AN ECOLOGICAL STUDY OF THE SPIDERS OF A RIVER-TERRACE FOREST IN WESTERN TENNESSEE[1]

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Studies dealing with the ecology of spiders are of two main types: (1) those which give ecological consideration to the entire animal population of the habitat and the spiders incidentally as members of that population, Adams (1915), Weese (1924), Blake (1926), and (2) those which give intensive consideration to the ecology of spiders exclusively of a particular habitat, Elliott (1930), Truman (1942). This study is of the latter nature.

PROCEDURE AND SCOPE OF WORK

Spiders were collected continuously every ten to fourteen days over a period of twenty-two months in a River-Terrace forest located along the secondary terrace of the Wolf river, a tributary of the Mississippi, in the region of Memphis, Tennessee. The land adjacent to the Mississippi River and its tributaries is characterized by typical swamp forest vegetation. As the land rises from the flood plain level, a secondary terrace forest is apparent, composed essentially of an Oak-Gum community along the lowland and Oak-Hickory along the upland, drier portion. Collections were made by beating branches of trees and shrubbery, sweeping herbage, sifting leaves and upper soil layer and removing the bark and wood from trees, stumps and logs. Species were identified by Dr. W. M. Barrows, of the Ohio State University.

THE SPIDER POPULATION OF THE RIVER-TERRACE FOREST

Species inhabiting the forest are listed alphabetically and numbered consecutively in order that they may be referred to by their numerical position in the table which appears below. The names given to the spiders are those, as far as possible, listed in the synonymic Index-Catalogue of Spiders of North, Central and South America (Petrunkevitch).

1. *Acacesia foliata* Hentz.
2. *Agassa cyaena* Hentz.
3. *Agelena americana* Keyserling.
4. *Agelena emertoni* Chamberlin & Ivie.
5. *Agelena naevia* Walckenaer.
6. *Agroeca* sp. ?
7. *Amaurobius americana* Keyserling.
8. *Antistea* sp.?
9. *Anyphaena fraterna* Banks.
10. *Anyphaena saltibunda* Hentz.
11. *Araneus arenatus* Walckenaer.
12. *Araneus benjaminus* Walckenaer.
13. *Araneus marmoreus* Clerck.
14. *Araneus miniatus* Walckenaer.
15. *Araneus stellatus* Walckenaer.
16. *Araneus thaddeus* Hentz.
17. *Araneus tusus* Petrunkevitch.
18. *Arctosa* sp.?
19. *Argiope aurantia* Lucas.
20. *Argiope trifasciata* Forskal.
21. *Argyrodes trigonium* Hentz.
22. *Argyrodes trituberculatus* Becker.
23. *Ariadne bicolor* Hentz.
24. *Aysha gracilis* Hentz.
25. *Bathyphantes micaria* Emerton.
26. *Callilepis imbecilla* Keyserling.
27. *Castaneira longipalpis* Hentz.
28. *Castaneira stupkai* Barrows.
29. *Ceraticelus fissiceps* Cambridge.
30. *Ceraticelus micropalpis* Emerton.

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31. *Ceraticelus minutus* Emerton.
32. *Ceratinopsis* sp.?
33. *Cesonia bilineata* Hentz.
34. *Chiracanthium inclusum* Hentz.
35. *Cicurina itasca* Chamberlin & Ivie.
36. *Clubiona pallens* Hentz.
37. *Crustulina guttata* Wider.
38. *Cyclosa conica* Pallas.
39. *Dendryphantes* (P) *audax* Hentz.
40. *Dendryphantes* (*M*) *capitatus* Hentz.
41. *Dendryphantes insignarius* Koch.
42. *Dendryphantes* (*P*) *whitmanii* Pecham.
43. *Dictyna armata* Banks.
44. *Dictyna bicornis* Emerton.
45. *Dictyna cruciata* Emerton.
46. *Dictyna frondea* Emerton.
47. *Dictyna sublata* Hentz.
48. *Dictyna foliacea* Hentz.
49. *Dictyna zaba* Barrows and Ivie.
50. *Dipoena nigra* Emerton.
51. *Dolomedes* sp.?
52. *Drassodes* sp.?
53. *Drasyllus aprilinus* Banks.
54. *Drasyllus dixinus* Chamberlin.
55. *Drasyllus fallens* Chamberlin.
56. *Drexelia directa* Hentz.
57. *Ebo latithorax* Keyserling.
58. *Epeira juniperi* Emerton.
59. *Erigone autumnalis* Emerton.
60. *Eperigone maculata* Banks.
61. *Ero* (*furcatus?*) Villers.
62. *Euryopis funebris* Hentz.
63. *Eustalia anastera* Walckenaer.
64. *Fuentes lineatus* Koch.
65. *Gea heptagon* Hentz.
66. *Gnaphosa bicolor* Hentz.
67. *Hahnia brunnea* Emerton.
68. *Harbrocestum pulex* Hentz.
69. *Hentzia basilica* McCook.
70. *Herpyllus vasifer* Walckenaer.
71. *Hyctia* sp.?
72. *Kaira alba* Hentz.
73. *Lepthyphantes sabulosa* Keyserling.
74. *Leucage venusta* Walckenaer.
75. *Linyphia communis* Hentz.
76. *Linyphia lineata* Linnaeus.
77. *Litopyllus rupicolens* Chamberlin.
78. *Loxosceles* (*rufescens?*) Dufour.
79. *Lycosa avara* Keyserling.
80. *Lycosa punctulata* Hentz.
81. *Lycosa rabida* Walckenaer.
82. *Maevia vittata* Hentz.
83. *Mangora gibberosa* Hentz.
84. *Mangora placida* Hentz.
85. *Marpissa undata* DeGeer.
86. *Micaria* sp.?
87. *Micrathena gracilis* Walckenaer.
88. *Micrathena reduviana* Walckenaer.
89. *Microneta cornupalpis* Cambridge.
90. *Microneta latidens* Emerton.
91. *Mimetus* sp.?
92. *Misumenops asperatus* Hentz.
93. *Misumenops celer* Hentz.
94. *Misumenops oblongus* Keyserling.
95. *Oedothorax* sp.?
96. *Originates rostratus* Emerton.
97. *Oxyopes aglossus* Chamberlin.
98. *Oxyopes salticus* Hentz.
99. *Pachylomerus* sp.?
100. *Pardosa nigropalpis* Emerton.
101. *Pechamia scorpionea* Hentz.
102. *Pallenes* sp.?
103. *Philodromus minutus* Banks.
104. *Philodromus pernix* Blackwell.
105. *Phlegra fasciata* Hahn.
106. *Phrurolithus alarius* Hentz.
107. *Phrurolithus divinulus* Gertsch.
108. *Phrurolithus dulcineus* Gertsch.
109. *Pirata arenicola* Emerton.
110. *Pirata minutus* Emerton.
111. *Pisaurina mira* Walckenaer.
112. *Sergolius variegatus* Hentz.
113. *Schizocosa crassipes* Walckenaer.
114. *Scoloderus tuberculifer* Cambridge.
115. *Sittious cursor* Barrows.
116. *Synaema parvulum* Hentz.
117. *Tapinopa bilineata* Banks.
118. *Tetragnatha laboriosa* Hentz.
119. *Thanatidius dubius* Hentz.
120. *Theridion differens* Emerton.
121. *Theridion dulcineum* Gertsch & Archer.
122. *Theridion frondeum* Hentz.
123. *Theridion globosum* Hentz.
124. *Theridion kentuckyense* Keyserling.
125. *Theridula opulenta* Walckenaer.
126. *Theridion studiosum* Hentz.
127. *Theridion waliacii* Gertsch & Archer.
128. *Thiodina sylvana* Hentz.
129. *Tmarus* (*angulatus?*) Walckenaer.
130. *Tmeticus* (*asetivalis?*)
131. *Trachelas tranquillas* Hentz.
132. *Uloborus americanus* Walckenaer.
133. *Wala mitrata* Hentz.
134. *Wala palmarium* Hentz.
135. *Xysticus ferox* Hentz.
136. *Xysticus funestus* Keyserling.
137. *Zelotes hentzi M.S.S.* W. M. Barrows
138. *Zygoballus bettini* Pecham.
139. *Zygoballus sexpunctatus* Hentz.

ECOLOGY OF THE RIVER-TERRACE FOREST SPIDERS

A summary of the findings with reference to ecological factors is given below in tabular form. Blank spaces in the table indicate insufficient data for the determination required. The symbols used in the table are as follows:

COLUMN I—Species as indicated by numbers given in the taxonomic listing on pages 38 and 39. A "D" alongside of the number representing the species indicates that the species characteristically inhabits the more moist lowland portion of the forest.

COLUMN II—The number of individuals collected of a particular species.

COLUMN III—Specific relation of the species to the forest. These determinations are based upon a comparative study made between species of spiders inhabiting this forest and those recorded for vegetational associations such as Oak-Hickory, Beech-Maple, Elm-Maple, Wet and Dry Prairie, etc. Also upon numerous collections made along the margins of the forest, the adjacent fields and meadows and other similar forests of the region. Symbols used in column III are:

R—Species typical of the River-Terrace forest.
E—Species usually found along the forest border or in regions where cutting of trees has resulted in a mixed grassland-forest community.
F—Field spiders, those found most often and in greatest numbers in cultivated areas, meadows or grassland.
Fo—Species reported for all forests on which data have been compiled and therefore exhibiting no habitat specificity in this regard.
O—Spiders which though present in the River-Terrace forest are more typical of Oak-Hickory.
Pw—Species characteristically inhabiting the wet prairie.
Pd—Species characteristically inhabiting the dry prairie.
Be—Spiders more typical of Beech-Maple and River-Terrace forest.

COLUMN IV—Characteristic stratal position of the spider population within the forest during the warm part of the year. Symbols used in column IV are:

G—Ground stratum.
H—Herb stratum.
S—Shrub stratum.
A—All strata.
U—Upper strata (herb-shrub-tree).
B—Species found characteristically under or in the crevice of bark.

COLUMN V—Approximate hatching periods for the species. (Suggested periods are good only for the vicinity of Memphis, Tennessee.) The determinations were made by comparing younger and younger stages of various species and by keeping the egg sac of others until hatching occurred. Though the suggested hatching periods are approximations in certain instances, the list is presented in the hope that it will stimulate further investigation on the part of those ecologically minded with resulting verification and necessary correction. Symbols: The months are numbered according to their occurrence in the year.

E—indicates the first half of the month.
M—indicates the mid-portion of the month.
L—indicates the last half of the month.

COLUMN VI—Period during which species matures. Symbols are the same as in Column V.

COLUMN VII—Hibernation stage of the species. In general the determination of the hibernation stage rests upon the mid-winter collection of spiders. Symbols used in Column VII are:

I—spiders that hibernate in immature or adult form.
E—spiders that overwinter in the egg sac as eggs or very young.

TABLE I

I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
1	16	E	H	9E	7L	E	8	2	.....	G?	.....	.....	.....
2D	1	R	G	.....	.....	.....	9	613	R	A	6M	5M	I
3	214	F	A	9E	7M	E	10	237	E	A	6M	5E	I
4	20	F	A	9E	7M	E	11	15	Fo	T	8L	6L	I
5	82	F	A	9E	7M	E	12	18	O	S	8L	6L	I
6	1	.....	H?	.....	.....	.....	13	1	Fo	S	.....	.....	E
7	3	Fo	G	6M	5E	I	14	2	R	S	.....	.....	I

TABLE I—(*Continued*)

I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
15	33	F	H	8L	6M	I	78D	2	R	S	.....	.....	.....
16	11	R	T	8L	6L	I	79	157	Rw	G	6E	4E	I
17	8	R	A	8L	6M	I	80	2	.....	G	.....	.....	E
18	13	.....	G?	.....	.....	I	81	75	E	GH	9L	7L	E
19	8	E	HS	4L	8L	E	82	69	E	H	7E	5L	I
20D	17	E	U	4M	8L	E	83	33	E	H	8L	6L	I
21	3	.....	S	.....	.....	I	84	86	R	H	7E	6L	I
22	2	R	S	.....	.....	I	85	17	O	B	7M	5E	I
23S	58	Fo	G	5M	4E	I	86	4	.....	.....	.....	.....	.....
24	118	O	A	6M	E5	I	87	1	E	T?	.....	.....	.....
25	7	E	H	.....	.....	I	88	2	R	.....	.....	.....	.....
26	71	E	GH	6M	5E	I	89	4	Be	G	5L	4M	I
27	6	Fo	G	8L	6L	.....	90	3	R	G	5L	4M	I
28	8	R	G	8M	7L	E	91	15	R	H	.....	.....	I
29	4	R	H	6M	5E	I	92	70	Fo	A	6E	5L	I
30D	1	R	G	.....	.....	.....	93	19	R	U	6E	5L	I
31	3	Fo	H	6E	4L	I	94	24	E	U	6E	5L	I
32?	1	.....	.....	.....	.....	.....	95?	1	.....	.....	.....	.....	.....
33	3	R	H	8L	6L	I	96	4	R	TS	.....	.....	I
34	12	R	H	6M	4M	I	97	239	R	A	7E	6M	I
35	1	R	G	.....	.....	.....	98	119	E	H	7L	5M	I
36	36	Fo	G	6M	5L	I	99?	.....	.....	.....	.....	.....	.....
37D	1	E	G?	.....	.....	.....	100D	14	E	G	5M	4L	I
38	3	.....	S	6M	5E	I	101?	2	F	.....	.....	.....	.....
39	72	E	U	7E	5L	I	102	3	.....	.....	.....	.....	.....
40	18	E	SH	HL	7E	I	103	11	R	T	6M	5E	I
41	179	R	A	7E	5L	I	104	39	O	A	6M	5E	I
42	51	O	A	.....	.....	I	105	1	R	G	.....	.....	.....
43	20	R	G	6M	5E	I	106	143	Fo	G	6M	5E	I
44	3	R	G	6M	5E	.....	107	4	.....	G	.....	.....	.....
45	135	R	U	6M	5E	I	108	1	F	G	.....	.....	.....
46	23	F	H	6M	5E	I	109	6	R	G	7E	5L	I
47	11	E	H	6M	5E	I	110	16	F	G	7E	5L	I
48	65	E	SH	6M	5E	I	111	286	E	H	8L	6M	I
49	177	E	A	6M	5E	I	112	2	R	H	7E	5M	I
50	1	.....	.....	.....	.....	.....	113	57	E	GH	5M	4E	I
51?	1	.....	.....	.....	.....	.....	114	18	R	U	8L	6L	I
52	1	.....	.....	.....	.....	.....	115D	1	F	.....	.....	.....	.....
53	1	.....	G?	.....	.....	.....	116	7	O	GH	5M	8M	I
54	2	R	G	6M	5E	I	117	2	.....	A	.....	.....	.....
55D	24	R	G	6M	5E	I	118	121	E	H	7E	6M	I
56	2	Pd	H	.....	.....	I	119	115	R	A	7E	5L	I
57	64	R	GH	6E	4L	I	120	22	E	U	6E	5E	I
58D	7	Fo	T	10L	7L	.....	121D	1	R?	.....	.....	.....	.....
59	6	E	U	4L	9L	I	122	5	E	H	.....	.....	.....
60	1	.....	G?	.....	.....	.....	123	42	R	H	6M	5E	I
61	1	.....	.....	.....	.....	.....	124	4	R	T	.....	.....	.....
62	5	Fo	U	6M	5E	I	125	33	E	A	8E	7M	I
63	23	Fo	HS	8E	5L	I	126D	63	R	T	7E	6M	E
64	31	E	G	7M	6E	I	127	2	.....	G	.....	.....	.....
65	5	R	H	8M	6L	I	128	90	R	A	7E	5E	I
66	2	E	G	.....	.....	.....	129	3	.....	.....	.....	.....	.....
67D	6	R	G	8L	L6	I	130	3	.....	G	.....	.....	.....
68D	9	E	A	6M	4M	I	131	4	E	.....	8L	6L	I
69D	9	R	U	8L	6L	I	132	49	Fo	H	9L	8E	I
70	6	Fo	A	6M	5E	I	133	8	R	S	6M	5M	I
71?	1	.....	.....	.....	.....	.....	134	2	O	T	.....	.....	I
72	7	R	H	6M	5E	I	135	31	E	GH	6M	4L	I
73	20	R	G	9L	8E	I	136	33	E	GH	6L	4L	I
74	80	Fo	U	7L	6L	E	137	6	E	G	8L	6L	I
75	40	F	H	6M	5E	I	138	1	R	H	.....	.....	I
76	101	F	H	6M	5E	I	139	28	R	H	6L	4L	I
77	1	.....	G	.....	.....	.....							

THE HABITAT

The River-Terrace forest, like the Deciduous forest in general, presents well defined strata. These are forest floor, herb layer, shrub layer and forest crown. Because of the influence of the forest crown and the absence of conditions such as exist in associations like arctic tundra and desert, environmental conditions are more uniform. Habitat situations within the forest, as pertaining to spiders, primarily reflect differences associated with the various vegetational strata from forest floor to forest crown. It is axiomatic that soil temperatures in general and especially forest soil temperatures are more stable than the overlying atmospheric temperature. Periodic checks of temperature, light and humidity in the strata of the forest under investigation substantiated the observations made by Weese, Blake and others that the forest floor has the lowest temperature of the strata generally during the summer, and highest during the winter. Humidity is greatest and light intensity lowest at the forest floor. The rate of evaporation was not checked, but it may be assumed that the evaporation rate is least at the ground-leaf layer. Weese (1924) has given proof of this for the Elm-Maple forest which he investigated. From the forest floor upward light intensity, temperature and evaporation increases while humidity decreases. Fluctuations in these physical factors of the environment occurs least in the ground-leaf layer and most in the forest crown, the reasons for this have been fully explained by Adams (1915), Weese (1924) and Blake (1926).

Spiders inhabiting the ground-leaf layer are species tolerant of little light, comparatively low temperature, a fair degree of moisture and low evaporation. The population of this stratum is the most constant of all the strata except during the winter months when migrants characteristic of other situations hibernate in it. This constancy of population is associated with physical factor gradients which exist between the ground-leaf layer and the adjacent herb layer. Spiders passing from one of these strata to the other undergo marked and sometimes very sharp changes.

Similar differences exist with regards to herb, shrub and tree strata but the gradients are not as steep nor as controlling in their effect.

The transitional nature of the forest under investigation affords a more varied habitat than more homogeneous vegetational associations such as Oak-Hickory or Beech-Maple forests because the River-Terrace Forest gradually changes from the more dense humid and shady forest of the lowland to the drier, more open Oak-Hickory association of the upland. Also, the presence of prairie vegetation in certain regions of the area adds further to the diversified nature of the habitat. Correlated with these varied biotic and physical features, there is much diversification in the spider population.

DISCUSSION

The stratal and habitat relations given above are not intended to indicate that the spiders are limited to the designated situations, but that the particular species are found most often and in greatest numbers in the micro-habitat or habitat suggested. Some of the spiders are apparently tolerant of a wide variety of conditions and can be found virtually in all situations in substantial numbers. Comparative abundance alone cannot be used as a criterion for determining habitat preferences, as the table shows, it often happens that a species characteristic of one habitat is numerically dominant in another; for example, *Agelena naevia*—a field form—and *Pisaurina mira*—a transitional form—are among the most numerous in the River-Terrace forest.

Physical factors are the dominant forces in the activities of the spiders during the winter. The habitat is essentially reduced to a single layer, the ground-leaf stratum. In southern Tennessee, however, a few species can be collected from

the remnant herb layer throughout the winter. As pointed out by Weese (1924), preceding hibernation there is a general downward migration of the spiders but certain species such as *Clubiona pallens* and *Ariadna bicolor* move upward with the advent of winter and hibernate under the bark of trees. Activity is reduced to a minimum during hibernation except on warm days when certain species move about on the dead leaves and herbs but even then evidence of predatory activity is lacking.

The mass hatchings indicated in the table during the late spring and the late summer result in two population peaks in the population density of the spiders when the young hatched at these periods mature. The fact that the hatching period and time of maturity of the species given above are somewhat earlier than published reports in this regard for the same species farther north, and that species reported as overwintering as eggs or egg-sized spiders in the north are readily collected from one-fourth to one-half grown in the Memphis area indicate the effect of environment on the reproductive and developmental processes of the spiders.

SPECIES DIAGNOSTIC OF THE HABITAT

Only thirty species were represented by fifty individuals or more in the collections. The total number of individuals of these thirty species constitute more than three-fourths of the 5,090 spiders taken. Among these principal or numerically dominant groups were some more typical of other habitats as the table shows. However, it is interesting to note that certain of these principal species occur in great abundance in this forest while being very scarce or absent in other vegetational communities studied. Further, according to published reports and information gained from collectors, one of the species (*Oxyopes aglossus*) though widely distributed, seems to be found in large numbers only in this type of habitat. Species of this nature are: *Oxyopes aglossus, Anyphaena fraterna, Thiodina sylvana, Mangora placida, Dictyna cruciata, Theridion studiosum* and *Ebo latithorax*. Collectively, they are diagnostic of the River-Terrace forest.

SUMMARY AND CONCLUSION

Although a great variety of species inhabit the forest, a comparatively few species make up the largest part of the total number of individuals collected. One hundred and thirty-nine species of spiders are reported for the forest. Thirty species, or approximately one-fifth of the total number, constitute 4,007 individuals or over three-fourths of the 5,090 individuals collected.

Principal species numerically are not always spiders typical of the forest, but may be forms more characteristic of other situations such as the forest border or field.

Of the spiders whose habitat relations were determined, 46 were typical River-Terrace forest spiders; 24 were forest spiders but more typical of other forests (Beech-Maple, Oak-Hickory, Elm-Ash-Maple, etc.); 33 were transitional forms and 11 were field spiders.

Seven species which we consider particularly diagnostic of the River-Terrace forest have been listed.

During the warm part of the year vertical distribution of the species is characterized by stratal communities. Stratification is associated with the physical factors and the vegetation.

Species composition of the stratal communities is not constant but shows seasonal variation.

Horizontal distribution is largely associated with varying moisture content of the soil.

Most of the spiders hibernate as immature forms or adults. Only 14% of the spiders whose hibernation stage was determined overwinter as eggs or egg-size spiders.

Over 90% of the species hibernate in the ground-leaf stratum, thus preceding hibernation there is a general downward migration. Apparently temperature is the chief factor affecting this vertical shifting.

The spiders exhibit two major hatching periods, late spring and late summer.

The mass hatchings of late spring and late summer result in two population peaks of adults when the spiders hatched at these times have matured.

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