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SEASONAL AND LATITUDINAL VARIATION IN SPIDER PREY OF THE MUD DAUBER *CHALYBION CALIFORNICUM* (HYMENOPTERA, SPHECIDAE)

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ABSTRACT

Spider prey of the Blue Mud Dauber, *Chalybion californicum* (Saussure), in eastern Missouri included 15 species representing four families. Araneidae was the most diverse family (nine species), but Theridiidae were more numerous, with *Steatoda americana* (Emerton) outnumbering all other species combined. Temporal abundances of the nine spider taxa most commonly captured by the wasps in Missouri suggest that wasps collect spiders in numbers relative to their seasonal and relative abundances, accessibility as prey, or size suitability. Spider prey of the same wasp species in northern Florida included 31 species representing nine families. Araneidae was both the most diverse (19 species) and most numerous family and exhibited a pattern of seasonal increase in abundance as prey of *C. californicum*. Theridiidae constituted a majority of the total individuals in both the Missouri survey and a similar survey from Maryland, while a corresponding study in southern Oklahoma resembled the Florida survey in having high proportions and numbers of Araneidae.

INTRODUCTION

Mud dauber wasps of the genera *Chalybion, Sceliphron,* and *Trypargilum* (Sphecidae) are well known to provision their nests with spiders (Araneae)

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collected from surrounding habitats as food for developing young. The contents of these wasps' nests have been examined by several investigators (Adato-Barrion and Barrion 1981; Brown 1974; Dorris 1969, 1970; Horner and Klein 1979; Irving and Hinman 1935; Obin 1981; Muma and Jeffers 1945; Peckham and Peckham 1898; Rau 1935a, b; Rau and Rau 1916; Sychevskaya 1973; Ward 1970). The predatory behavior of *Chalybion californicum* (Saussure) is described by Coville (1976) and that of *Sceliphron caementarium* (Drury) by Eberhard (1970). Rau (1915) describes behavioral reactions of both *C. californicum* and *S. caementarium* to manipulations of the spider prey in their nests. Obin (1981) gives an interesting account of the relations between the wasps and spiders that live near their nests.

Chalybion californicum (= *caeruleum* of authors) is a common steel-blue wasp distributed from southern Canada into northern Mexico (Bohart and Menke 1963). The species is exclusively an inquiline of other mud dauber genera; that is, *C. californicum* females do not build their own nests but instead re-use nest cells of other mud dauber species (early natural history literature incorrectly ascribes nest construction to *Chalybion*). We present here taxonomic analyses of the spider prey of *Chalybion californicum* in eastern Missouri and northern Florida and compare the results with those of two previous studies, that of Muma and Jeffers (1945) and of Horner and Klein (1979). Temporal variation in both prey species and numbers taken by *C. californicum* suggests that the wasps capture spiders not only according to size and habitat but also to relative and seasonal abundances. Proportional representation of araneid and theridiid prey in the four surveys suggests a latitudinal patterning of prey collection by *C. californicum*

STUDY SITES AND METHODS

Study sites.—In Missouri, the study site was Washington University's Tyson Research Center, near Eureka in southwest St. Louis County. The Research Center is largely mature second-growth oak-hickory forest (described quantitatively by Hampe 1984) with clearings maintained as early successional oldfields by biennial mowing. Substantial populations of *Sceliphron caementarium* nest in old warehouses and on abandoned railroad loading platforms that are near both oldfield and forest habitats. *C. californicum* is a common inquiline of the *S. caementarium* nests.

In Florida, field studies were conducted on *C. californicum* at several sites in Alachua Co. Two of these, Lake Wauburg and "ABC", yielded data for the present study. The Lake Wauburg site consisted of two structures. One, a wooden crawl space with an unfinished pine ceiling and open sides, was within 5 m of the lakefront. The structure was surrounded on three sides by a frequently mowed lawn that was dotted with palms and turkey oaks. A stand of palmetto and hardwoods was located approximately 100 m away. Wasps also nested on the painted, exterior walls of a wooden garage situated 150 m from the lake shoreline immediately next to a small plot of palmetto-hardwood forest.

The "ABC" nesting site consisted of the underside of a wooden bridge spanning Rocky Creek, ca 1 km from State Road 121. The site is situated in the middle of a mesic hammock through which the creek runs. The hammock forest is replaced by cleared, agricultural plots and secondary growth within several hundred meters of the site.

Methods.—In Missouri, 11 spiders were taken in 1983 from *C. californicum* returning to their nests with prey. Three nests of *C. californicum* (with one active cell each) were also collected, opened, and their spider contents were evaluated. Sixty-six cells in 59 additional nests were collected and opened in May through September of 1984. Sampled nests were generally ones in which provisioning had been observed on the day of collection. Nests were collected intact, and individual cells were opened. The fresh spiders (the wasps sting and immobilize but do not kill their prey) were collected and preserved in 70% ethanol. Spiders mutilated by feeding larvae such that they could not be identified were not collected. Voucher specimens of all collected taxa are deposited in the Department of Biology's Museum of Natural History, University of Missouri—St. Louis.

In Florida, sixty-two nests cells in 55 nests were examined for spider contents in 1980 and 1981. As in Missouri, nests were collected intact and the cells opened. Spiders were removed and placed into 70% ethanol and held for identification. Voucher specimens of all taxa are housed in the collections of H. J. Brockmann and M. S. Obin, Department of Zoology, University of Florida, Gainesville.

RESULTS AND DISCUSSION

In Missouri, 56 of the 62 nests had only a single active *C. californicum* cell; five nests had two active cells, and one nest had three. Thirty-four cells were fully provisioned and sealed; 35 were only partially provisioned and were open. Sealed cells contained from 8 to 33 spiders; unsealed cells had from 2 to 22. The total of 860 spiders included 15 species representing four families (Table 1). Thirteen immature *Araneus* could not be identified to species. *Steatoda americana* (Emerton) (Theridiidae) represented 73% of the total collection.

In Florida, not all nest cells were completely provisioned. The number of spiders per cell ranged from one to 37. As in Missouri, full, sealed cells containing an egg or larva were considered completely provisioned. The total of 741 spiders included 31 species representing nine families (Table 1).

The nature and diversity of habits near the wasps' nests may have influenced the diversity and abundance of spiders collected as prey. The warehouse complex that was the Missouri study site is poorly maintained. Consequently, many cracks and crevices exist in the structures and their concrete foundations as well as in the abandoned railroad platforms. These fissues provided abundant web suspension sites favored by theridiid spiders (Kaston 1948) as well as some araneids (Muma and Jeffers 1945). Immediately adjacent oldfield habitats and foliage provided sites where other araneid spiders preferentially placed their webs. The abundance of theridiid and araneid spiders in the wasps' nests may thus reflect in part spider abundance in the habitats nearest the wasps' nesting area. Obin (1981) has observed that *C. californicum* and their spider prey in Florida have similar selections of particular habitats and structures.

Seasonal prey patterning.—Patterning of the monthly abundances of the nine major prey species found in *C. californicum* nests in Missouri is shown in Table 2. The range of dates across which any prey species was taken is in each case encompassed by known dates for seasonal activity as reported by such authors as Kaston (1948, 1970, 1976) and Levi (1973). The data of Table 2 may in some cases directly reflect such phenology. For example, the diminished number of *Steatoda americana* taken by wasps in August and September may reflect

Table 1.—Taxa and abundance of spider prey of *Chalybion californicum* (Saussure) at Tyson Research Center, St. Louis Co., Missouri (MO) in 1983 and 1984 and at the Lake Wauburg and "ABC" sites in Alachua Co., Florida (FL) in 1980 and 1981.

FAMILY	SPECIES	*N* (individuals) MO	FL
ARANEIDAE	*Acanthepeira stellata* (Marx)		29
	Acacesia hamata (Hentz)		1
	Araneus cingulatus (Walckenaer)	18	
	Araneus marmoreus Clerck	24	
	Araneus miniatus (Walckenaer)		3
	Araneus pegnia (Walckenaer)		5
	Araneus sp.	13	2
	Araniella displicata (Hentz)	1	
	Arigope aurantia Lucas	26	122
	Argiope sp.		8
	Eustala anastera (Walckenaer)		21
	Gea heptagon (Hentz)	7	166
	Larinia borealis Banks		1
	Leucauge venusta (Walckenaer)		10
	Mangora gibberosa (Hentz)		11
	Mecynogea lemniscata (Walckenaer)		113
	Metazygia wittfeldae (McCook)		1
	Micrathena mitrata (Hentz)	1	
	Micrathena sagittata (Walckenaer)	3	8
	Neoscona arabesca (Walckenaer)	23	8
	Neoscona domiciliorum (Hentz)		2
	Neoscona hentzi (Keyserling)	3	
	Neoscona sp.		2
	Nephila clavipes (L.)		25
CLUBIONIDAE	*Clubionoides excepta* (L. Koch)		1
MIMETIDAE	*Mimetus* sp.		1
OXYOPIDAE	*Peucetia viridans* (Hentz)		3
PISAURIDAE	*Pisaurina undulata* (Keyserling)		1
SALTICIDAE	*Eris marginata* (Walckenaer)		1
	Metaphidippus protervus (Walckenaer)	1	
TETRAGNATHIDAE	*Tetragnatha guatemalensis* (Seeley)		1
THERIDIIDAE	*Argyrodes globosus* Keyserling		1
	Latrodectus mactans (Fabricius)		42
	Latrodectus variolus (Walckenaer)	48	2
	Steatoda americana (Emerton)	629	
	Steatoda borealis (Hentz)	9	
	Steatoda grossa (C. L. Koch)		18
	Theridion frondeum Hentz	53	
	Theridion pictipes Keyserling		113
	Tidarren sisyphoides (Walckenaer)		11
THOMISIDAE	*Misumenops asperatus* (Hentz)		6
	Misumenops oblongus (Keyserling)		2
	Philodromus washita Banks	1	
	TOTAL	860	741

diminished abundance in those months (Kaston 1948). The occurrence of *Latrodectus variolus* (Walckenaer) as prey only after mid summer does not accurately reflect the known April to November phenology of that species (Wilson 1967), however, and suggests that the wasps shifted to it as a prey item of lower preference as numbers of *S. americana* in the environment diminished. Analogous phenomena may explain the similar shift in frequency in nest cells

Table 2.—Monthly patterning of the numbers of individuals of the nine spider taxa most frequently collected from nest cells of *Chalybion californicum* (Saussure) in St. Louis Co., Missouri, in 1983 and 1984. Numbers in parentheses beneath the months indicate the number of nests and the number of cells sampled, respectively, for that month.

TAXA	MAY (1,1)	JUNE (13,15)	JULY (27,31)	AUG. (17,18)	SEP. (4,4)
THERIDIIDAE					
Steatoda americana	31	198	312	87	1
Theridion frondeum	—	35	18	—	—
Latrodectus variolus	—	—	3	22	23
Steatoda borealis	—	—	1	2	6
ARANEIDAE					
Araneus cingulatus	—	17	1	—	—
Neoscona arabesca	—	10	6	7	—
Araneus marmoreus	—	—	4	16	4
Argiope aurantia	—	—	22	4	—
Gea heptagon	—	—	3	4	—

from *Araneus cingulatus* (Walckenaer) to *A. marmoreus* Clerck (Table 2). The patterning for *Argiope aurantia* Lucas probably reflects size suitability; though the spiders are known to be active until October (Levi 1973), spiders in late summer and fall are too large to be placed into a mud dauber cell. Thus the data of Table 2 together with information on spider phenologies and growth patterns suggest that the number of individuals of any spider species in the nest cells reflects components of seasonal occurrence, seasonal size patterning, wasp preferenda, or combinations of these. Such phenomena may also explain the increased frequency of Araneidae between April and August as prey of *C. californicum* in Florida (Table 3), for Obin (1981) notes that small-sized araneid spiders (e.g., *Mecynogea lemniscata* (Walckenaer), *Gea heptagon* (Hentz)) are found in Florida throughout the summer.

Latitudinal differences.—The present survey from Missouri and one from Maryland (Muma and Jeffers 1945) had more than two thirds of the total number of individual spiders in the Theridiidae, while a survey in southern Oklahoma (Horner and Klein 1979) and the present survey from Florida had more than two thirds of the total number of individuals in the Araneidae (Table 4). Latitude is a correlate of this observed difference in nest contents. The present Missouri survey, at 38°31′N latitude, and the Maryland survey, at ca 39°0′N, are north of the Oklahoma and Florida surveys, at ca 34°30′N and ca 29°37′N, respectively. The number of species per family and their proportions of the total

Table 3.—Seasonal variation in prey capture by the mud dauber *Chalybion californicum* at two sites in Alachua County, Florida during 1980 and 1981. The relative frequency of capture for each spider family is given as a proportion of all spider prey during the period indicated. Numbers in parentheses beneath the sample dates indicate the number of nests and the number of cells sampled, respectively.

TAXA	APRIL 1-MAY 31 (10,15)	JUNE 1-JULY 1 (11,12)	JULY 16-OCTOBER 1 (34,35)
ARANEIDAE	136/245 (55.5%)	84/128 (65.6%)	318/368 (86.4%)
THERIDIIDAE	106/245 (43.3%)	34/128 (26.6%)	47/368 (12.8%)
Other	3/245 (1.2%)	10/128 (7.8%)	3/368 (0.8%)

Table 4.—Proportional representation by family of the numbers of individuals of Araneae in four surveys of the prey of *Chalybion californicum* (Saussure). MO = St. Louis Co., Missouri (N = 860; present study); MD = Maryland (N = 927; Muma and Jeffers 1945); OK = Comanche Co., Oklahoma (N = 446; Horner and Klein 1979); FL = Alachua Co., Florida (N = 741; present study). The latitudes of the study sites are given beneath the column headings. Totals do not equal 1.000 due to rounding error.

TAXA	MO 38°31′	MD 39°0′	OK 34°30′	FL 29°37′
Anyphaenidae	—	0.001	—	—
Araneidae	0.138	0.269	0.699	0.726
Clubionidae	—	—	—	0.001
Linyphiidae	—	0.001	—	—
Lycosidae	—	—	0.002	—
Mimetidae	—	0.001	—	0.001
Oxyopidae	—	0.016	—	0.004
Philodromidae	—	—	0.004	—
Pisauridae	—	—	—	0.001
Salticidae	0.001	0.016	—	0.001
Tetragnathidae	—	—	—	0.001
Theridiidae	0.859	0.677	0.294	0.252
Thomisidae	0.001	0.018	—	0.011
TOTALS	0.999	0.999	0.999	0.998

number of species captured at a site show a similar but not identical pattern; only the most northerly survey, in Maryland (Muma and Jeffers 1945), had Theridiidae with the largest number and proportion of species (Table 5).

At least two factors may underly these latitudinal differences in prey taxa of *C. californicum*. First, behavioral components of prey search and capture may vary between northern and southern wasp populations. Obin (1981) suggests that individual wasps may vary in their responses to spiders as a function of searching locale, which suggests that the wasps may form search images for specific spider taxa. Second, composition of the spider fauna may vary with latitude and/or specific features of the habitat surrounding each study site. Obin (1981) suggests that the lower percentage of *Latrodectus mactans* (Fabricius) taken by *C. californicum* in Florida than in Maryland (Muma and Jeffers 1945) reflects the availability of appropriately sized (i.e., small) araneid prey throughout the summer in Florida. The most southerly survey had the highest number of species, suggesting a latitudinal component of spider diversity, but the most northerly survey, which is based on the largest number of specimens, has the second highest species number suggesting that sampling intensity may also affect the data.

Our study demonstrates that the proportional representation of theridiid and araneid prey abundance can differ greatly between sites (Table 4, columns MO and OK) even though the number of available prey species and the number of species per family (= diversity) are similar (Table 5, columns MO and OK). We suggest, therefore, that surveys of wasp-collected spider taxa be implemented at two or more sites in conjunction with independent, parallel surveys of spider abundance and diversity. Such studies could reveal if *C. californicum* females consistently select a particular subset of the full araneid diversity available to them. If so, the relatively easy technique of sampling spiders from recently provisioned mud dauber nests could provide a useful diagnostic tool for

Table 5.—Number of species per family and their proportions of the total number of species per survey in four surveys of the spider prey of *Chalybion californicum* (Saussure). MO = St. Louis Co., Missouri (present study); MD = Maryland (Muma and Jeffers 1945); OK = Comanche Co., Oklahoma (Horner and Klein 1979); FL = Alachua Co., Florida (present study). The latitudes of the study sites are given beneath the column headings. Proportion totals do not equal 1.000 due to rounding error.

TAXA	MO 38°31′	MD 39°0′	OK 34°30′	FL 29°37′
Anyphaenidae	—	1/0.052	—	—
Araneidae[a]	9/0.600	[b]4/0.201	7/0.538	17/0.548
Clubionidae	—	—	—	1/0.032
Linyphiidae	—	1/0.052	—	—
Lycosidae	—	—	1/0.076	—
Mimetidae	—	1/0.052	—	1/0.032
Oxyopidae	—	[b]2/0.105	—	1/0.032
Philodromidae	—	—	2/0.153	—
Pisauridae	—	—	—	1/0.032
Salticidae	1/0.066	2/0.105	—	1/0.032
Tetragnathidae	—	—	—	1/0.032
Theridiidae	4/0.266	[b]7/0.368	3/0.230	6/0.193
Thomisidae	1/0.066	[b]1/0.052	—	2/0.064
TOTALS	15/0.998	[b]19/0.987	13/0.987	31/0.997

[a]Immature *Araneus* that could not be determined to species are not included.
[b]These are minimum estimates of the number of species; actual numbers may have been higher.

biogeographic analysis of spider diversity within the limits of wasp prey taxa and prey size preferenda.

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