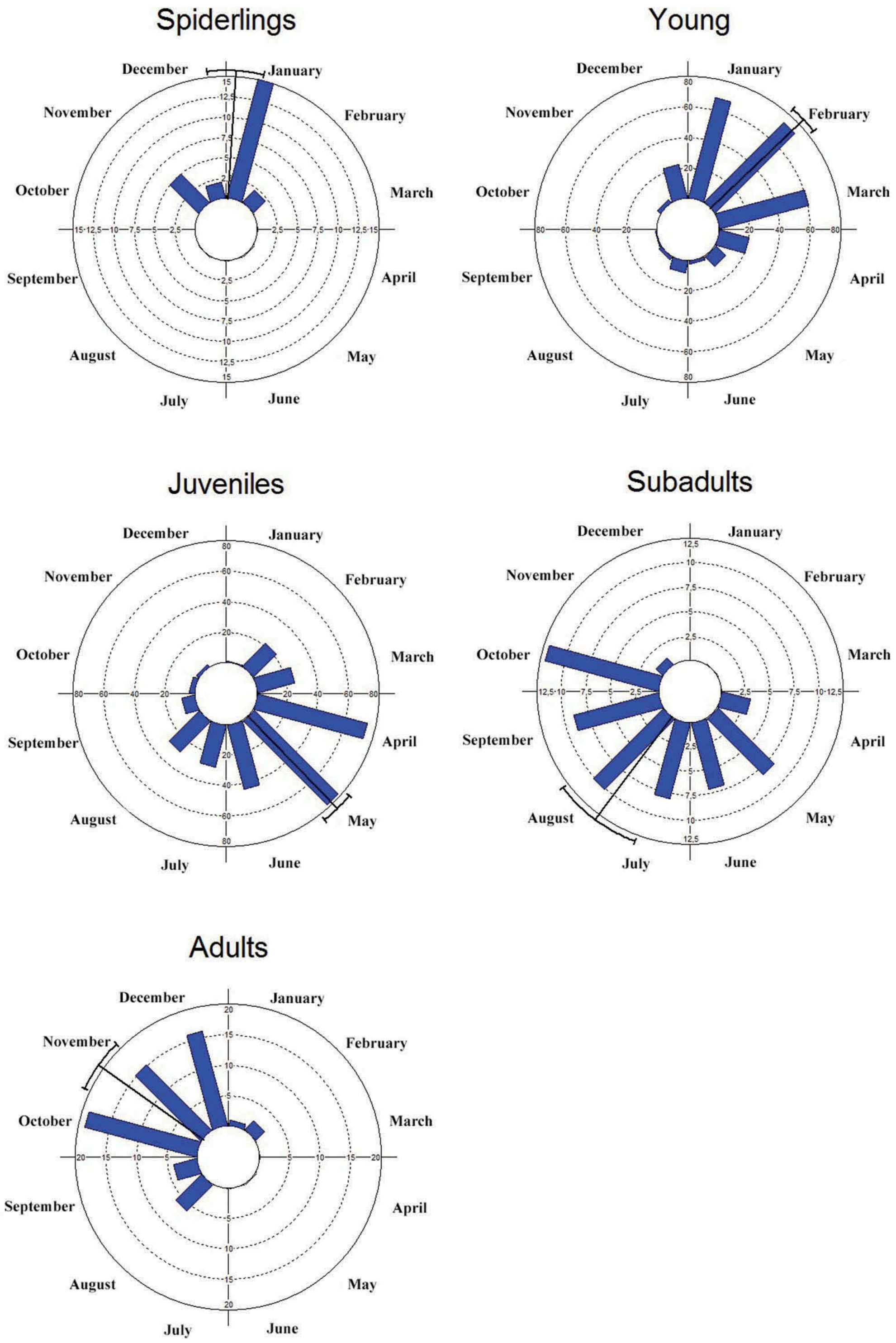

Figure 7. Circular histograms of the frequency of age structure established for the population of *Peucetia rubrolineata* (Oxyopidae) from July 2013 to December 2015 in Serra do Japi, SP, Brazil. The black line vector inside the circle indicates the angular mean or direction of the data. The transverse line in the sector outside the circle indicates the 95% confidence interval.

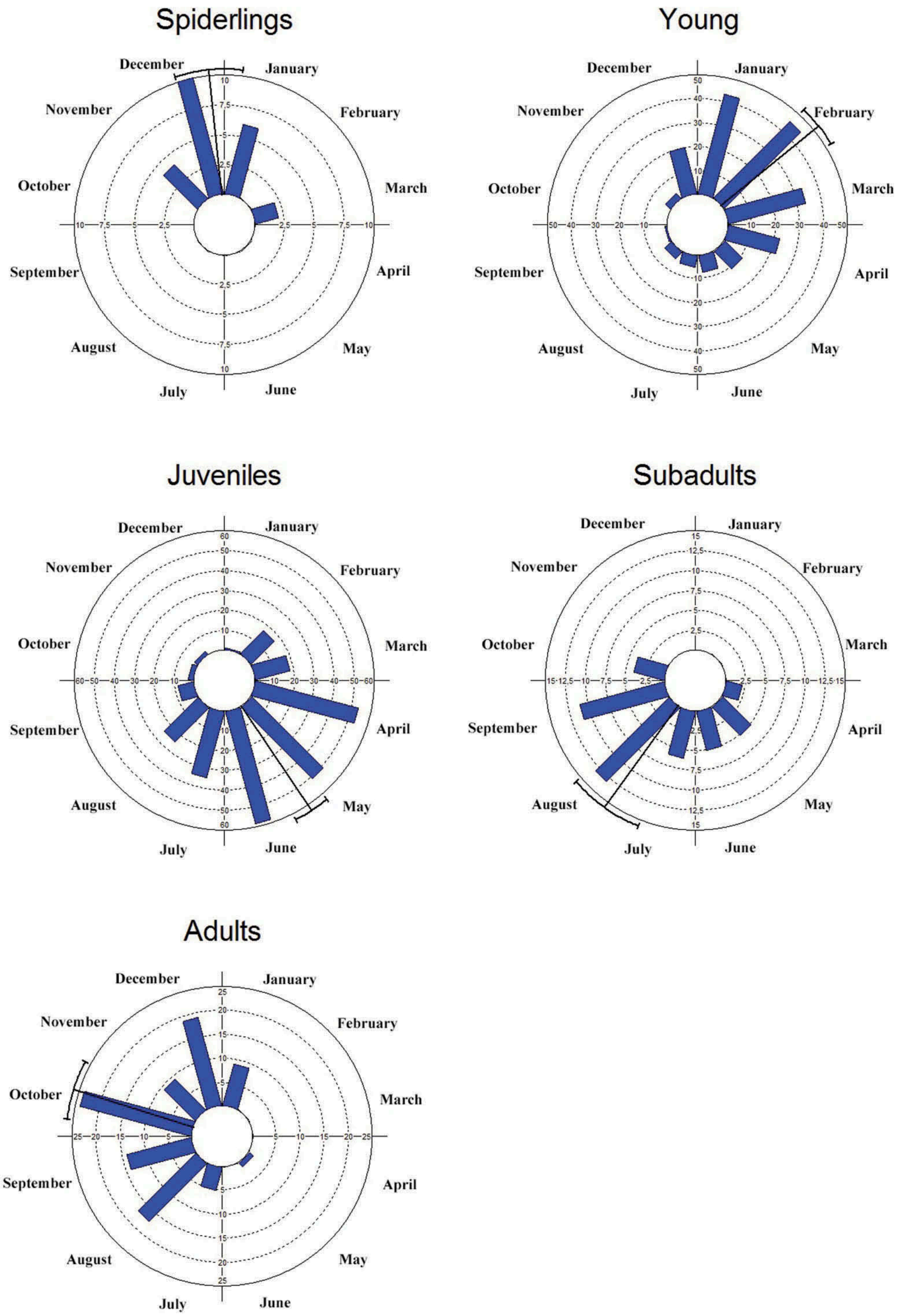

Figure 8. Circular histograms of the frequency of the age structure established for the population of *Peucetia flava* (Oxyopidae) from July 2013 to December 2015 in Serra do Japi, SP, Brazil. The black line vector inside the circle indicates the angular mean or direction of the data. The transverse line in the sector outside the circle indicates the 95% confidence interval.

Synchrony due to natural events

Abundance of *P. rubrolineata* and *P. flava* individuals was directly correlated with rainfall and temperature. However, the events did not occur synchronously, with time lags of 2 and 3 months, respectively (Table 2).

Discussion

Our observations indicate that the populations of *P. rubrolineata* and *P. flava* present a stenochronic pattern in spring with a very marked period of adult spider activity at a defined time in the year – according to the classifications of Tretzel (1954) and Paquin and Dupérré (2001). Our study suggests that both *P. rubrolineata* and *P. flava* present a single reproductive period in the spring followed by the deposition of eggs and recruitment of new individuals in summer (January–December). Subsequently, the juveniles (fifth and sixth instars) appear mainly in autumn and winter when temperatures and precipitation are low. From a developmental point of view, this phase is longer, probably due to limited availability of prey. During the dry year 2014 this effect was exacerbated in the age structure of both *P. rubrolineata* and *P. flava*. Morais-Filho and Romero (2009) reported contrasting results in a different location, wherein *P. flava* revealed seasonal stability and overlapping generations resulting from consistent fecundity throughout the year. On the other hand, populations of *Misumenops argenteus*, *Eustala taquara* and *Eustala perfida* revealed phenological patterns similar to the two *Peucetia* species studied (Romero and Vasconcellos-Neto 2003; Souza 2013). In these studies conducted at the Serra do Japi, all species had similar age structures with successive peaks of the developmental stages of spiders appearing throughout the year.

Climatic variables were the most important factors influencing the age structure of *P. rubrolineata* and *P. flava* populations. We observed a positive correlation between rainfall and temperature and the abundance of both species. It is known that summer (when temperature and rainfall are usually higher) shows an increase in insect and arthropod populations (Wolda 1988; Tidon 2006; Pereira da Silva et al. 2011; Kishimoto-Yamada and Itioka 2015), thereby increasing prey availability for the spiders. Romero and Vasconcellos-Neto (2005b) reported the presence of several types of insects on *T. adenantha* between November and January (summer). These results indicate strong bottom–up effects since, with increasing rainfall, the increase in the insect populations on *T. adenantha* plants should, in our view, positively affect the abundance of the two spider species. Another population study conducted in Yucatan, Mexico on the spider *P. viridans* also revealed similar relationships between precipitation and population. In the Yucatan study, *P. viridans* also presented a time lag; in other words, an increase in the number of individuals was observed a few months after rainfall and prey availability changed (Arango et al. 2000). Since the study was not conducted for the whole year, it is not possible to infer the population levels of *P. viridans* during the initial few months in the year. Studies with other spiders also demonstrate strong effects of climatic variables on population fluctuation. For example, in a plant–spider system (plant *T. adenantha* and spider *Misumenops argenteus*), bottom–up effects were also observed, wherein the increase in precipitation positively affected the productivity of vegetative branches, which increased the number of arthropods associated with this plant and benefited the spider population (Romero and Vasconcellos-Neto 2003).

A study performed on social spiders in the Serra do Japi also reported seasonal patterns of populations. Marques et al. (1998) recorded similar life cycle patterns in two sympatric species *Anelosimus jabaquara* and *Anelosimus dubiosus* (Theridiidae). These species also presented marked peaks of adults in late spring and during early summer, which points to a single reproductive period in these species. These authors also recorded developmental stages and found that the reproductive period of *A. jabaquara* occurred in December whereas for *A. dubiosus* it occurred in November. The short reproductive period windows observed in *P. rubrolineata* and *P. flava* could therefore, diminish the competition between emerging spiderlings and facilitate coexistence of congeneric sympatric species. However, this has not been tested in the field and other resource partitioning mechanisms may contribute to the coexistence of the two species studied (e.g. differential use of micro-habitat, different diet). Additionally, in the field no predation events were observed among the species studied. Furthermore, in very few instances the two spider species were recorded on the same plant (personal observation).

Despite the significant climatic effects observed in the Serra do Japi, the population profile observed in this study was not always repeated in other species of spiders. The bark-dwelling spider *Selenops cocheleti* (Selenopidae) maintains stable population composition throughout the year (Villanueva-Bonilla and Vasconcellos-Neto 2016). Because this selenopid maintains a stable population level it is possible that some generations overlap. Such overlapping generations and the continued availability of adult females results in constant oviposition and reproduction and, consequently, constant recruitment of individuals.

In summary, we report that the population fluctuation and age structure of *P. rubrolineata* and *P. flava* inhabiting *T. adenantha* were similar. Ecologically similar populations share resources diligently to reduce or avoid competition (Hutchinson 1957). If these two spiders have similar ecological timescales, i.e. if both have similar abundance peaks occurring in identical climatic stations throughout the year, then the interspecific competition could be intense. However, from our study it appears that different feeding strategies and/or preference to occupy specific microhabitats within the host plant may favour the coexistence of these two congeneric species.

Acknowledgements

We thank the Prefeitura Municipal de Jundiaí, SP, Brazil for granting permission to work at the Biological Reserve of the Serra do Japi. The authors also thank Instituto de Estudos dos Himenóptera Parasitóides da Região Sudeste Brasileira (INCT HYMPAR – SUDESTE-CNPq, FAPESP, CAPES), Yuri Fanchini Messas, Hebert Silva e Souza and anonymous reviewers for helpful comments on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

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