Possible niche differentiation of two desert wandering spiders of the genus *Syspira* (Araneae: Miturgidae)

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Abstract.   When species with similar morphological and ecological characteristics occupy the same habitat, selection should minimize resource competition and promote coexistence by means of spatial partitioning. Competing species might exploit resources at different times or specialize in distinct resources. From July 2005 through May 2006 we examined the niche axes of two endemic sympatric desert species, *Syspira tigrina* Simon 1885 and *Syspira longipes* Simon 1885 in the State of Baja California Sur, looking for evidence that coexistence is fostered by differences in choice of microhabitat, temporal activity, occupation of space, or size. The results show high monthly microhabitat overlap (> 0.9). However, we found subtle differences in temporal activity and marked differences in juvenile and male body size, as well as some evidence of mutual spatial segregation. We conclude that body size and spatial segregation appear to be the dominant niche axes that facilitate coexistence of these species.

Keywords: Ecological segregation, morphological segregation, niche overlap

A central goal of ecology is to understand the forces that maintain species diversity within communities (Hutchinson 1959; Pacala & Tilman 1993; Chesson 2000). Hardin (1960) suggested that sympatric similar species competing for the same resources cannot stably coexist because one species will always be more efficient than the others and will quickly drive them to extinction. Consequently, coexistence requires some form of resource partitioning between co-occurring species to reduce or prevent interspecific competition (Amarasekare 2003). Hutchinson (1959), Chesson (2000), and Davies et al. (2007) state that partitioning can occur in three ways. First, species might differ in where they experience and respond to a limiting factor (spatial habitat partitioning). Second, different species may be limited by the same resources, but differ in the time when they exploit the resource (temporal partitioning). Third, co-occurring species may specialize in different resources (resource partitioning). These kinds of partitioning would be the result of selection for ecological character divergence among sympatric populations (Brown & Wilson 1956; Dayan & Simberloff 2005; Davies et al. 2007).

Different types of segregation have been reported among coexisting spiders. Among diurnal sympatric web-builders, scientists have observed a clear microhabitat segregation pattern in tetragnathids and linyphiids (Aiken & Coyle 2000; Wright & Coyle 2000). Henaut et al. (2001) have reported prey partitioning among araneids. Among nocturnal sympatric araneids and tetragnathids, researchers have noted temporal and spatial segregation (Ward & Lubin 1992).

Among diurnal wandering spiders, Uetz (1977) and Turner & Polis (1979) found seasonal specialization to be the predominant niche dimension facilitating coexistence of some gnaphosoids, while spatial (Suwa 1986) and microhabitat segregation (Moring & Stewart 1994; Carrel 2003) were the key to coexistence in some lycosids. Cutler & Jennings (1992)

found that habitat partitioning is common among congeneric jumping spiders. Among syntopic, congeneric, nocturnal wandering spiders, only ctenids have been studied, and the results suggest that among *Ctenus* species there is no clear niche partitioning (Gasnier & Höfer 2001), but that *Cuppiennus* species could be separated by differences in phenology on a seasonal basis (Schuster et al. 1994).

In the desert of Baja California Sur, there are two sympatric *Syspira* species: *Syspira tigrina* Simon 1885 and *S. longipes* Simon 1885 (Araneae: Miturgidae). These endemics (Olmstead 1975), are medium sized (8–12 mm) ground-dwelling spiders that are active during the night. Pitfall trap collections indicate that they represent up to 50% of all wandering spiders where they are found, so they are an important component of the desert ground spider assemblage (Nieto-Castañeda 2004). This genus has not yet been used as a model in ecological studies.

By documenting small-scale patterns of sympatric populations of *S. tigrina* and *S. longipes*, we wished to look for patterns of microhabitat occupation, microhabitat overlap, spatial segregation, temporal activity, and size segregation over a span of one year. Specifically, we asked the following questions: 1) What is the structural microhabitat occupied by the two species? 2) Is there evidence of overlap in microhabitat? 3) Are there indications of mutual spatial exclusion? 4) Is there evidence of temporal separation in activity? 5) Are there indications of size segregation? The answers to these questions will help us understand how co-occurrence of these two congeners takes place.

METHODS

Study area.—We selected four localities in the southern extension of the Sonoran Desert (León de la Luz et al. 2000) to represent a diversity of ground habitats, including three oases with varying availability of water and one locality without a water source. The oases are Presa de la Buena Mujer (24°05′N, 110°11′W, 180 m a.s.l.), a reservoir; Laguna San Pedro (23°56′N, 110°09′W, 6 m a.s.l.), a lagoon on the Pacific coast; El Novillo (23°55′N, 110°13′W, 220 m a.s.l.), a small pond in the hills, and El Comitán (24°07′N, 110°25′W, 20 m a.s.l.), a dry area (Fig. 1). The region is a subtropical desert with hot

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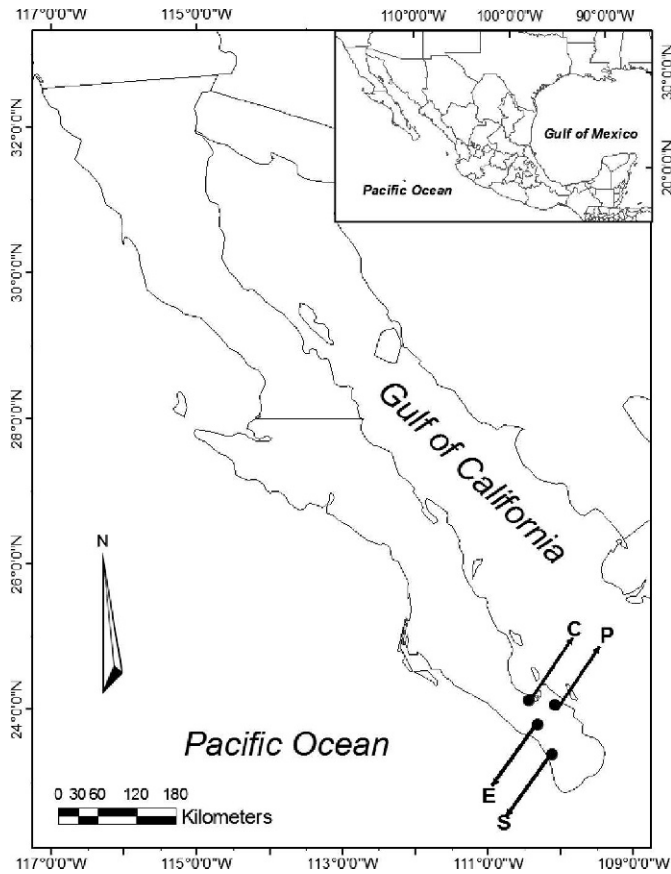
Figure 1.—Map of study sites where the two *Syspira* spider species were collected. S: Laguna San Pedro, P: Presa de la Buena Mujer, E: El Novillo, C: El Comitán.

Figure 2.—Dorsal view of carapace pattern of adults of *S. tigrina* (A) and *S. longipes* (B).

summers and a sporadic rainy season between July and October, and warm winters with little or no rain between November and February. The vegetation is subtropical desert shrub (León de la Luz et al. 1996).

Field work.—At each site, we plotted two belt transects (100 m × 1 m), separated by 50 m. Transects were divided into 20 quadrants (5 m × 1 m). We only sampled odd-numbered quadrants to avoid disturbance to the contiguous ones. We sampled the same quadrants every time because sizes of monthly catches of *Syspira* did not decline over a year (Nieto-Castañeda 2004) in a previous study of Baja California's wandering ground spiders using pitfall traps. Exhaustive hand collections with headlamps were made by a three-member team, which spent one night at each locality every 3 mo from July 2005 through May 2006. This sampling pattern included two rainy seasons (July and January) and two dry seasons (October and May), totaling 16 collecting days. Sampling started at dusk when *Syspira* spiders become active and continued for 4–5 h, until spiders were no longer present. The spiders were preserved in 70% ethanol.

Characterization of microhabitats.—When a spider was found, we drew a 0.19 m² circle (based on a 25 cm radius) around it and measured ten variables to characterize the microhabitat. The percentage of the following five ground surfaces was identified: (1) bare soil, (2) fallen logs and branches, (3) leaf litter and twigs, (4) gravel and pebbles (2–64 mm dia.), and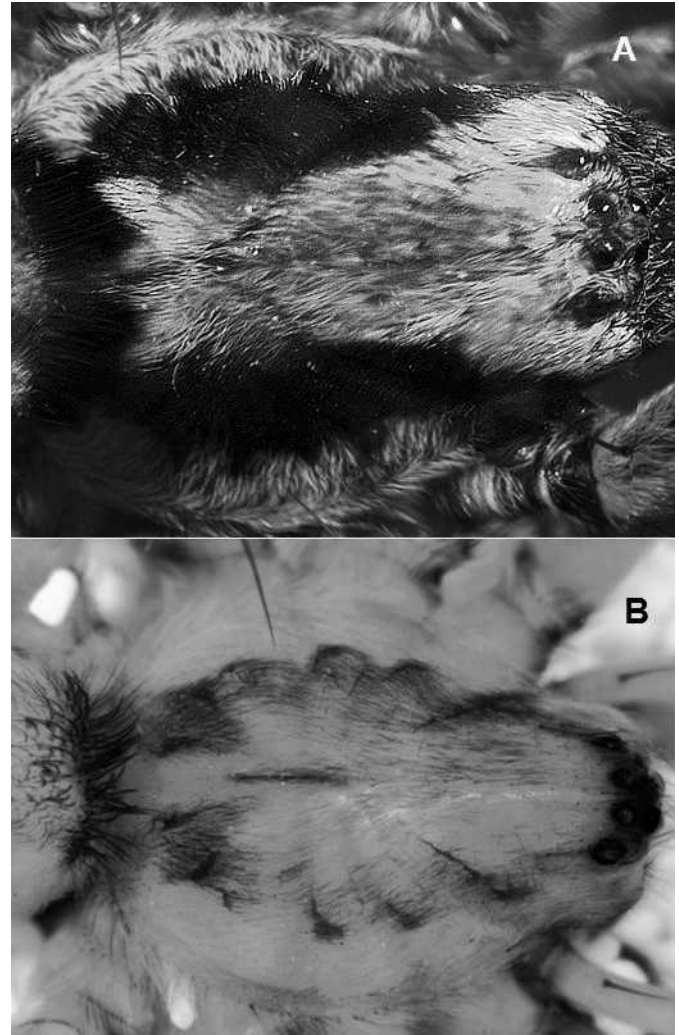 (5) cobbles (64–256 mm dia.). Next, we immediately estimated the percentage of above-ground vegetation (6). We then recorded (7) plant life forms (trees, shrub, herbs), (8) soil texture [measured as categorical variable 1: 100% of sand, 2: <100, and >70% of sand, 3: <70% of sand) by the wet feel method (Thien 1979)], (9) temperature, and (10) relative humidity at the bare soil surface with a thermo-hygrometer (HI-8564, Hanna).

Species identification and measurements.—All spiders were identified to species level using Olmstead (1975) and then sexed if they were mature. We included the immature spiders because they are necessary for any objective community analysis (Sackett et al. 2008). These spiders, even young specimens, are easily identified by the markings on the carapace. *S. tigrina* has three dark stripe markings: two are longitudinal and almost parallel, beginning near coxa I and ending before the posterior edge of the carapace; these stripes are separated by at least the distance between the anterior lateral eyes. The third stripe is perpendicular to the other two and is closer to the posterior edge of the carapace (Fig. 2A). *S. longipes* has reticulated markings (Fig. 2B).

The total tibia I length and the carapace width of every spider was measured as an indicator of body size (Hagstrum

Table 1.—Number of juveniles (J), adult males (M), and adult females (F) of two *Syspira* species sampled each month in study.

Species	July			October			January			May			Total
	J	M	F	J	M	F	J	M	F	J	M	F	
S. tigrina	59	11	18	76	4	1	105	0	4	56	2	3	339
S. longipes	21	8	2	27	0	3	21	0	1	7	1	2	93

1971; Toft 1976). We did not measure total body length because that can change quickly with alterations in foraging success. Measurements were performed with a stereoscopic microscope, using a micrometer. Voucher specimens were deposited in the Arachnological and Entomological Collection of the Centro de Investigaciones Biológicas del Noroeste (CAECIB).

Data analysis.—*Characterization of microhabitat:* To test whether species occupied different microhabitats with respect to the month sampled, we used principal components analysis (PCA) with varimax rotation of the correlation matrix. This reduced the ten continuous microhabitat variables to a smaller number of variables that explained most of the variation in the raw data. Prior to conducting the PCA, we log$_{10}$-transformed temperature and relative humidity, after adding 1 to improve normality and reduce heteroscedasticity. Then percentages were converted to proportions and transformed by arcsine square root (Goodman 2007). PCA was separately conducted for each season, which generated four sets of PC axes. PC axes with eigenvalues greater than 1.0 and eigenvectors with scores greater than 0.7 were considered informative. The first two principal components were plotted against each other to find structure in the data that could distinguish *S. tigrina* specimens from *S. longipes* specimens. All analyses were performed with STATISTICA v. 6.0 software (StatSoft, Inc).

Overlap of microhabitat: Using the most informative variables in PCAs, we calculated Pianka's Index of microhabitat overlap by sampled month with the ECOSIM v. 7.0 software (Gotelli & Entsminger 2008). We then determined the statistical significance of the observed microhabitat overlap by comparing it with the RA3 algorithm, where the niche breadth was retained and the zero states were reshuffled. In the monthly presence-absence matrices, each row represented the two *Syspira* species and each column represented a different microhabitat category, in which the observed data on resource utilization were randomized between the two species in 5000 simulations with proportional representations of the two *Syspira* species and resources (Gotelli & Entsminger 2008).

Spatial segregation: With an abundance matrix by sampled month in place, where rows represented the two *Syspira* species, columns represented different quadrants (80 by month, 320 in total), the co-occurrence module of ECOSIM v. 7.0 was used to test for non-random patterns of species co-occurrence. We calculated co-occurrence scores (C-score) as the numbers of checkerboard units, based on 5000 interactions with proportional representations of species and quadrant sites. Species representations (rows) and quadrant location representations (columns) were kept 'proportional' because these conditions best reflected differences between species in terms of trapping and spatial heterogeneity in trapping probability. We calculated the expected C-scores (null models) and subsequently tested for whether the occurrence of *S.*

tigrina and *S. longipes* deviated from random occurrence (Gotelli & Entsminger 2008).

Temporal activity pattern: We used a Fisher exact test by species to test for independence of spider abundance between transects. We then performed a chi-squared goodness of fit test to determine monthly differences in species abundance. All analyses were performed with the Stata v. 9.1 software (StataCorp, College Station, TX).

Size segregation: We also conducted a multivariate two-group Hotelling's T-squared test with Stata v. 9.1 software, which tested for significant monthly size differences in the carapace width and total tibia length between *Syspira* species by developmental stage. Statistical significance was set at $P < 0.05$.

RESULTS

Spiders collected.—During this study, we collected 432 *Syspira* spiders. Immature spiders represented almost 87% of all *Syspira* spiders and were more abundant in January, while adults were more abundant in July. *S. tigrina* was the most abundant species in every month (Table 1).

Characterization of microhabitat.—PCAs with microhabitat variables organized by month were used to characterize the microhabitats occupied by each species. The first two components of the four PCAs accounted for ∼ 50% of the variation (Table 2). *S. longipes* were always within the microhabitat conditions occupied by *S. tigrina*. Positive scores for PC1 correlated with moist areas during July, October, and January and dry areas during May. Negative scores for PC1 were associated strongly with cool areas in July, October and January and warm areas during May. According to PC1, *S. longipes* was restricted to the areas that were cooler and had higher relative humidity than areas occupied by *S. tigrina* during July and January and to the areas that were warmer and had lower relative humidity occupied by *S. tigrina* during October and May. During May, positive scores were linked with low sand soil texture. There were slight differences in the structural microhabitat variables correlated with PC2. During July, positive scores showed a relationship with higher bare soil surface, negative scores were correlated with higher leaf litter and twigs surface. During October and January, positive scores for PC2 were interconnected with high leaf litter and twig surface, and negative scores correlated with high bare soil surfaces. During May, PC2 was positively correlated with vegetation coverage above ground and life form, but PC2 did not distinguish *S. longipes* from *S. tigrina* (Fig. 3).

Overlap of microhabitat.—Monthly microhabitat overlap for both species was high, indicating an almost complete overlap. This result was significantly higher than expected by chance ($P \leq 0.05$) (Table 3).

Spatial segregation.—The two species shared only a small number of the 320 quadrants in all months, and most

Table 2.—Correlations of ten structural microhabitat variables with the first two axes obtained from PCA (PC1, PC2) for each month. Bold numbers indicate the most important variables. Eigenvalues and total variance explained are provided too.

| Variable	July		October		January		May	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Bare soil	0.38	**0.86**	−0.08	**−0.91**	0.26	**−0.91**	0.00	−0.06
Fallen logs and branches	−0.09	0.00	0.39	−0.28	0.05	0.19	0.02	−0.52
Leaf litter and twigs	−0.02	**−0.84**	0.01	**0.90**	0.14	**0.95**	−0.19	0.16
Gravel and pebbles	−0.48	−0.22	−0.17	−0.06	−0.73	−0.03	0.24	0.34
Cobbles	−0.31	0.01	0.50	0.12	−0.25	−0.07	0.12	−0.49
Above ground vegetation	0.56	−0.33	0.03	0.07	0.10	0.16	−0.29	**0.69**
Life form	0.21	−0.57	0.09	0.19	0.13	0.22	0.05	**0.77**
Soil texture	−0.65	−0.09	−0.39	0.21	−0.24	0.23	0.74	−0.19
Temperature	**−0.76**	0.15	**−0.84**	0.00	**−0.83**	0.03	0.95	0.01
Relative humidity	**0.84**	−0.11	**0.88**	0.10	**0.88**	−0.09	**−0.91**	0.04
Eigenvalue	2.55	1.98	2.38	1.89	2.70	2.17	2.92	1.70
% Total variance	25.50	19.77	23.84	18.93	27.00	21.69	29.16	17.03
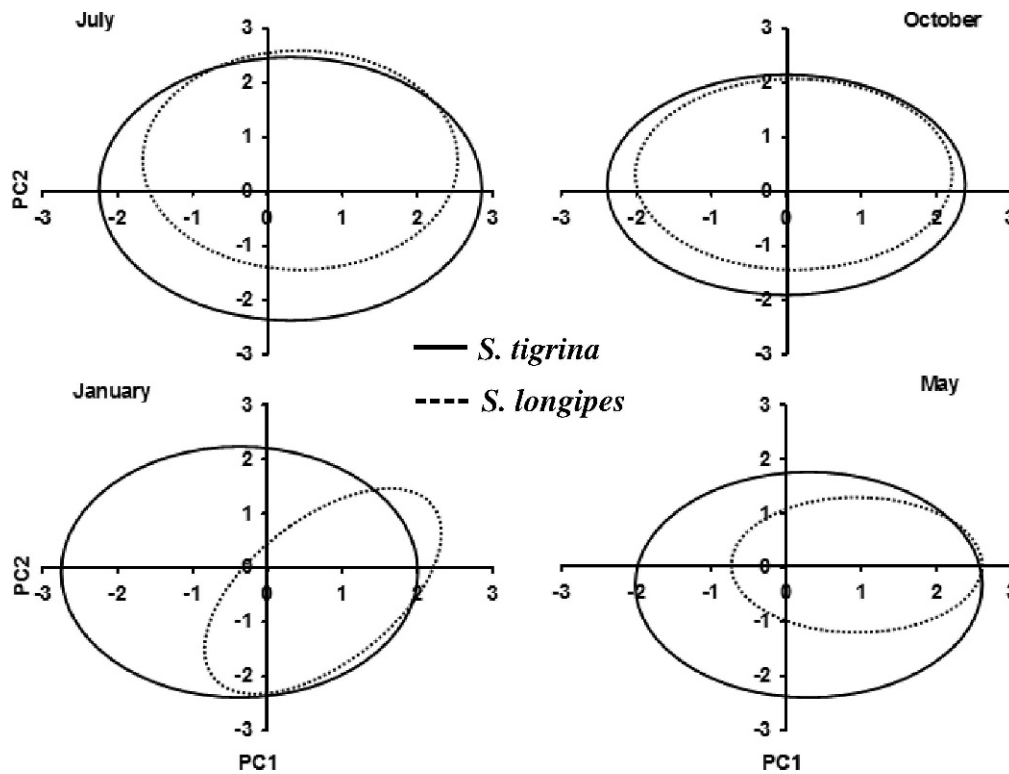
Figure 3.—Structural microhabitat occupied by two *Syspira* species each month in two-dimensional ecological space based on principal components scores (PC1 and PC2).

Table 3.—Observed and expected Pianka's overlap indices for each month. Indices are given as the mean ± SD. Expected values are based on 5000 interactions with proportional representation of species and resources.

Month	Overlap Index	
	Observed	Expected
July	0.95	0.79 ± 0.08
October	0.97	0.75 ± 0.09
January	0.94	0.73 ± 0.09
May	0.92	0.87 ± 0.03

quadrants were exclusively occupied by one species. In all months, C-scores were significantly higher than expected by chance, which indicated interspecific spatial segregation ($P \leq 0.05$) (Table 4).

Temporal activity pattern.—We found that *S. tigrina* had significantly different patterns between transects ($\chi^2_3 = 20.79$, $P < 0.05$), but *S. longipes* did not; neither species had the same monthly abundance pattern ($\chi^2_3 = 4.21$, $P > 0.05$) (Fig. 4).

Size segregation.—Juveniles of neither species had the same average tibia and carapace size among months (July: $F_{2,77} = 7.38$, October: $F_{2,100} = 40.77$, January: $F_{2,123} = 60.02$, May:

Table 4.—Frequency of quadrants (for each month = 80; total = 320) occupied by one, both, or neither *Syspira* species. Observed and expected C-scores are given. Indices are given as the mean ± SD. Expected values are based on 5000 interactions with proportional representation of species and trap quadrants.

Month	Species in quadrants			C-score	
	None	Single	Both	Observed	Expected
July	31	41	8	310	111 ± 41
October	32	34	14	208	96 ± 35
January	28	44	8	259	108 ± 46
May	40	36	4	155	59 ± 32

$F_{2,60} = 12.96$, $P < 0.05$). Females of neither species exhibited significantly different tibia and carapace sizes in most months (October: $F_{2,1} = 0.02$, January: $F_{2,2} = 0.23$, May: $F_{2,2} = 0.96$, $P > 0.05$) except in July ($F_{2,17} = 6.35$, $P < 0.05$). Males of both species had significantly different tibia and carapace sizes in July ($F_{2,16} = 20.10$, $P < 0.05$), but in the other three months the sample size was too small to test. *S. longipes* spiders had a longer tibia I and a wider carapace than *S. tigrina* in all stages and months (Fig. 5).
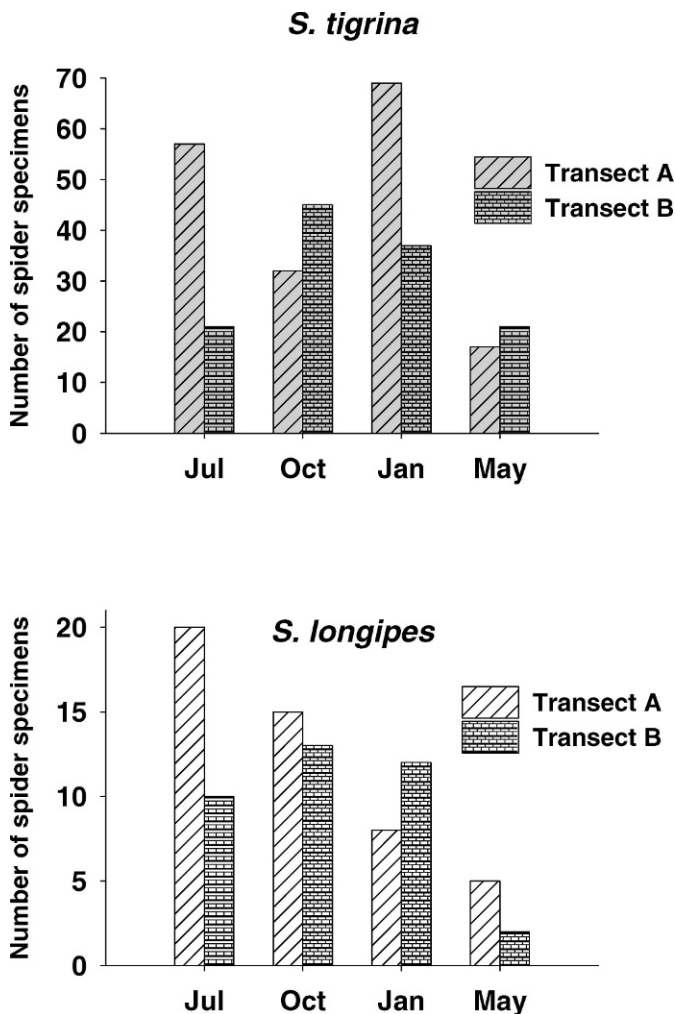

Figure 4.—Monthly numbers of active *Syspira* species in two transects (A, B) sampled at each site.

DISCUSSION

Large similarities in microhabitat occupancy indicate that *Syspira* species should compete intensely (Holt et al. 1994), with limited species overlap (Goodman 2007). Additionally, members of the species should segregate in other dimensions, as has been observed for other wandering spiders (Schuster et al. 1994; Gasnier & Höfer 2001). In co-occurring, congeneric, web-building spiders of the families Araneidae, Tetragnathidae, and Linyphiidae in Nearctic regions, microhabitat segregation appears to be a main factor allowing coexistence (Aiken & Coyle 2000; Wright & Coyle 2000). This type of segregation between congeneric species has been documented in burrowing wolf spiders of the genus *Geolycosa* in Florida (Marshall et al. 2000; Carrel 2003) and ground-wandering *Pardosa* species in Japan (Suwa 1986). There is, however, no evidence of habitat segregation among nocturnal, congeneric, terrestrial cursorial spiders.

The constrained occupancy of the microhabitat of *S. longipes* relative to *S. tigrina*, with respect to temperature and relative humidity, suggests possible differences in their metabolism, since these environmental factors affect spider performance (Huey & Kingsolver 1989). Spatial arrangements of *Syspira* species appear unrelated to leaf litter and twigs or bare surfaces, even in desert communities that lack much structural complexity, although these features are considered to be one of the most critical microhabitat variables affecting community structure (Melville & Schulte 2001; Goodman 2007).

We were not surprised to find significant spatial segregation between these *Syspira* species during all months since there are several studies suggesting that similar sympatric spider species differ principally in spatial distribution. For example, four wandering *Ctenus* species in Central Amazonia segregate spatially (Gasnier & Höfer 2001) and four sympatric orb weavers (Araneidae and Tetragnathidae) that inhabit coffee plantations in Mexico reduce competition by building webs of varying structures in different locations (Henaut et al. 2001). Congeneric species of *Pardosa* have the same daily and seasonal pattern, but segregate by vertical or horizontal stratification (Greenstone 1980; Suwa 1986).

As expected, we found slight differences in temporal segregation; however, it has not been well documented in congeneric wandering spiders, although Turner & Polis (1979) and Uetz (1977) stated that temporal segregation was an important factor in reducing niche overlap. Yet this type of segregation has been reported in other co-ocurring species, namely *Pardosa milvina* (Hentz) with *Hogna helluo* (Walckenaer) on soybean farms in Ohio (Marshall et al. 2002). Ward & Lubin (1992) found that six nocturnal orb-weavers (Tetragnathidae and Araneidae) occupied the same habitat, but had different daily and seasonal activity patterns.

Competition for food has long been considered a keystone of community ecology. Therefore, differences in the average monthly size of juveniles, and sometimes adults, of both species may enable trophic divergence because body size is a reliable determinant of prey size, non-web-building spiders typically consuming prey of similar size to themselves (Gertsch & Riechert 1976; Nentwig & Wissel 1986). The significant overlap in average body size between females of
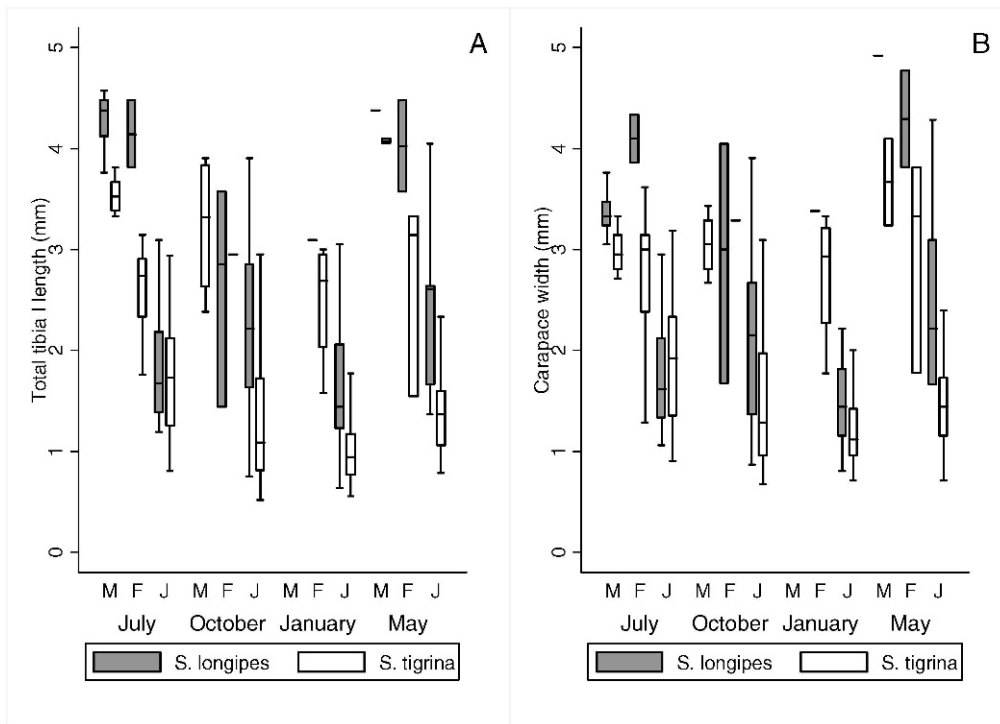
Figure 5.—Box plots of tibia I length (A) and carapace width (B) of both *Syspira* species. M: males, F: females, J: juveniles.

both species from October to May suggests that competition for prey or other resources may be high. There are many cases among animals that highlight the important role of phenotypic divergence between sympatric species as a way to avoid competition for food: bill size and shape in passerine birds (Newton 1967); body size among amphibians, reptiles, insects, and rodents; canine teeth diameter in carnivores (Pimm & Gittleman 1990); and neck height or incisor arcade structure in herbivorous mammals (Gordon & Illius 1988; Du Toit 1990).

Differences in size may also be attributable to character displacement (Guilleman et al. 2002; Dayan & Simberloff 2005). Such displacement occurs when selection, during extended periods of sympatry among animals that partition resources, results in an accumulation of morphological differences that reduces or resolves competition. However, such differences in morphology may have arisen before the species came into sympatry, and these differences may have been responsible for facilitating coexistence at its initial stages. In either case, morphological distinctiveness is likely to be a major contributor to stable coexistence of potential competitors (York & Papes 2007). Few studies actually address phenotypic divergence between sister sympatric species. Many researchers assume that closely related species are more likely to compete than distantly related ones (Dayan & Simberloff 2005). There are no studies in which phenotypic differences among sympatric spider congeners are correlated as a consequence of character displacement.

These two *Syspira* are closely related sympatric species that have probably evolved similar life histories, and, since they use the same microhabitats, have similar resource use. The spatial, temporal (to a lesser degree), and size differences between the two species may be the key factors permitting their coexistence.

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