Spider Prey of *Trypoxylon lactitarse* Saussure (Hymenoptera: Sphecidae)[1]

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Abstract Surveys of prey use by *Trypoxylon lactitarse* Saussure (Hymenoptera: Sphecidae) were conducted in Clemson, SC, by placing trap-nests in four habitat types: a planted loblolly pine stand, a naturally-occurring mixed hardwood forest, an area of mowed grass containing scattered mature oaks, and a mowed pasture. *Trypoxylon lactitarse* only provisioned trap-nests in the planted pine and mixed hardwood habitats. All recovered trap-nests were found between 1 and 19 July 1991. In the pine habitat, two fully provisioned trap-nests were recovered that contained a total of 91 spiders in the families Araneidae (93.4%), Mimetidae (5.5%), and Tetragnathidae (1.1%). In the mixed hardwood forest, eight fully provisioned trap-nests were recovered, containing a total of 721 spiders in the families Araneidae (97.2%), Philodromidae (2.6%), and Mimetidae (0.1%). In the pine habitat, spiders consisted predominantly of *Araneus* spp. juveniles (58.2%) and the araneid *Eustala cepina* (Walckenaer) (28.6%); whereas, in the hardwood habitat *E. cepina* (81.8%) was the most abundant prey. Although prey use varied between the two habitats, within each habitat contents of individual trap-nests suggests that *T. lactitarse* exhibits a relatively high degree of prey constancy.

Key Words *Trypoxylon lactitarse*, provisioning wasps

Trypoxylon lactitarse Saussure (Hymenoptera: Sphecidae) is widely distributed throughout eastern North America west to Arizona and south to Argentina (Krombein et al. 1979). This species has been previously referred to as *T. albopilosum planoense* Rohwer, *T. albopilosum* Fox, *T. cinereum* Cameron, and *T. striatum* Provancher, and has been placed in the genus *Trypargilum* Richards (Krombein et al. 1979).

Early reports of *T. lactitarse* (as *Trypoxylon albopilosum*) behavior, biology, and prey use were made by Peckham and Peckham [as *Trypoxyllon*] (1895) and Rau (1928). Previous studies have reported that spiders in the families Araneidae, Tetragnathidae, Theridiidae, Mimetidae, Thomisidae, Pisauridae, Gnaphosidae, Anyphaenidae, Clubionidae, and Salticidae are used as prey by *T. lactitarse*, with Araneidae being the most common prey (Krombein 1967, Medler 1967, Krombein et al. 1979, Coville 1981, Camillo and Brescovit 1999).

In this study we determined the composition of spider prey of *T. lactitarse* in northwestern South Carolina, compared prey composition between pine and hardwood habitats, and compared prey composition within and between trap-nests.

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Materials and Methods

This study was conducted in Clemson, Pickens Co., SC in 1991. Trap-nests, similar to those described by Krombein (1967), were constructed from untreated pine lumber. Each trap-nest was constructed from a block measuring 17 × 4 × 4 cm. Prior to boring the nest hole, which measured 0.94 cm diam × 13.5 cm deep, each block was sawed lengthwise and the halves nailed together so trap-nests could be easily opened after provisioning occurred in order to remove the spider prey for identification. Trap-nests were attached to a wooden backboard (30.5 × 8.9 × 1.9 cm) in sets of four with the trap-nest openings oriented in alternating directions (Fig. 1). Three such sets of trap-nests were placed in each of four habitats: a planted loblolly pine [*Pinus taeda* (L.)] stand (approximately 1 ha), a naturally-occurring mixed hardwood forest dominated by several oak species (*Quercus* spp.) (approximately 6 ha), near the center of a pasture (approximately 10 ha), and in an area of mowed grass containing several scattered white oak (*Q. alba* L.), red oak (*Q. rubra* L.), and live oak (*Q. virginiana* Mill.) trees (approximately 2.5 ha), all of which were >40 cm dbh. In the pine, mixed hardwoods, and grass-oak areas, backboards were tied to standing live

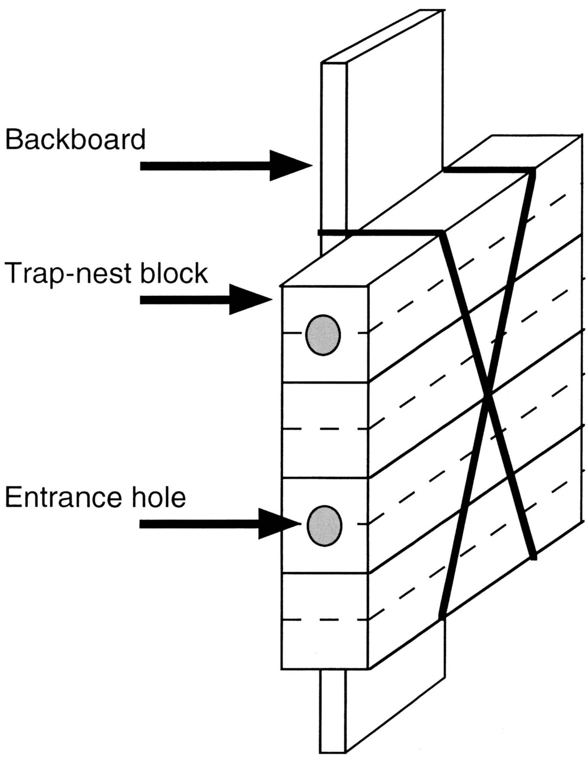

Fig. 1. Trap-nest design showing one set of four individual trap-nests mounted to a backboard. Individual trap-nests measure 4 × 4 × 17 cm, with a 0.94 × 13 cm nesting hole.

trees, while in the pasture they were tied to existing metal fenceposts. The lowest trap-nest on a backboard was between 0.8 and 1.2 m above the ground surface, and within each habitat, the three sets of trap-nests were separated by at least 10 m. All trap-nests were within 0.6 km of all others.

Trap-nests remained in the field from 30 May until 15 October 1991 and were checked weekly until provisioning began in late June. They were then checked every Monday, Wednesday, and Friday until no provisioning activity was observed at any trap-nest for 10 d. From mid-August until mid-October they were checked bi-weekly. Provisioning was considered complete either when the open end of the trap-nest contained an obvious mud plug, or when no adult *T. lactitarse* was observed at a nest where one had previously been active. Only trap-nests considered to have been completely provisioned were included in the analyses. Provisioned trap-nests were returned to the laboratory and opened on the observation date when provisioning was complete. Spiders from individual cells were placed together in vials of 80% EtOH until identified. Individual cells were numbered with the innermost cell being designated as Cell 1.

Primary spider identifications were made by MWR, with positive identifications of those in the genus *Araneus* made by J. Redner (Biosystematics Research Centre, Agriculture Canada). Representative specimens of all species have been deposited in the Clemson University Arthropod Collection (CUAC). Specimens of *Araneus ni-*

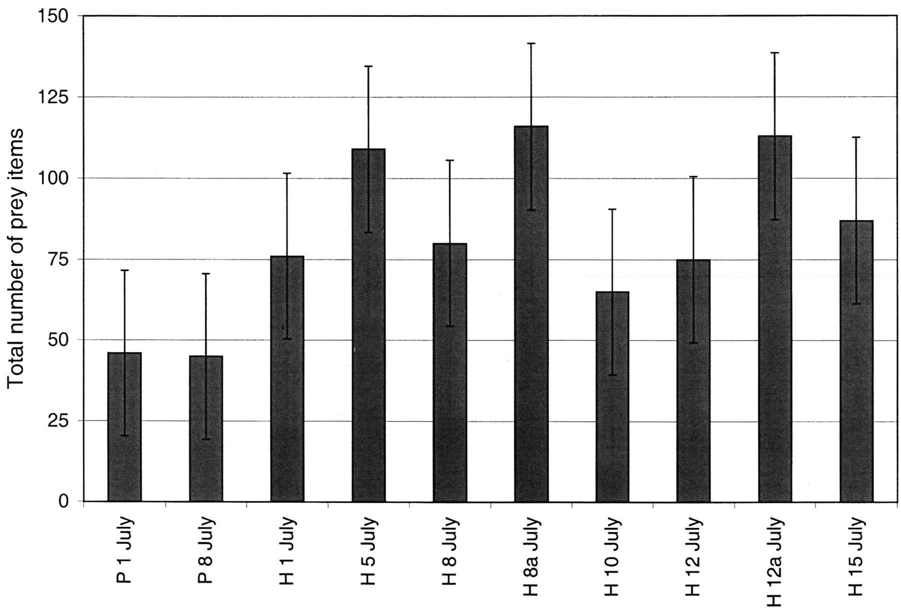

Fig. 2. Total number of prey items per trap-nest provisioned by *T. lactitarse* in Clemson, SC in 1991. Vertical bars indicate ±1 SD of these 10 observations. Habitat is indicated by P (pine habitat, or H (hardwood habitat). Trap recovery dates followed by an a indicate the second trap recovered within a habitat on a given date.

veus (Hentz), *A. cingulatus* (Walckenaer), and *A. guttulatus* (Walckenaer) also have been deposited in the Biosystematics Research Centre, Agriculture Canada.

Data collected from each trap-nest included habitat, completion date, number of provisioned cells, number of spiders per cell, and identifications of spiders recovered from each cell. References to individual trap-nests are made in the following format: P or H (for pine or hardwood habitat) date provisioning was considered complete (i.e., P 1 July would indicate a trap-nest from the pine habitat collected on 1 July). On both 8 and 12 July, two provisioned trap-nests were recovered in the hardwood habitat. Those trap-nests are designated as 8 and 8a July and 12 and 12a July. Within these 10 trap-nests, three individual cells were found to contain <5 spiders and a near fully developed wasp larva. Because the majority of the spiders in these cells had been consumed, these cells were excluded from any analyses of prey composition. Because of potential foraging differences required to capture adult females, adult males, or juvenile spiders of a given species, each prey species was divided into these three prey groups for analyses.

Because the data consisted of total prey counts from each provisioned cell, chi-square analyses were used to determine whether the numbers of spiders within provisioned trap-nests or habitats were equally distributed among the prey groups recovered. For the total number of prey items per trap-nest, number of prey groups per cell, number of provisioned cells per trap-nest, and number of prey items per cell, a difference of more than 1 SD from the mean of all ten provisioned trap-nests was considered to indicate significance. Bruillouin's diversity index (*H*) and evenness

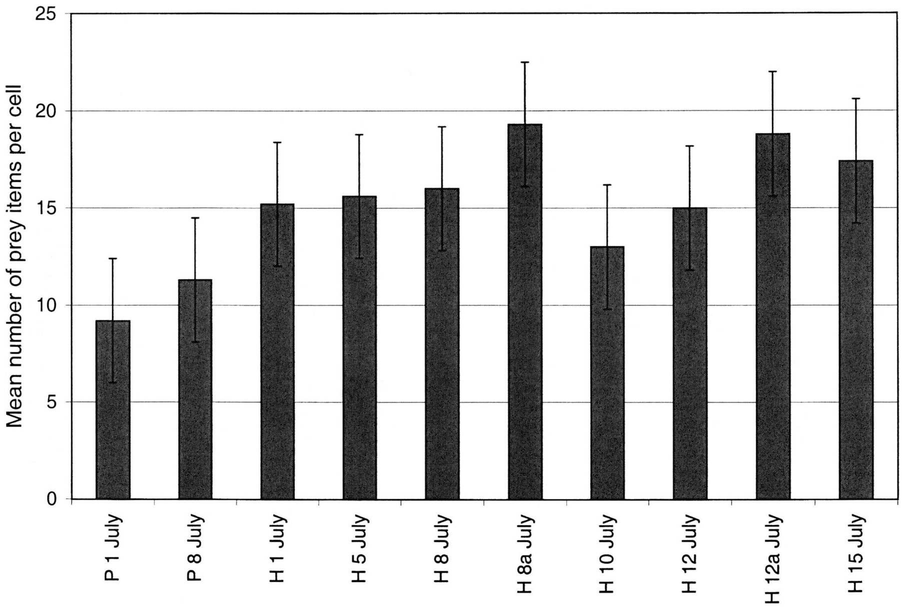

Fig. 3. Mean number of prey items per cell in trap-nests provisioned by *T. lactitarse* in Clemson, SC in 1991. Vertical bars indicate ±1 SD of these 10 observations. Trap designations are as in Fig. 2.

measure (J) were used because we were comparing completely known data sets from provisioned nests, and were not randomly sampling spider prey from these trap-nests (Poole 1974). To assess similarity among trap-nests, or individual cells within or among trap-nests, the modified Morisita-Horn index (C_{MH}) was used because it has been reported to be the most effective similarity measure for quantitative data and is not influenced by either sample size or sample diversity (Wolda 1981). A C_{MH} value of >0.70 was chosen to indicate a high degree of similarity for all comparisons.

Results and Discussion

Of the four habitats examined, no provisioned trap-nests were found in either the pasture or grass-oak habitats, suggesting that *T. lactitarse* either does not forage or does not use nest sites in open habitats, or that their spider prey are not found in these types of habitats. Two completely provisioned trap-nests were recovered in the pine and eight in the hardwood habitats. Six additional trap-nests were recovered, two in the pine and four in the hardwood habitats, in which the wasp larva had consumed all prey except for those in the outermost one or two cells. Data from these six trap-nests were only used to determine the seasonal activity period of *T. lactitarse.* All provisioned trap-nests were recovered between 1 and 19 July 1991. Because no provisioned trap-nests were recovered from 30 May to 30 June or from 20 July to 15

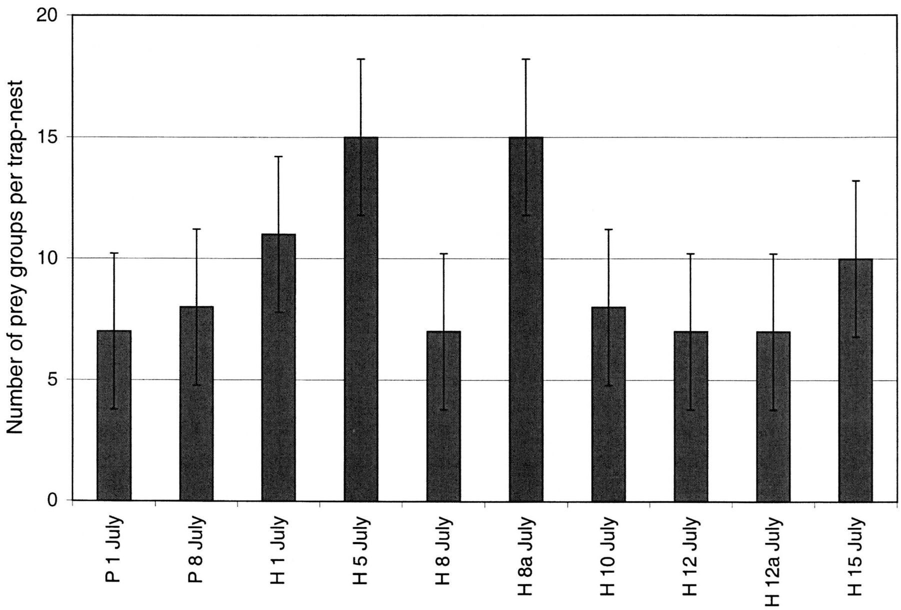

Fig. 4. Total number of prey groups (females, males, or juveniles of each prey species) in trap-nests provisioned by *T. lactitarse* in Clemson, SC in 1991. Vertical bars indicate ±1 SD of these 10 observations. Trap designations are as in Fig. 2.

Table 1. Number of individuals of each prey group recovered from ten provisioned *Trypoxylon lactitarse* trap-nests from pine and hardwood habitats, Clemson, SC

Species	Group	Pine 1 July	Pine 8 July	Hardwood 1 July	Hardwood 5 July	Hardwood 8 July	Hardwood 8a July	Hardwood 10 July	Hardwood 12 July	Hardwood 12a July	Hardwood 15 July	Total P/H
Araneidae												
Acacesia hamata (Hentz)	I	—	—	—	1	—	2	—	—	—	—	0/3
Araneus cingulatus (Walckenaer)	F	—	—	1	1	—	3	2	—	1	2	0/10
	M	—	—	—	—	—	—	—	—	—	1	0/1
Araneus guttulatus (Walckenaer)	I	—	—	2	—	—	1	—	—	—	1	0/4
	F	—	2	—	1	—	4	1	3	4	2	2/15
	M	—	—	1	—	2	1	5	2	—	—	0/11
Araneus niveus (Hentz)	F	—	—	—	2	1	3	1	—	—	2	0/9
	M	1	—	—	—	—	—	—	—	—	1	1/1
Araneus spp. juveniles	I	36	17	5	3	2	3	15	—	2	—	53/30
Eustala anastera (Walckenaer)	F	—	2	—	—	—	—	—	1	—	—	2/1
Eustala cepina (Walckenaer)	I	4	7	13	16	6	26	2	23	12	—	11/98
	F	2	12	26	70	53	58	25	65	76	44	14/417
	M	—	1	18	4	13	6	12	2	3	17	1/75
Mecynogea lemniscata (Walckenaer)	F	—	—	—	—	—	1	—	—	—	—	0/1
	M	—	—	—	1	—	1	—	—	—	—	0/2

Table 1. Continued.

		Pine		Hardwood								
Species	Group	1 July	8 July	1 July	5 July	8 July	8a July	10 July	12 July	12a July	15 July	Total P/H
Metepeira labyrintha (Hentz)	I	—	—	4	2	—	3	—	—	—	—	0/9
	F	—	—	2	3	—	1	—	—	—	—	0/6
	M	—	—	2	2	—	—	—	—	—	1	0/5
Wixia georgia Levi	F	—	1	—	1	—	—	—	—	—	—	1/1
Wixia spp. juveniles*	I	—	—	—	1	—	1	—	—	—	—	0/2
Tetragnathidae												
Leucauge venusta (Walckenaer)	F	1	—	—	—	—	—	—	—	—	—	1/0
Mimetidae												
Mimetus puritanus Chamberlin	F	1	3	—	—	—	—	—	—	—	—	4/0
Philodromidae	M	1	—	—	—	—	1	—	—	—	—	1/1
Philodromus keyserlingi Marx	F	—	—	2	1	3	3	—	2	4	4	0/19

* Probably juveniles of *W. georgia.*

October, it would suggest that *T. lactitarse* is active only during the first 3 wks of July in northwestern South Carolina. Rau (1928) and Fischer (1974) both reported that this species actively provisioned from late June through August in North America, while Camillo and Brescovit (1999) reported year-round provisioning by *T. lactitarse* in Brazil.

In our study, the completely provisioned trap-nests had either five (n = 6), six (n = 3), or seven (n = 1) provisioned cells. Other studies have reported finding between one and 12 provisioned cells in trap-nests of *T. lactitarse* (Krombein 1967, Medler 1967, Coville 1979, Camillo et al. 1993). Coville and Griswold (1983) reported one to eight provisioned cells for *T. xanthandrum* Richards.

The lowest numbers of total prey per trap-nest were in the P 1 July and P 8 July trap-nests, although these only differed by more than 1 SD from trap-nests H 5 July, H 8a July, and H 12a July (Fig. 2). The two pine habitat trap-nests also had the lowest mean number of prey items per cell, although these only differed by more than 1 SD from the H 8a July and H 12a July trap-nests (Fig. 3). The total number of prey groups (species × female, male, or juvenile) per trap-nest were highly variable and showed no obvious patterns (Fig. 4).

In the pine habitat, the two complete trap-nests contained a total of 91 spiders of seven species plus *Araneus* spp. juveniles (Table 1). The Araneidae made up 93.4%, Mimetidae 5.5%, and Tetragnathidae 1.1% of the prey in the pine habitat. In the hardwood habitat, 721 spiders of 11 species, plus *Araneus* spp. and *Wixia* spp. juveniles were recovered from eight complete trap-nests (Table 1). Araneidae made up 97.2%, Philodromidae 2.6%, and Mimetidae 0.1% of the total prey in the hardwood habitat. Although we recovered only four families of spiders in *T. lactitarse* trap-nests, our data are consistent with those of Krombein (1967), Medler (1967), Fischer (1974), Krombein et al. (1979), Coville (1981), and Camillo and Brescovit (1999), in that the Araneidae was the most common family used by *T. lactitarse* in provisioning trap-nests. The Araneidae also have been reported as the most common prey taxa for *T. aestivale* Richards and *T. antropovi* Coville (Camillo 1999), *T. orizabense* Richards (Coville 1979), *T. rogenhoferi* Kohl (Camillo and Brescovit 2000), *T. tenoctitlan* Richards (Coville and Coville 1980), and *T. tridentatum tridentatum* Packard (Jiménez and Tejas 1994). This study reports the first record of *L. venusta* (Tetragnathidae) as prey of *T. lactitarse* in the United States. Camillo and Brescovit (1999) reported *Leucauge* sp. in *T. lactitarse* trap-nests in Brazil, and Coville et al. (2000) reported juvenile tetragnathids as prey of *T. vagulum* Richards in Costa Rica.

Eustala cepina was the most commonly recovered prey species in both the pine (28.4%) and hardwood (81.8%) habitats (Table 1). Camillo and Brescovit (1999) reported that *Eustala* (identified as species 1 through 5) comprised 47.1% of the total prey recovered from *T. lactitarse* trap-nests in Brazil. *Eustala* spp. also have been reported as abundant prey of *T. monteverde* Coville (Coville 1982, Brockmann 1992), *T. politum* Say (Cross et al. 1975), and *T. tridentatum tridentatum* (Jiménez and Tejas 1994).

Use of females, males, and juveniles of the 12 identifiable prey species varied among species (Table 1). *Eustala cepina* in both habitats, and both *A. guttulatus* and *M. labyrintha* in the hardwood habitat were represented in the prey by females, males, and juveniles. *Mimetus puritanus* in the pine, and *A. cingulatus, A. niveus,* and *M. lemniscata* in the hardwood habitat, were recovered as both females and males. A single *L. venusta* female was found in the pine habitat; whereas, only females of *P. keyserlingi* were recovered in the hardwood habitat. Only females of *E. anastera* and

W. georgia were recovered in both habitats. Juveniles of *Araneus* spp. were found in both habitats, whereas those of *Wixia* spp. were found only in the hardwood habitat. Chi-square analyses of individual trap-nest data indicated that for those prey species consisting of more than one group, only *E. cepina* were not evenly distributed among females, males, and juveniles, with females being used as prey more often than males or juveniles (Fig. 5). When data from all trap-nests were pooled within each of the two habitats, *E. cepina* in the pine habitat had significantly more females and juveniles used as prey than males (χ^2 = 10.65; df = 2; P < 0.001); whereas, in the hardwood habitat significantly more females were used as prey than males or juveniles (χ^2 = 371.55; df = 2; P < 0.001) (Fig. 5, Table 1). In the pooled hardwood habitat data, females of *A. cingulatus* were significantly more abundant in the prey than were males (χ^2 = 12.70; df = 1; P < 0.001) (Table 1). When all prey items were pooled within each habitat, females were used significantly more often than males or juveniles in the hardwood habitat (χ^2 = 350.40; df = 2; P < 0.001), and juveniles more often than

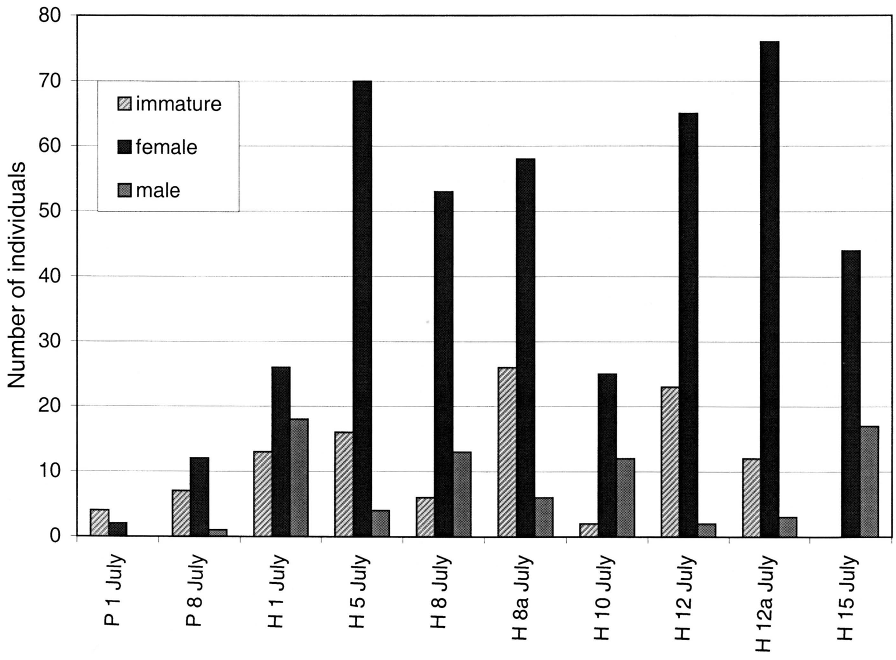

Fig. 5. Total numbers of female, male, and juvenile *E. cepina* recovered from *T. lactitarse* trap-nests in Clemson, SC in 1991. Chi-square analyses examined either whether distributions differed from 1:1 (if two prey groups were present) or 1:1:1 (if three prey groups were present (P 1 July, χ^2 = 0.67, 1 df, P > 0.05; P 8 July, χ^2 = 9.06, 1 df, P < 0.05; H 1 July, χ^2 = 4.53, 2 df, P > 0.05; H 5 July, χ^2 = 82.40, 2 df, P < 0.001; H 8 July, χ^2 = 53.58, 2 df, P < 0.001; H 8a July, χ^2 = 45.87, 2 df, P < 0.001; H 10 July, χ^2 = 44.42, 2 df, P < 0.001; H 12 July, χ^2 = 59.24, 1 df, P < 0.001; H 12a July, χ^2 = 83.71, 2 df, P < 0.001; H 15 July, χ^2 = 24.36, 2 df, P < 0.001).

females or males in the pine habitat (χ^2 = 59.76; 2 df; P < 0.001). Coville (1981) and Camillo and Brescovit (1999) have reported that *T. lactitarse* prey consisted largely of juvenile spiders in Brazil and Costa Rica, respectively. Juveniles also have been reported to make up the majority of prey for *T. arizonense* Fox (Matthews and Matthews 1968), *T. monteverdae* (Coville 1982, Brockmann 1992), *T. nitidum schultessi* Richards (Coville 1981), *T. occidentalis* Coville (Coville 1982), *T. orizabense* (Coville 1979), *T. politum* (Barber and Matthews 1979), *T. saussurei* Rohwer (Coville 1981), *T. subimpressum* F. Smith (Genaro and Alayón 1994), *T. superbum* F. Smith (Coville and Griswold 1984), *T. tenoctitlan* (Coville and Coville 1980), *T. texense* Saussure (Kurczewski 1963), *T. tridentatum tridentatum* (Jiménez and Tejas 1994), and *T. xanthandrum* Richards (Coville and Griswold 1983).

In this study, we did not determine population densities for all spider species within the two habitats and so were not able to determine if use of a particular prey, such as *E. cepina* in hardwoods or *Araneus* spp. juveniles in pines, was due to *T. lactitarse*'s hunting strategy or to the abundance of these particular prey groups. The abundance of females as prey in the hardwood habitat supports Rehnberg's (1987) hypothesis that female spiders may be preferred due to their larger size.

Prey diversity, as measured by Bruillouin's *H*, varied considerably among the ten completely provisioned trap-nests. The seven trap-nests having *H* values >1.0, each had between 8 and 17 prey groups (species × females, males, juveniles), while the three trap-nests with *H* values <1.0 (P 1 July, H 12 July, H 12a July) each contained only 7 prey groups (Tables 1, 2). Evenness (*J*) values also varied widely among the

Table 2. Bruillouin's diversity (*H*) and evenness (*J*) values for entire trap-nests provisioned by *Trypoxylon lactitarse* in pine and hardwood habitats in Clemson, SC in 1991

	H	*J*
Pine		
Total	1.27	0.52
1 July	0.73	0.42
8 July	1.42	0.78
Hardwood		
Total	1.52	0.51
1 July	1.65	0.76
5 July	1.25	0.50
8 July	1.01	0.56
8a July	1.53	0.62
10 July	1.50	0.73
12 July	0.53	0.32
12a July	0.95	0.52
15 July	1.39	0.62

Table 3. Modified Morisita-Horn similarity (C_{MH}) values among *Trypoxylon lactitarse* trap-nest data from pine and hardwood habitats in Pickens Co., SC, 1991

Trap-nest*	P 1 July	P 8 July	H 1 July	H 5 July	H 8 July	H 8a July	H 10 July	H 12 July	H 12a July	H 15 July
P 1 July	***	0.74	0.19	0.12	0.10	0.13	0.46	0.05	0.11	0.07
P 8 July		***	0.64	0.60	0.56	0.65	0.81	0.47	0.59	0.57
H 1 July			***	0.79	0.82	0.87	0.86	0.63	0.77	0.92
H 5 July				***	0.97	0.96	0.78	0.94	0.99	0.94
H 8 July					***	0.92	0.82	0.94	0.96	0.96
H 8a July						***	0.79	0.82	0.96	0.95
H 10 July							***	0.68	0.74	0.84
H 12 July								***	0.94	0.83
H 12a July									***	0.92
H 15 July										***

* P = pine; H = hardwood.

trap-nests examined, with those having low numbers of prey groups with only a single numerically abundant prey group having the lowest values. Despite the variation in H and J values among individual trap-nests, H values for pooled data within each habitat indicated higher prey diversity in the hardwood than the pine habitat, while evenness values were similar between the two habitats (Table 2). Camillo and Brescovit (1999) and Camillo and Brescovit (2000) reported Shannon-Weaver H' and J' values for *T. lactitarse* and *T. rogenhoferi*, respectively, in Brazil based on pooled trap-nest data recovered within each of three geographic regions. They report considerable variation in both diversity and evenness of prey among geographic regions and among months within regions for both wasp species.

The modified Morisita-Horn similarity index values indicated that while prey compositions within each of the two habitats were relatively similar, the pine habitat trap-nests were not similar to those found in the hardwood habitat (Table 3). Geographic differences in Sorenson similarity (*SQ*) and percentage similarity (*PS*) values, have been reported by Camillo and Brescovit (1999) for prey of *T. lactitarse* and Camillo and Bresocvit (2000) for *T. rogenhoferi* prey based on pooled trap-nest data from three geographic areas in Brazil.

The wide range of diversity and evenness values suggests that *T. lactitarse* is a generalist predator utilizing a wide range of spider species, gender, and age classes as prey. However, our data, as well as that of previously published reports, also suggest that *T. lactitarse* exhibits a general search image for either araneid webs or retreats. In addition, the abundance of female prey in hardwoods and juveniles in pines, and the high C_{MH} index values within each habitat indicates that *T. lactitarse* exhibits a relatively high degree of prey constancy within the habitat immediately surrounding a trap-nest.

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