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Strong phenological differences between two populations of a Neotropical funnel-web wolf spider

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Comparisons of phenological patterns among populations within a species are uncommon in arachnids. *Aglaoctenus lagotis* is a wolf spider that lives in funnel-webs across South America. The aim of this study was to describe the phenological patterns of two distant populations of *A. lagotis* (central Argentina, CA, and southern Uruguay, SU). Individuals of each population were sighted along transects, every month for two years. The CA and SU populations differed in their phenological patterns (Wald χ^2 = 966.94, df = 66; p <0.001). The CA population showed a spring–summer unified reproductive season and immature individuals overwintered. SU showed the sexual period during autumn, the maternal period during spring–summer and the females, mostly mated, overwintered. These strong differences imply temporal isolation in mating possibilities between both populations. The differences encountered could be due to phenotypic plasticity or have a phylogenetic basis. Interpopulation studies of other features of *A. lagotis* would show whether they also vary, suggesting speciation.

Keywords: phenology; populations; sedentary lycosid; *Aglaoctenus lagotis*; Neotropics

Introduction

Phenology is the study of seasonal distribution of periodic life-cycle events of individuals. This distribution is a structural component of animal populations, affecting food availability to mating systems (Forkner et al. 2008; Elias et al. 2011; Welch et al. 2011). Knowing this biological characteristic enables its fluctuations to be predicted during the year and selection of the best time or species for ecological and behavioural studies, particularly for reproductive researches (Baena and Macías-Ordóñez 2012). Several phenological studies have been performed on plants (e.g. Fenner 1998; Ferreira-Nunes et al. 2012) and migratory birds (Stervander et al. 2005; Tøttrup et al. 2008), many regarding the effect of climate change on life-cycles of species (Cotton 2003; Thorup et al. 2007). Phenological patterns have also been reported in several spider groups (e.g. Berry 1971; Wise 1984; Schaefer 1987; Costa and Pérez-Miles 2002; Viera et al. 2007; Miyashita et al. 2012), as in studies that evaluate the role of these arthropods as biological control agents. (Miliczky et al. 2008). Although wolf spiders were examined preferentially (e.g. Merret 1968; Costa 1995; Framenau 1998;

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Marshall et al. 2002; Hendrickx and Maelfait 2003; Cera and Spuņģis 2011; Dolejš et al. 2012), studies on the web-building ones are almost none existent (Sordi 1996).

The most common approach to phenology is the description of periodic life-cycle events for a species or group of species, either in plants (Fenner 1998; Ferreira-Nunes et al. 2012) or animals such as birds (Cotton 2003; Stervander et al. 2005), insects (Wolda 1998; Forkner et al. 2008), scorpions (Araújo et al. 2010) or spiders (Costa 1991; Marshall et al. 2002; Costa et al. 2006). However, the search of variants in phenological patterns among populations of a species is scarce for plants and animals in general (Peterson 1995; Monteiro and Furness 1998; Figuereido-Goulart et al. 2005) and spiders are no exception (Hendrickx and Maelfait 2003; Fernández-Campón 2010). Populations of a species with different phenological patterns can lead to speciation, especially if the temporal location of the sexual periods between them differ, generating reproductive isolation (Monteiro and Furness 1998; Kirkpatrick and Ravigne 2002; Hendrickx and Maelfait 2003; Santos et al. 2007). However, this relationship between phenological patterns and speciation does not always occur, depending on other factors such as the magnitude of the temporal isolation between the sexual periods or the existence of intermediate phenological patterns that make gene flow possible, at least indirectly (Peterson 1995).

Species that are widely distributed are more likely to experience diversity of environmental conditions and to exhibit differences in life history traits in response to this variation, such as in seasonal distribution of developmental stages of individuals (Elias et al. 2011). The Neotropics, a highly diverse and complex region in terms of climates, show a mosaic of environmental conditions (Brown 1991; Morrone 2001), which in turn results in complex selective pressures upon organisms, generating assorted and unique reproductive behaviours and morphological traits. Furthermore, since areas of homogeneous environmental conditions seem to be more fragmented in the Neotropics compared with other tropical regions, it is expected that a single species inhabiting this region experiences a wider set of environmental variables and a higher intraspecific variation in mating strategies than those species living in the Paleotropics (Macías-Ordóñez et al. 2014). In addition, this may result in higher rates of speciation due to sexual selection (Ritchie 2007; Seddon et al. 2008).

Web-building wolf spiders are members of Sosippinae (Brady 2007) and Venoniinae (Lehtinen and Hippa 1979), small and poorly studied subfamilies. Both have been largely considered basal in the evolution of Lycosidae (Foelix 2011), although controversial views also exist (Murphy et al. 2006). Sosippinae is located in the Neotropics and shows a chaotic taxonomic history (Santos and Brescovit 2001) with three genera currently recognised. Two of them are exclusive to South America (Brady 2007; Piacentini 2011), with *Aglaoctenus* being the genus with the greater number of species. *Aglaoctenus lagotis* was the first species described in the genus and several previously existing species became synonymous after the work published by Santos and Brescovit (2001). Currently, it is the only confirmed species of Lycosidae from South America with a completely web-living life. This also makes it of interest in relation to clarifying webs and sedentary life origins in a family characterised by wandering members.

A. lagotis constructs funnel-webs, which only adult males abandon to search for females (Bucher 1974). The geographical range of this species covers much of South America, from southern Uruguay to Venezuela (Piacentini 2011). Previous studies reported the presence of *A. lagotis* in different environments and vegetal strata

(Rubio et al. 2005), as well as the existence of variations in patterns of body coloration, in sexual behaviour repertoire and genital morphology (Bucher 1974; Santos and Brescovit 2001; Stefani et al. 2011; González et al. 2013). Additionally, current studies suggest the existence of different polyandry rates between populations (M. González, unpublished data). However, with respect to phenological patterns we only found one report from populations of southeastern Brazil (Sordi 1996), with concordant general comments reported by Stefani et al. (2011) and Stefani and Del-Claro (in press) for near areas, and by Bucher (1974) for northwest Argentina. Although these reports defined *A. lagotis* as being an annual cycle species with the entire reproductive season (sexual, oviposition and spiderlings) occurring in spring–summer, some variations are suggested. Additionally, some field collects in southern areas of South America reinforced the hypothesis that there may be large differences between populations (M. González, personal observation).

Given the variations suggested for other features of *A. lagotis* (body coloration pattern, sexual behaviour, genitalia and polyandry rates), its wide geographical distribution in a heterogeneous region such as the Neotropics and its recently suggested limited dispersal ability (Stefani and Del-Claro, in press), it would be expected that phenological patterns will differ between distant populations. The aim of the present study is to give detailed descriptions of the phenological patterns in two populations of *A. lagotis* distantly located (central Argentina and southern Uruguay) and to compare such patterns with the only existing report for the species. Southern Uruguay is located at the southernmost point given for the species distribution, whereas central Argentina is located intermediately between the southern Uruguay population and the Brazilian populations of which the phenological pattern has been reported. Although we hope to find a general similar phenological pattern in both populations (in agreement with the previously described for the species), we expect to detect some temporal differences in the periodic life-cycle because of latitudinal climatic conditions (i.e. variation due to geographical distributions, already largely studied) (Coyne and Orr 2004). The phenological analysis offered by the present study, rare in arachnids, will promote further discussions on the isolation or cohesion of the species, historically known for its taxonomic problems.

Methods

The study was carried out in two populations of *A. lagotis* placed in the hillsides of 'Sierras Chicas', Córdoba, Argentina (CA; 30°57′00.10″S, 64°10′00.28″W) and the grassland of 'Piedras de Afilar', Canelones, Southern Uruguay (SU; 34°36′44.83″S, 54°27′24.22″W) (Figure 1). Hills with scrubby vegetation predominate in CA while grassland vegetation is dominant in SU (Cabrera 1971; Grela 2004) (Figure 2). In CA, the temperatures are higher, humidity is lower and the winter shorter than in SU (Figure 3).

Two researchers visited each population every month for two years (2009 and 2010), with the first author always present. The fieldwork lasted three hours, during which one of the researchers walked the study area from north to south and the other from east to west in straight line transects, guided by GPS. Each transect was parallel separated from the other by 5 m. We located animals in webs, either by the presence of the barrier threads, the platform or their silk tube. On each visit, we registered the developmental and sexual categories of all individuals as adult male, adult female,

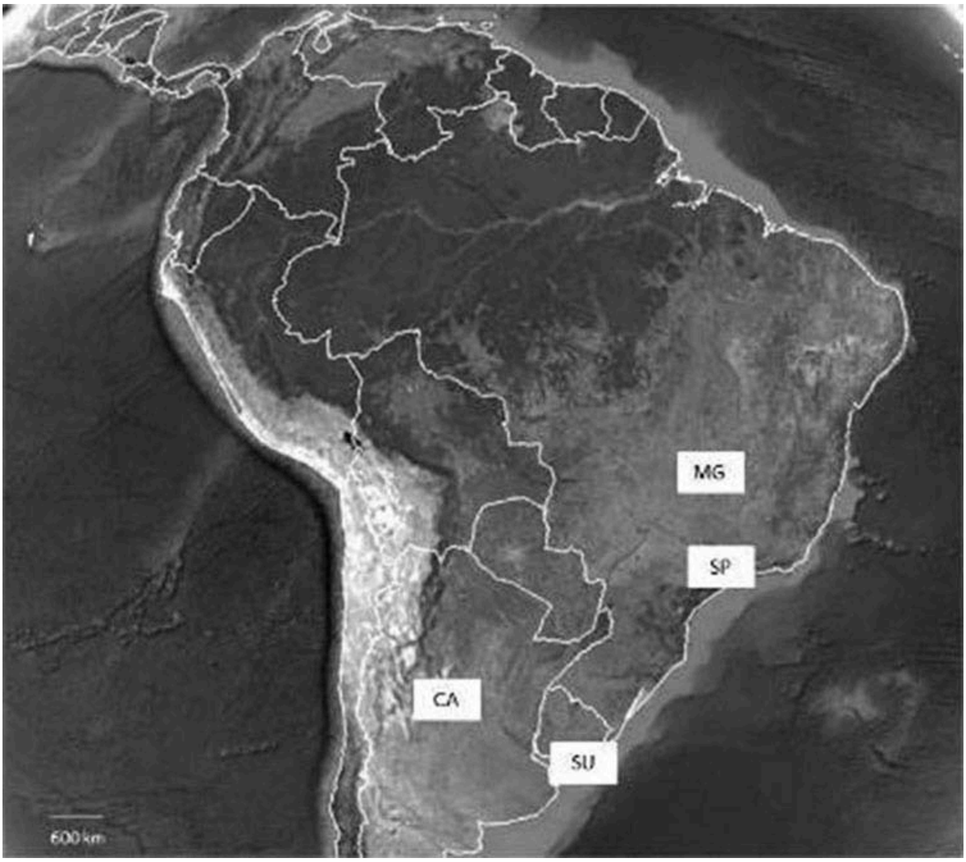

Figure 1. Location of *A. lagotis* populations: central Argentina (CA) (Ascochinga, Sierras Chicas, Córdoba, Argentina), southern Uruguay (SU) (Piedras de Afilar, Canelones, Uruguay) and Brazilian populations of Minas Gerais (MG) and São Pablo (SP).

female carrying eggsac, female carrying spiderlings and immature (penultimate and juvenile spiders) that both researchers had been able to sight from transects. When it was not possible to identify individuals' categories just by looking them on their web, we captured the specimens (manually, by blocking their silk tubes) and immediately after categorization set them free at the same place. Only when identification was not possible in the field did we carry specimens to the laboratory for determination with a dissecting microscope.

The reproductive season includes the sexual period (when females and males are present and matings occur) as well as the maternal period (when females carry the eggsac and then the spiderlings). All the sighted individuals were in their webs; this implies that those adult males encountered had not started to search for females (Sordi 1996). This feature of the sampling method chosen (based exclusively on individuals inhabiting webs) would then cause bias in the proportions of each gender observed, attributable to the fact that we will be excluding those males who had left their webs to search for females. Bias would be also expected due to the shorter life of males (Stefani and Del-Claro 2011). In both populations the number of individuals

Figure 2. Characteristic landscape of both locations under study: (A) central Argentina, (B) southern Uruguay.

encountered did not differ between the two studied years (CA: $U = 3176$, $Z = -1.25$, $p = 0.21$; SU: $U = 3338$, $Z = -0.75$, $p = 0.46$). Therefore, the findings from both years were examined together as a whole for each population. Voucher specimens (10 females and 10 males of each population) were deposited in the scientific

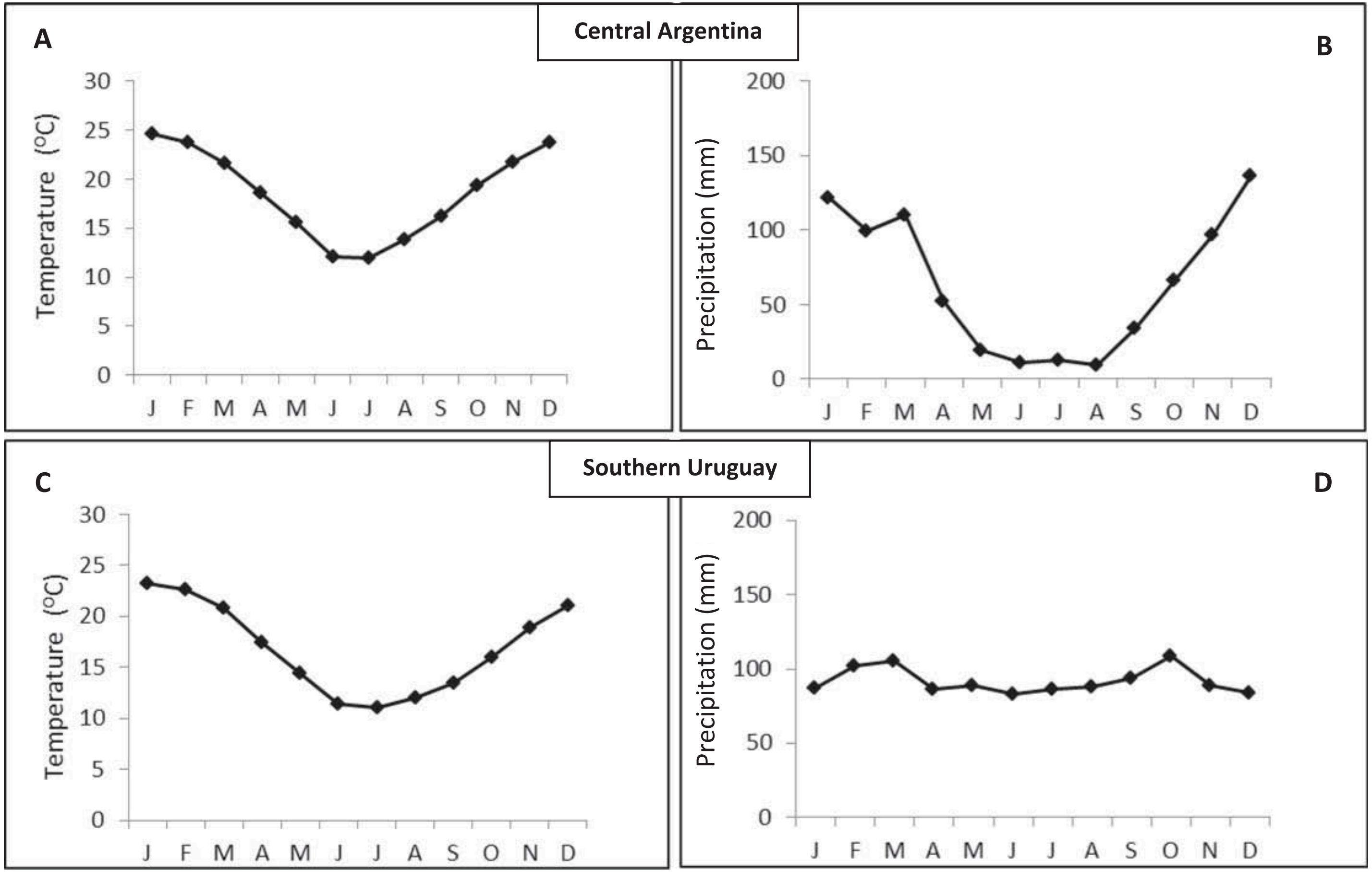

Figure 3. Mean temperature and annual rainfall during 2010–2011, according to the Portal Oficial del Gobierno de la Provincia de Córdoba (Argentina) and the Dirección Nacional de Meteorología (Uruguay).

arachnological collections of the Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay, and the Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina.

Normal distribution of the data was examined using the Shapiro–Wilk test and the homogeneity of variances with the Levene test. We performed the Mann–Whitney U-test for nonparametric analysis and used generalised linear models (GLM) with Poisson distribution and log link functions to perform parametric analyses. The statistical package used was InfoStat Professional v.2011p (Di Rienzo et al. 2011), with an alpha value of 0.05 to assess significance of results.

Results

The sighting frequency was of 5.21 individuals per hour per researcher for CA and 3.5 individuals per hour per researcher for SU. The total number of individuals sighted during the year is shown in Figure 4. For both populations, months with the lowest frequency of individuals' sighting corresponded to those in which only females or females with eggsacs occurred (November–January for CA and June–October for SU). In contrast, the highest values of sighting corresponded to those with predominance of immature individuals (March–October for CA and November–April for SU). Overall, a higher number of sightings was obtained in CA than in SU. The total numbers of individuals sighted during the fieldwork, discriminated by developmental and sexual categories, are shown in Table 1. Although the numerical relation female/male was approximately 2:1 for both populations, the numerical relation penultimate female/penultimate male was near 1:1.

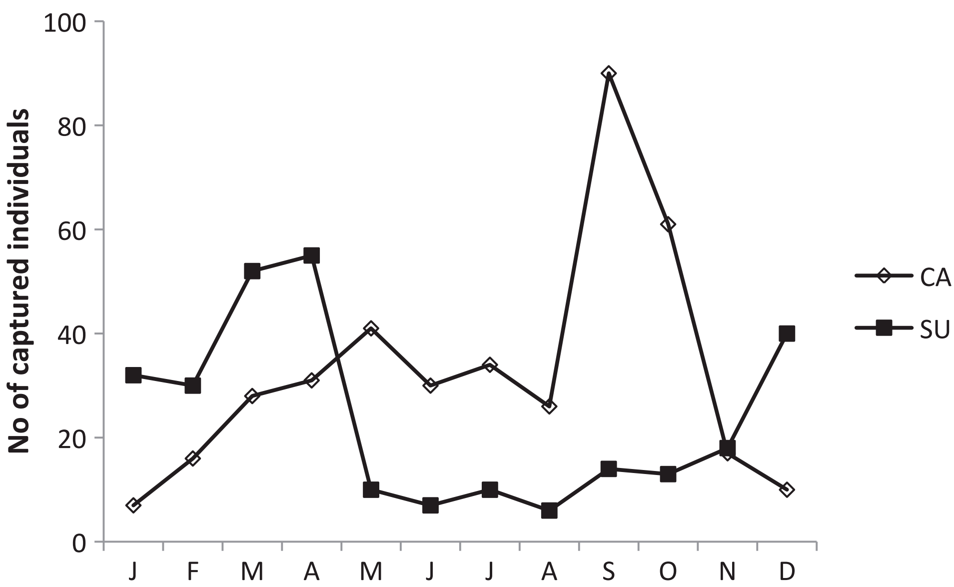

Figure 4. Number of individuals captured in webs during the year from central Argentina (CA) and southern Uruguay (SU) populations of *A. lagotis.*

Table 1. Number of individuals sighted during fieldwork in both populations; central Argentina (CA) and southern Uruguay (SU).

		CA	SU
Immature individuals	**Juveniles**	180	82
	Penultimate ♀	47	35
	Penultimate ♂	53	41
Adult individuals	♀	35	46
	♂	24	20
	♀**with eggsac**	18	16
	♀**with spiderlings**	18	12
	Total	**375**	**252**

The proportion of individuals on each category in both populations during the year is shown in Figure 5. We found statistical differences in the number of individuals per category and per month between populations (GLM Poisson distribution and log link function, Wald $\chi^2 = 966.94$, df = 66; $p < 0.001$). In CA the reproductive season occurred during spring and summer (September–February), during which the sexual period is followed by the maternal period. During the rest of the year we found immature individuals of different sizes, including winter months (June–August) (Figures 5 and 6). In SU the reproductive season appears to be partitioned by the winter, with the sexual period occurring during autumn (March–May) and the maternal period during spring (September–November). From December to March we found immature individuals of different sizes (Cephalothorax width from 0.7 to 3.8 mm). Only females, included mated ones, overwintered (Figures 5 and 6). Individuals' stages of development showed a small overlap among months, especially in SU, where synchrony appears more accentuated than in CA (Figure 5). CA showed a longer sexual period than SU, even partly overlapped with the maternal period (November and December) (Figure 6).

Discussion

Our results strongly suggest the existence of temporary disruption for the occurrence of interpopulation matings (i.e. an allochronic reproductive isolation). Although both populations of *A. lagotis* showed stenochrony (where spiders reproduce in definite season of the year, *sensu* Schaefer 1987) and an annual cycle that has already been reported for the species (Sordi 1996), they exhibit strongly different phenological patterns. Firstly, spring–summer unified reproductive season (i.e. sexual and maternal periods consecutive in time) characterizes the central Argentina population. In contrast, a clearly partitioned reproductive season occurs in the southern Uruguay population (i.e. sexual period during autumn and maternal period during spring–summer). Secondly, during the winter the central Argentina population presented immature individuals of diverse sizes whereas the southern Uruguay population presented only adult females, mostly mated ones.

The phenological pattern of the central Argentina population agrees with Schaefer's classification of spring/summer stenochronous species, with matings during spring and early summer and individuals overwintering as immature stages (Schaefer

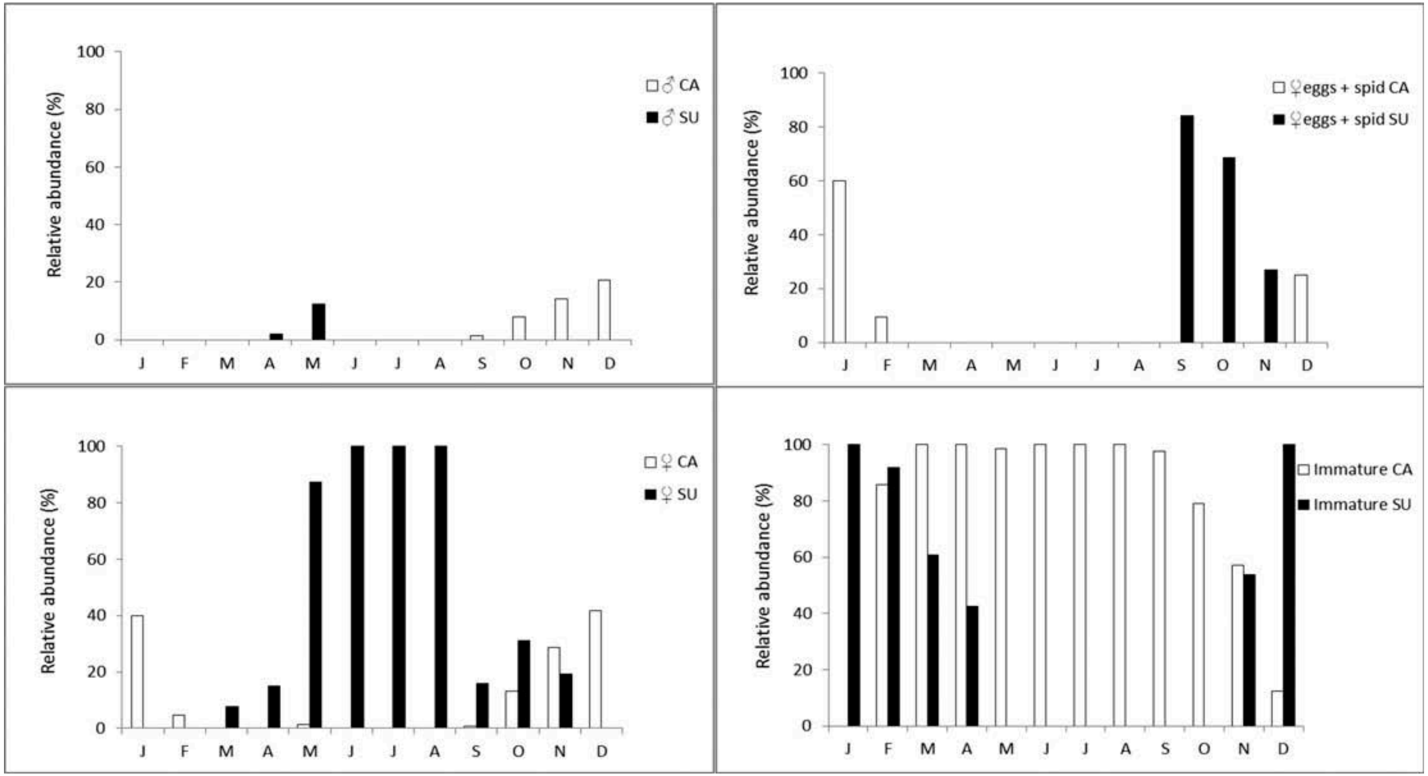

Figure 5. Relative abundance of males, females and immature individuals from both studied populations of *A. lagotis* during the year (2011–2012). Categories are compared in pairs. ♂CA: males from central Argentina; ♂SU: males from southern Uruguay; ♀CA: females from central Argentina; ♀SU: females from southern Uruguay; ♀eggs + spid CA: females from central Argentina carrying eggsac or spiderlings (maternal period); ♀eggs + spid SU: females from southern Uruguay carrying eggsac or spiderlings (maternal period); immature CA: immature (juveniles and penultimate) individuals from central Argentina; immature SU: immature (juveniles and penultimate) individuals from southern Uruguay.

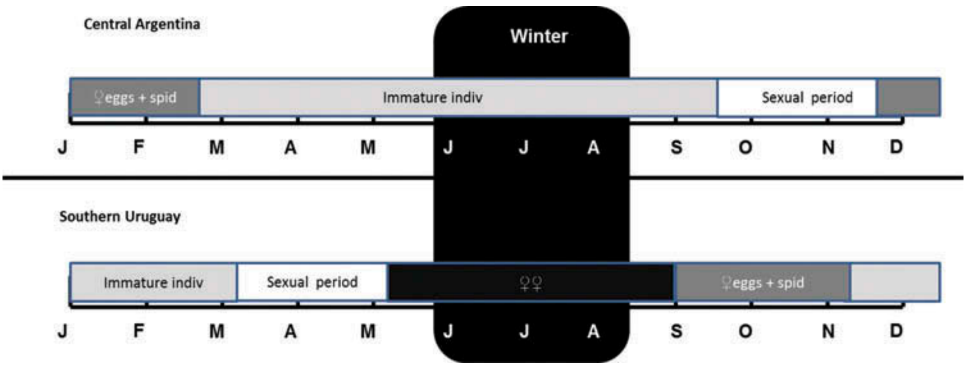

Figure 6. Schematic diagram showing the phonological patterns of central Argentina (CA) and southern Uruguay (SU) populations during the year. Note the clear temporal separation between the sexual periods of both populations and the overwintering only of females in SU as well as only of immature individuals in CA. ♀eggs + spid: females carrying eggsac or spiderlings (maternal period); Immature indiv: immature (juveniles and penultimate) individuals; ♀♀: females (most of them mated).

1987). In contrast, the southern Uruguay population presents a phenological pattern that is autumn stenochronous, with matings during autumn and only females, mostly mated ones, overwintering. In the phenological pattern previously described for *A. lagotis* (southeastern Brazil, Sordi 1996), the sexual period occurs from August to November and maternal period from September to December, and the coldest months, from May to July, are only pierced by immature individuals (Sordi 1996). Although the reproductive season of the southeastern Brazil populations starts earlier than that of the central Argentina population, it is clear that both populations show great similarity. In addition, a similar pattern also appears in a population from northwest of Argentina (province of Tucumán), in which the sexual period occurs from October to January (Bucher 1974). The southern Uruguay population shows the most different phenological pattern of all the *A. lagotis* populations studied to date.

The phenological pattern of the southern Uruguay population (sexual period in autumn) resembles those seen in other Uruguayan spiders such as the anyphaenid *Senogasta backauseni*, the caponiid *Caponina notabilis* (F. Costa unpublished data) and the lycosid *Schizocosa malitiosa.* The last species presents higher number of adult males and females during autumn, although they are found during the rest of the year as well (Costa 1991). *Lycosa arenaris,* a riparian species from temperate Australia, also presents this phenological pattern with an autumnal sexual period and a spring–summer maternal period (Framenau 1998). Nevertheless, in temperate zones spiders showing a sexual period during spring and summer is the most common pattern (Foelix 2011), as described for the other populations of *A. lagotis* (central Argentina and southeastern Brazil). This trend also occurs in other arachnids such as most scorpions (Polis 1990), and harvestmen (Machado and Macías-Ordóñez 2007), with females laying eggs and/or hiding the offspring in protected places during the cold season (e.g. Tallamy and Schaefer 1997; Machado and Macías-Ordóñez 2007).

As the eggsac in wolf spiders must be ripped by the mother to enable spiderlings to emerge (Foelix 2011) from a long winter, as occurs in Southern Uruguay, this may result in only adult females enduring that season, being capable of resisting the climatic conditions (i.e. cold and scarcity of prey). Later, females that survived winter build the eggsac at the beginning of the warmer months, and then take care of it and the emerged spiderlings. The climatic conditions and food resourced in late spring favour the rapid growth of the offspring before autumn, by when it must have reached the adulthood and be ready for mating. In a different way, populations located in lower latitudes (e.g. central Argentina or those of Brazil) have shorter winters and more warmer months, and, therefore, more time for the occurrence of matings, oviposition, spiderlings emergence and offspring development, overwintering as immature individuals. In other words, there is no high pressure on the reproductive season for the imminent arrival of winter. Although no differences seem to exist between size, body condition (González et al. 2013) or clutch size of individuals from *A. lagotis* populations, polyandry rates appear to be higher for central Argentina than for southern Uruguay (M. González, unpublished data). The currently reported phenological patterns could be related to those rates. Therefore, lower polyandry levels in the southern Uruguay population would relate with the shorter sexual period observed. More studies will be necessary to understand this possible relationship.

The different phenological patterns found in *A. lagotis* could be associated with the expression of phenotypic plasticity due to environmental factors, such as climate conditions or vegetational phytophysiognomies, quite diverse throughout the Neotropics or be related to differences in genetic information between populations (Fernández-Campón 2010; Velásquez et al. 2013; Macías-Ordóñez et al. 2014). In terms of environmental factors, central Argentina has hillsides with spinal vegetation and southern Uruguay has temperate grasslands (pampas) where grazing is common. In central Argentina temperatures reach more extreme values and winters are shorter than in southern Uruguay. Additionally, in central Argentina the climate is drier, in particular the winter (with frequent fire events) and annual precipitation levels are lower, occurring almost exclusively from September to April (from the beginning of spring to the beginning of autumn). In contrast, precipitation levels in southern Uruguay are higher and distributed almost homogeneously throughout the year and grazing is common. In southeastern Brazil, the study encouraged by Sordi (1996) was in moist tropical semi-deciduous forest and, although average temperatures remain higher than in central Argentina throughout the year, the rainy season goes from October to March (Instituto Nacional de Meteorología, www.inmet.gov.br) as found in Argentinian populations. Concerning the variation in genetic information, Stefani and Del-Claro (in press) report two sites of a different size (about 10 km away), the product of the habitat fragmentation, and two forest fragment sites close together where the sizes of individuals and of their webs differ but genetic data among them is very similar. Comparative genetic analysis among the populations mentioned in this study will be very useful to reveal if the differences mentioned above are also reflected in their genetic material.

However, we recently found a spatial overlap between both populations of *A. lagotis* in geographical intermediate locations (Departamento de Rio Negro, Uruguay), where individuals coexist that resemble those of central Argentina and others which resemble those of southern Uruguay. This association is based on a body pigmentation pattern previously reported for each population (González et al. 2013) and the respective phenological patterns described in the present study. This finding suggests that, even if climate conditions were factors that promoted phenological patterns differentiation in the past, they are not the ones that currently maintain it. Instead, more local microhabitat conditions (e.g. more or less dense vegetation) are related to the presence of one or the other ‘form’, or populations may present a genetic basis to differentiate and remain differentiated beyond being under the same environmental conditions. In other words, if the reported difference emerged through phenotypic plasticity in response to environmental conditions, genetic factors or microhabitat characteristics would be currently maintaining them. This would explain why the ‘forms’ remain distinct, even when they co-occur and are exposed to the same climatic conditions. The Rio Negro locality therefore offers us the possibility to investigate causes of the reported differences and further studies will focus on this target.

The possibility of mating occurrence between populations, and the genital morphology of their individuals, is currently being examined by experimental trials in the laboratory (M. González, unpublished data). Given that a single species may experience a wide set of environmental variables in the Neotropics (Macías-Ordóñez et al. 2014), leading to higher intraspecific variation (Fernández-Campón 2010), more interpopulation studies are needed. The present study attempted to offer this approach in relation to the phenology. Other studies could help in clarifying whether the heterogeneity of the features mentioned (body pigmentation pattern, sexual behaviour, phenological pattern), extends to other features within the species or if they are accompanying a speciation process of isolation (Kirkpatrick and Ravigne 2002).

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