BIOLOGY AND BEHAVIOR OF A JUMPING SPIDER, *HABRONATTUS AGILIS*

by 2215

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INTRODUCTION

Habronattus agilis Banks is a small (5-6.5 mm) jumping spider of the family Salticidae having certain unusual behavior patterns which are probably unique among salticids. All jumping spiders construct silk cocoons or retreats for resting at night, molting, hibernating, and for rearing the young to the second instar, but this species, and at least 2 other Habronattus spp., are the only ones known to incorporate additional material, in this case, sand, into the cocoons. In addition, the behavior of H. agilis suggests a primitive colonialism. After briefly considering the biology and life history of H. agilis, this study deals mainly with its behavior.

MATERIALS AND METHODS

Individuals of all instars of H. agilis were studied over a period of 15 months, from May 1970 to July 1971. The original 10 males and 11 females were captured during May and June of 1970 near Manhattan, Kansas in 2 areas described in the section on habitat. The young spiders on which the growth and molt data have been based were the progeny of 10 females. Two of those original females and only one of their female offspring also laid eggs during 1971.

The original spiders were kept in 1-pint, wide-mouth Mason jars with wire mesh screening in the lid. As soon as the spiderlings emerged from the egg cocoon, they were separated and housed in plastic dishes (7 cm diameter, 1.5 cm deep). The lids had a 1-cm hole with fine mesh screening for ventilation. Small cotton wads, moistened every few days, provided moisture, and the bottom of the container was covered with a thin layer of sand. Second instars were fed Collembola (Sinella curviseta), and all others Drosophila sp. Initially, house flies were used for food, but the spiders more easily caught fruit flies

without injury.

Humidity, temperature, and light were not controlled in this study. Daylight was supplemented by overhead flourescent lamps for 9-10 hours a day, and the temperature ranged between 19 and 30 C.

Observations were made almost entirely with a dissecting microscope surrounded by a curtain of translucent Mylar plastic to decrease the disturbance of the spiders, who otherwise reacted to any movement by the experimenter. Photographs were taken with an Alpa 10-D and a Leicaflex SL mounted on the dissecting microscope, using Tri-X film and electronic flash.

BIOLOGY OF *HABRONATTUS AGILIS*

Taxonomic Review of the Genus

Species now included in *Habronattus* have been placed in various genera since the first species was originally described by Hentz (1846) who named all jumping spiders *Attus*. Since then, the species have been included under *Habrocestum* (Peckham 1883), *Ephippus* (Keyserling 1884), *Hasarius* (Emerton 1891), *Evarcha* (Simon 1902), *Pellenes* (Peckham 1909), and *Habronattus* (Bryant 1941).

The original description of *Habronattus* (Cambridge 1901) was based on *H. mexicanus* from Mexico. Of the 11 species listed, 2 were from North America, *coecatus* and *viridipes*, and were transferred from Habrocestum (Peckham 1888). Species were distinguished by characteristics of the genitalia.

Habronattus was not mentioned again until 1941. Bryant considered that *Habronattus* was separate from the genus *Pellenes* due to certain consistent variations in the shape of the male palpus and the female epigynum. Several spiders formerly placed in the genus *Habrocestum* have been transferred to *Habronattus* based largely on characteristics of the legs and genitalia (Chickering

1944, Chamberlin and Ivie 1944, Kaston 1948). A good description of the genus is taken from Kaston (1948):

"The females all have an epigynum with a single opening at the posterior end of a centrally arched or conical structure. In the palp of the male the bulb is more or less circular; the embolus starts on the retrolateral side of, or at least at the proximal end of, the bulb, and parallels the margin of the cymbium; paralleling the embolus, but not quite as long as the latter, is a strong, spine-like conductor. In both sexes, the relative length of the legs is 3142, with the males of some species possessing peculiar modifications of form, color, or ornament on Leg 1 or 3 or both."

Description of Habronattus agilis

The species Habronattus agilis was first described by Peckham (1888) as Habrocestum auratum, a new generic designation for Attus auratus Hentz. However, Banks (1893) found the 2 to be dissimilar and proposed a new species name, agilis. When Peckham revised the North American Attidae in 1909, he recognized the European genus Pellenes to which he assigned Habrocestum agilis. This name was retained by Emerton (1909), Comstock (1912 and 1940), and Kaston (1938). In all of these, leg modifications were described but genitalia were not.

Chickering (1944) redescribed 4 species of Habronattus, among them agilis. His description included leg ornamentation, cheliceral teeth, genitalia, hairs, bristles, and coloration.

The particular individuals used in this study vary slightly from the usual descriptions of Habronattus agilis (Kaston 1948, Chickering 1944). The following description is based on these spiders, with variations noted in the text. Since hairs and scales are often confused, hairs have been considered to

be those epidermal derivatives which stand away from the body, scales to be those which lie flat against the body.

Male.-Length 5.0-6.0 mm. Legs 3412 (compare with Kaston's description of Habronattus). Leg 1 (Fig. 1): Femur fringed dorsally and ventrally with white or yellow hairs, the hairs decreasing in length distally in the dorsal fringe, increasing in length to the midpoint of the ventral fringe; prolateral surface loosely covered on dorsal half with yellow and white hairs, thickly covered on ventral half with mixed yellow scales and hairs. Patella expanded distally with dorsal and ventral fringes, white hairs blending to yellow distally; prolateral surface covered with yellow hairs, blending to blue-green distally, and centrally marked by a heavy black spine. Tibia with yellow dorsal and ventral fringes on the proximal half only; prolateral surface covered with blue-green hairs and marked centrally with a heavy black spine; 3 pairs of ventral spines. Metatarsus and tarsus without fringes, prolateral surface covered with yellow scales; 2 pairs of ventral spines on metatarsus. Retrolateral surface of Leg 1 and both pro- and retrolateral surfaces of remaining legs loosely covered with yellow scales. Ventral surface of tibia and metatarsus 4 dark brown. [Compare Emerton's drawing of Leg 1 (Fig. 2)]. Palp (Fig. 3) with all segments loosely covered with yellow scales; femur with dorsal fringe of long white hairs; tibia short and broad, drawn out retrolaterally into a long stout sinuous black apophysis; tarsus round and flattened laterally; embolus arises near tibial apophysis and makes a complete circle around the periphery of the cymbium, ending near its origin; conductor arises near the center of the bulb, extends proximally to the base of the tarsus, then turns abruptly and curves around parallel to the embolus to 1/3 the circumference of the bulb. [Compare Kaston's diagram of the palp (Fig. 4)]. Color (Fig. 6):carapace brown to black, covered with mixed black and light brown scales, with greatest density

of brown scales in ocular quadrangle; several long black bristles scattered in region of anterior lateral eyes (ALE), posterior lateral eyes (PLE), and posterior median eyes (PME); numerous shorter and heavier bristles form a row above the AME; 2 stripes, composed of white scales, beginning behind the AME and continuing posteriorly above the PME, encircling the dorsal 3/4 of the PLE and converging slightly toward the posterior border where they merge with a white stripe extending from across clypeus and encircling ventral edges of the carapace just above a narrow black border; a second short stripe extends medially from a point behind the AME to midway between the PLE, sometimes replaced by a triad of white spots; abdomen with 3 dorsal white stripes, 2 extending across anterior border around lateral edges of abdomen and ending just above spinnerets where stripes remain width of spinnerets apart, third stripe extending from anterior end of abdomen posteriorly along midline and ending just short of spinnerets; remainder of dorsum covered with black and brown scales and scattered long black bristles. Venter of abdomen covered with cream-colored scales (Fig. 7).

Female.-(Fig. 8). Length 5.0-6.5 mm. Legs 3412, covered loosely with cream-colored scales. Coloration essentially like male but majority of scales forming stripes and covering dorsum are cream-colored mixed with black; stripes similar to those on male except central abdominal stripe broken into a series of spots; short reddish-brown stripe extends ventrally from each AME (Fig. 9), becoming a thin black stripe extending from lateral edge of clypeus around lateral wall of carapace, just above a slightly broader cream-colored stripe. Venter of abdomen with a broad yellow stripe within which are 3 brown stripes extending from epigastric furrow to base of spinnerets. Epigynum with a recurved anterior, crescent-shaped margin, single tubular opening, and 2 obliquely placed spermathecae (Fig. 5).

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Fig. 1. Prolateral view of Leg 1 of a male Habronattus agilis observed in this study shows light colored fringes and hairs on femur, patella, and tibia. Central dark areas on patella and tibia conceal stout black spines. Compare with Figure 2.

Fig. 2. Drawing of prolateral view of Leg 1 of a male H. agilis (redrawn from Emerton 1902). Shows the femur with black fringes and hairs, the patella with a white dorsal and a black ventral fringe, and the tibia with black fringes and hairs except for a white spot at the distal end. The metatarsus and tarsus have white hairs.

Fig. 3. Ventral view of palp of male H. agilis observed in this study is virtually identical to the drawing in Figure 4 for H. agilis.

Fig. 4. Drawing of ventral view of the palp of H. agilis (Kaston 1948).

Fig. 5. Epigynum of female H. agilis (Kaston 1948).

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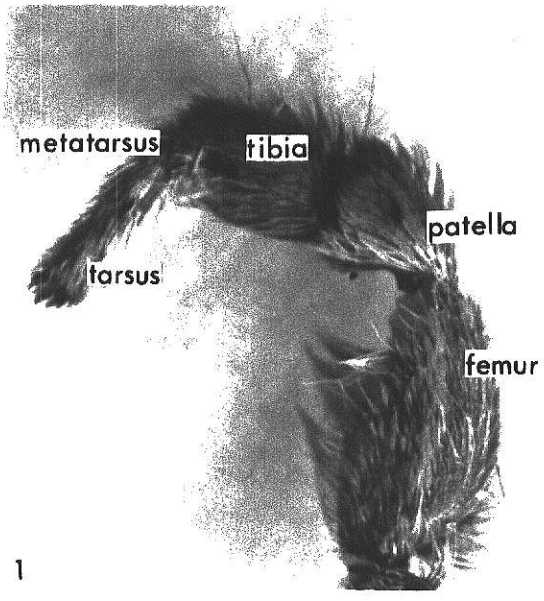
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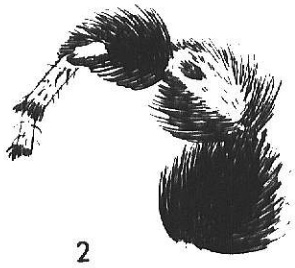

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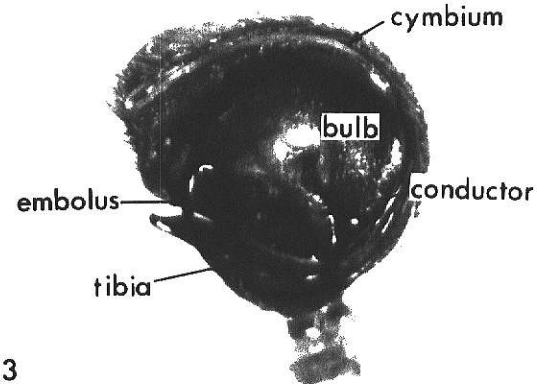
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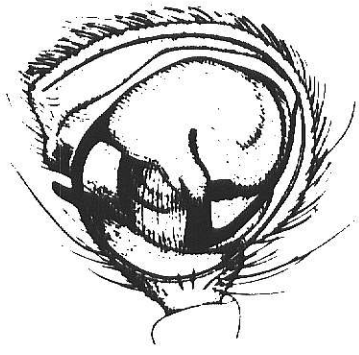

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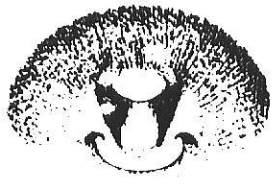

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Fig. 6. Dorsal view of male Habronattus agilis showing striped pattern and usual position of the legs.

Fig. 7. Ventral view of male H. agilis.

Fig. 8. Dorsal view of female H. agilis showing striped pattern and abdominal spots.

Fig. 9. Anterodorsal view of female H. agilis showing stripes below AME.

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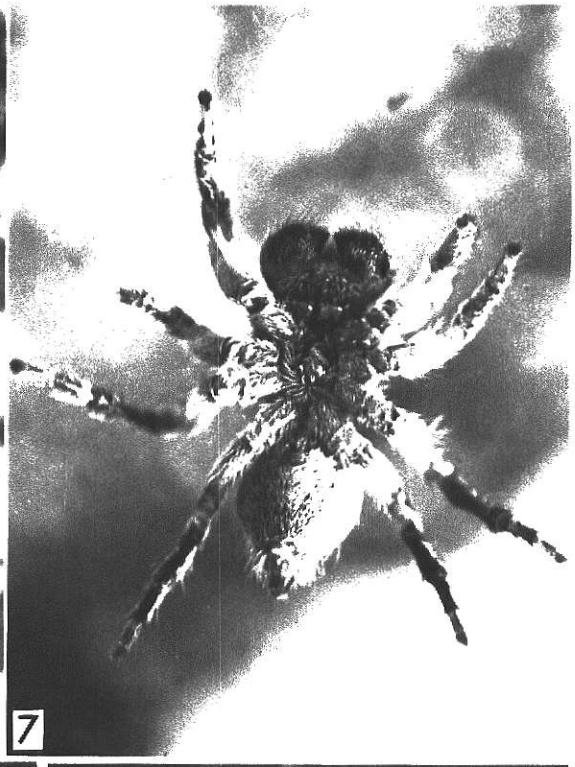

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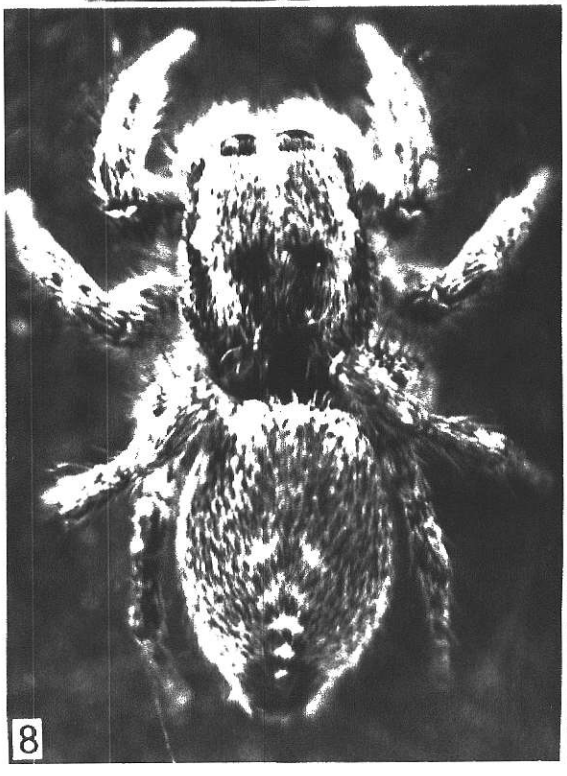

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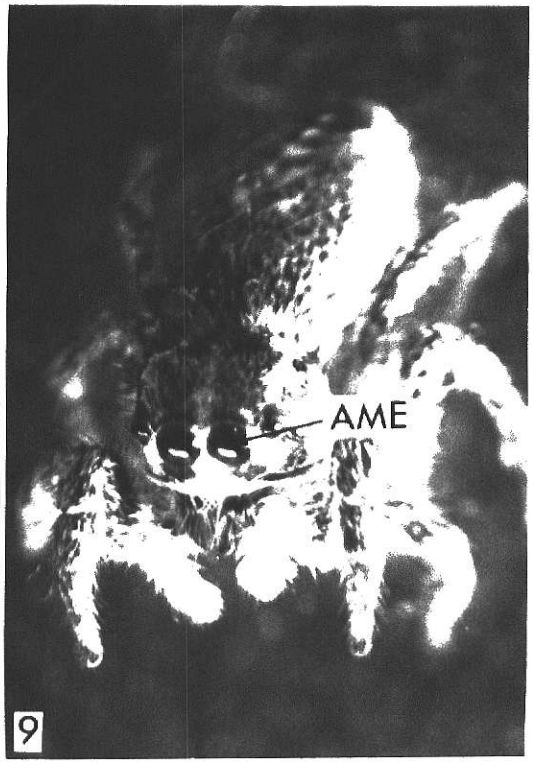

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A male and female are being deposited in the collection of the National Museum in Washington, D.C.

Habitat

Habronattus agilis is fairly common in the United States east of the Rocky Mountains. Although it occurs frequently along sea shores, among marsh grass, and under sticks and stones (Barnes 1954, Kaston 1948), it also has been found inland in Texas, New Mexico, and Kansas.

The spiders observed in this study were taken in Pottawatamie County, Kansas, mainly from 2 isolated sandy pockets. Such areas occur frequently in Kansas along streams and rivers and on the flat tops of a few hills where they form small desert-like areas.

The first study area is about 25 miles north of Manhattan, Kansas near Randolph (39° 24' 34"N, 96° 41' 23"W) and has been named the Little Gobi Desert (Fig. 10-11). Much of this area has become overgrown in recent years with grasses, but there are still some patches of bare sand where many cryptic arthropods and H. agilis may be found. The total area of this site is approximately 1 hectare.

The second area is located along a stream on U.S. Highway 24 about 5 miles east of Manhattan (39° 12' 17"N, 96° 24' 18"W). Flat sandy areas stretch on either side of the stream for about 15 m long by 8 m wide (Fig. 12-13). Willows, grasses, and low weeds are common here, along with many cryptic arthropods. H. agilis was found only on the west side, which was 1-1.5 m higher than the east side and not as subject to flooding.

Fig. 10-11. The "Little Gobi Desert". Numerous small patches of bare sand are visible along the fence and in the foreground of Figure 10 and in the entire central area of Figure 11. H. agilis was most often found in these bare patches.

Fig. 12-13. The stream area. The lower mud flats on the east side of the stream (Fig. 12) frequently flooded, prohibiting H. agilis from living there. That section is visible as the upper part of Figure 13. H. agilis was found in considerable numbers on the higher level which was 1-1.5 m above the mud flats and had many bare patches of sand.

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Microhabitat

The work of Chew (1961) on distribution of desert spiders suggests that Habronattus agilis may prefer sand substrate, but it may occur on vegetation from low grasses to bushes. During this study, H. agilis was frequently found in low vegetation, seldom more than 50 cm above the ground. The sexes varied in plant-type preference. Males were most often found on low green vegetation, whereas females were more likely to be found on dried plants and leaves to a height of 50 cm, or on the sand where their dull brown coloration rendered them rather difficult to see. Males were found wandering about on the tops of leaves while females remained motionless in one spot or jumped along the ground in pursuit of small arthropods.

Seasonal Occurrence

Active adults of Habronattus agilis were found in the field from April 27 to late October. From June onward, females were increasingly difficult to find because of brood care activities. Juveniles first appeared in late June and became only slightly more numerous as the season progressed.

Life Cycle

Ten female Habronattus agilis, collected as adults, were observed in separate jars with 5-6 mm of sand covering the bottom. This method proved unsatisfactory because it was impossible to observe activities inside the egg cocoons and to obtain data on development of the spiderlings, Hence, all data for the first broods of spiderlings started from instar 2 or 3. Later broods in 1971 were raised in transparent plastic containers (7 cm diameter, 1.5 cm deep) with a layer of sand one grain deep on the bottom. This caused the

females to construct only the dome of their egg cocoons, leaving the bottom open to view. The cocoons from these females provided data on egg development and instar 1.

Eggs

Ten females laid 29 egg masses, 1-4 egg masses per female, during the summer of 1970. The average number of eggs per mass was 11.3 with a range of from 3-25, and all were fertile. Dates of laying and times between egg masses are given in Table 1. Eggs were laid from June 1 to September 9. The mean intervals between egg masses were 28 days between masses 1 and 2,and 2 and 3, and 26 days between masses 3 and 4. Mean time between all egg masses was 27.6 days with a range of 15-33 days.

Embryonic Development

Newly-laid eggs measured 0.8-1.0 mm in diameter and were pale yellow with a pearly luster. The following developmental series was taken from the brood of a female who failed to construct a sand cocoon. However, she remained over the cluster of eggs similar to females with normal cocoons. Two eggs failed to develop.

Day 9: No major externally visible changes occurred in the embryo until day 9 when the anterior and posterior ends of the body were distinguishable. Legs and palpi appeared as ridges on either side, and the egg membrane started to lift around the legs (Fig. 14).

Day 10: The egg membrane broke across the cephalothorax and along the proximal leg attachments. The legs were free from the body distally (Fig. 15).

Day 11: Retinal pigment was visible as internal clusters of reddish-brown pigment in the region of the AME. Lenses do not develop until the

Table 1. Intervals between egg masses and oviposition dates of Habronattus agilis.

Spider No.	Date of 1st eggs	Days between egg masses	Date of 2nd eggs	Days between egg masses	Date of 3rd eggs	Days between egg masses	Date of 4th eggs
3	Jun. 1	28	Jun. 29	25	Jul. 24	33	Aug. 26
71	Jun. 4	33	Jul. 7	29	Aug. 5	21	Aug. 26
73	Jun. 4	33	Jul. 7	26	Aug. 2	23	Aug. 25
79	Jun. 8	21	Jun. 29	30	Jul. 29	28	Aug. 26
11	Jun. 11	15	Jun. 26				
12	Jun. 26	34	Jul. 30	27	Aug. 26		
77	Jun. 29						
45	Jun. 30	30	Jul. 30				
81	Jul. 9	30	Aug. 8	32	Sept. 9		
75	Jul. 13	31	Aug. 13				
Mean		28		28		26	

second instar, judging from an examination of the first instar exuviae. The legs were free from the body, and body regions were noticeably separate. Chelicerae began to develop, and palpi and spinnerets were visible as unsegmented knobs. Color of the abdomen remained a plae yellow, while the cephalothorax became clear. Egg membranes were free from the body (deutovum stage) (Fig. 16).

Day 12: The legs elongated and retinal pigmentation of the AME darkened.

Day 13: Retinal pigmentation was visible in the remining eyes, reddish brown bristles were visible on legs, abdomen, and cephalothorax. The spinnerets were visible as 3 pairs. Leg segmentation had begun proximally and small leg movements occurred.

Day 14: The deutovum membranes were shed and the first instar spiderlings were able to move about rather uncoordinatedly. The legs could not yet support the body, nevertheless, the first instars were able to leave the central area to one centimeter and return. Leg segmentation was complete and mouthparts were capable of slight movements. The bristles were elevated and retinal pigment in all eyes was dark. Dark pigments on the abdomen appeared as a faint median stripe and lateral spots (Fig. 17).

Day 15: The female left the spiderlings which were still capable of only limited motion. Black pigmentation on the abdomen continued to darken and began on the cephalothorax as a median line extending from the ALE to the posterior border and as dark areas behind the PLE. Reddish brown annulations appeared on the distal ends of all femurs.

Day 21: 6 days later, the first instars were much more coordinated and all coloration had darkened. The AME retinae, still lighter than those of the other eyes, displayed lateral movements (Fig. 18).

Day 25: The second instars appeared after 25 days and were very agile,

scopulae were present on the tarsi, and all eyes except the AME showed fully darkened pigmentation.

Day 26: The second instars left the egg cocoon (Fig. 19).

The 10 females spent an average of 16.8 days inside the egg cocoons and 10.7 days between their emergence from one cocoon and laying of another mass. During this interval, females fed frequently, one female consuming 9 *Drosophila* in a morning. Copulation was not observed during these intervals.

Molting and Growth

Data taken in the laboratory on growth from the second instar may not be equivalent to that under natural conditions, particularly for the final 2 molts. It has been found that spiders overwintering indoors experience an accelerated growth to maturity and early death (Gardner 1967). When molting to adults was attempted during what would normally be a hibernation period, all the spiders died. It was first thought that the dry heat in the laboratory was causing this high mortality, but results were the same under humidities from under 10% to almost 100%. Larger species of salticids, maintained simultaneously in the laboratory managed to molt successfully, but the majority of them died early in the spring. When raising hunting spiders in captivity, it is probably advisable to maintain them at sufficiently low temperatures during their natural winter to render them inactive if one wishes to observe the spiders under as nearly natural conditions as possible. This will allow the natural cycling to proceed, so that development in the spring will continue normally.

Table 2 lists 12 spiders and the duration of each instar from one to 7. Data for instars one to 3 have been taken from another group of spiders raised during 1971, for reasons mentioned previously. Data for Table 3 were all

Fig. 14. Day 9 of Habronattus agilis embryo development. Legs and palpi appear as ridges on the embryo to the far right. The dark area on the posterior border of Leg 4 is the rupturing egg membrane. The embryo on the lower right shows an indentation between cephalothorax (upper) and abdomen (lower).

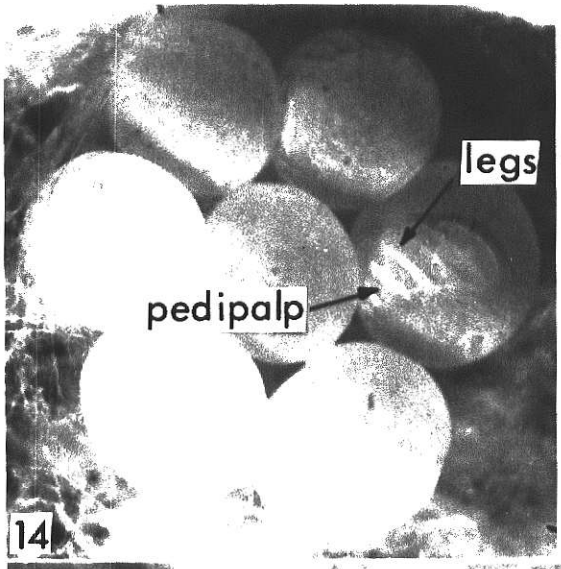
Fig. 15. Day 10. Embryo at the far right shows greater elevation of the leg ridges and further rupturing of the egg membrane across the proximal leg attachments. Embryo on the upper left shows greater division between cephalothorax and abdomen.

Fig. 16. Day 11. Embryo at the far left shows legs free from the body and from each other, as well as distinct cephalothorax and abdomen. Chelicerae appear as knobs at ventral edge of cephalothorax.

Fig. 17. Day 14. Early first instar spiderling shows leg segmentation complete and dark annulations on the distal ends of all femurs. Bristles are numerous and faint stripes of color appear on the abdomen. Retinal pigmentation is apparent as rings around each eye.

Fig. 18. Day 21. Late first instar shows well developed retinal pigmentation and abdominal stripes.

Fig. 19. Emerged second instar has well developed movement and vision, and has a full cover of scales and hairs. The carapace is completely dark and distal ends of all leg segments have dark annulations.



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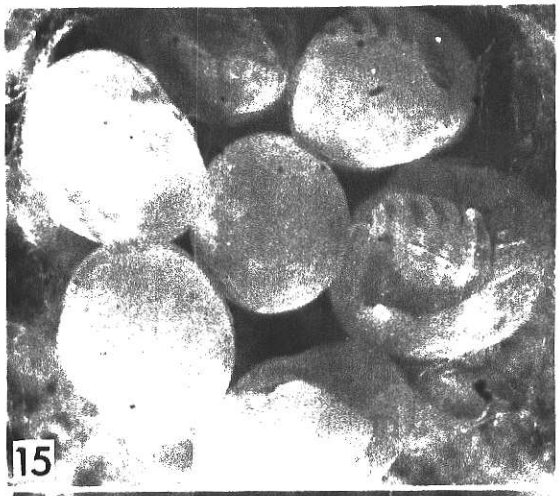

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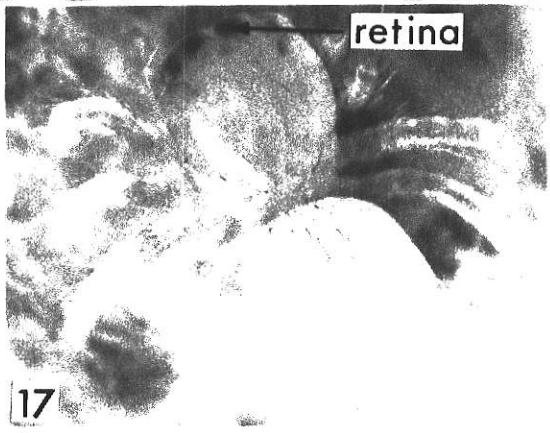

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Table 2. Duration of instars 1-7 in Habronattus agilis (days).

Spider No.	Instar 1	Instar 2	Instar 3	Spider No.	Instar 3	Instar 4	Instar 5	Instar 6	Instar 7
O2A1	28	29	14	5a1	12	14	16	33	34
O2A3	28	36	12	5a2	12	17	19	56	
W1A1	18	24	16	5b	14	15	14	42	35
W1A3	18	39	14	5c1	13	18	13	45	29
W1A4	18	24	15	5c2	11	18	16	54	29
W1A6	18	51	14	5d1	17	16	18	52	
W1A7	18	37	15	5d2	21	12	15	43	
W1A8	18	29	12	12a	24	18	17	65	30
W1A9	18	59	14	24a1	13	12	20	197	
O1A7	23	37	15	24a2	18	19	15	195	
				44b	18	19	22	51	
				48a	21	20	12	60	166
Mean	20.5	36.5	14.1		16.2	16.5	16.4	41.9[a]	31.4[b]

[a]Mean excludes spiders 24a1 and 24a2 which matured in the spring of 1971.

[b]Mean excludes spider 48a which matured in the spring of 1971.

Table 3. Total body length (mm) of Habronattus agilis instars 1-7 following each molt.

Spider No.	Instar 1[a]	Instar 2	Instar 3	Spider No.	Instar 2	Instar 3	Instar 4	Instar 5	Instar 6	Instar 7
02A1	1.5	2.0	2.6	5a1	2.0	2.7	3.5	4.7	5.0	5.4
02A3	1.5	2.4	3.0	5a2	2.5	3.0	3.5	4.5	5.0	
W1A1	1.6	2.0	2.6	5b	2.4	2.6	3.2	4.0	4.4	5.0
W1A3	1.6	2.4	2.6	5c1	1.9	2.5	3.0	4.1	4.5	4.9
W1A4	1.6	2.0	2.7	5c2	2.4	2.6	3.0	3.1	4.5	4.9
W1A6	1.6	2.1	2.7	5d1	2.2	2.3	2.9	3.1	4.0	4.5
W1A7	1.6	1.9	2.4	5d2	2.0	3.2	3.8	4.1	4.5	
W1A8	1.5	2.0	2.4	12a	2.0	3.0	4.0	4.7	4.9	
W1A9	1.5	2.1	3.0	24a1	2.5	3.0	3.3	4.0	4.3	4.9
01A7	1.6	2.1	2.6	24a2	2.0	2.7	2.9	4.2	5.0	
				44b	2.1	2.6	3.1	4.0	4.9	
				48a	2.0	2.3	2.8	3.5	4.6	
Mean	1.6	2.1	2.7		2.2	2.7	3.3	4.0	4.6	4.9
Mean Growth		.5	.6			.5	.6	.7	.6	.3
Per cent Increase		35	21			20	17	11	11	6

[a]After shedding of deutovum membranes.

obtained by measuring the spiders before they left the molt cocoon, since as soon as they began to feed, their abdomens enlarge.

Instar 2 is critical as the newly emerged spiderlings are particularly vulnerable to predation and are limited to a very small prey size. However, the per cent increase in length during this instar was the greatest and duration was about twice that of instars 3-5. Instar 3 is given twice to compare growth for 2 different groups of spiders. The first had more numerous and larger prey (Drosophila) available to it, the second had only Collembola. Duration was the same for both groups in this instar, and so were the mean growth and per cent increase in length. Therefore, food may not have been as critical a factor in the early instars as might be supposed. Spiders having only Collembola available to them may have compensated by eating a larger number of smaller prey than those fed Drosophila. However, duration of instars may be largely controlled by hormones which regulate molting. Instars 6 and 7 were the longest (41.9 and 31.4 days). Spiders matured to adults during these 2 instars, usually during the fall of the year, but some matured the following spring, as shown by the figures 197, 195, and 166 days. There seemed to be no correlation between maturation and length of the pre-adult instar.

The mean growth for all instars was nearly the same. Per cent increase in length, however, declined from 35% at instar 2 to 6% at instar 7. In effect, most instars required approximately the same amount of time to increase their length by nearly equal increments. They were, however, growing less rapidly. These spiders, when mature, were an average of 1.0-1.5 mm smaller than wild H. agilis. The decline in growth of the laboratory-raised spiders probably occurred during instars 5-6, which show the per cent increase in length to be cut by almost one half. The spiders kept during the summer of

1971 were, at the time of this writing, reaching the fifth instar and they were increasing their mean length by about 20%. If each instar increased its length by 20% at each instar, the length of the adults would range between 4.9 and 6.9 mm, the approximate range of length in wild spiders.

THE BEHAVIOR OF HABRONATTUS AGILIS

Vision

The Salticidae are so dependent on vision that a brief review of the more important findings regarding vision of jumping spiders will be helpful in discussing the behavior of H. agilis. The AME are the major "seeing" eyes, the other 6 serving as a peripheral detection system allowing nearly a 360° viewing range. When a moving object comes within this field, the entire body is rotated until the AME are fixed upon it. The events which follow determine the spider's reaction.

Land (1969) has listed 4 types of retinal movement as they occur in a normal sequence: (1) spontaneous activity, a rapid periodic side to side movement by which the AME detect the object; (2) saccades, which bring the object to the center of focus from the periphery of the retinae; (3) tracking, or fixation on the object; and (4) scanning, in which the target is watched for up to 10 seconds, following which the spider may stalk and capture, raise its first legs and court (if a male), remain still and watch (if a female), turn and run, or walk away. This highly elaborate visual system allows the spider to detect potential prey, distinguish between edible and inedible objects by their geometry, and to navigate in the appropriate direction (Land 1969). A spider watching a prey insect that has passed behind an object will continue rotating its body in the same direction, and can usually relocate the prey.

The first 3 events in the above sequence (spontaneous activity, saccades, and tracking) occur too quickly to be separately distinguished. In H. agilis, as in most other salticids, this was observed as a rapid turning by the spider to face a prey insect, or any other moving object that entered its visual field. Scanning was accompanied by what appeared to be a color change in the AME, but what was actually the movement of the retinae to establish the identity of the object, and, if a prey, to assess the distance to it. H. agilis is apparently able to distinguish between potential prey, a member of its own species, an enemy, or an indifferent object in a few seconds.

Movement and Locomotion

The locomotion of H. agilis is characteristic of the more highly advanced salticids, designated "hoppers" by Jocelyn Crane (1949) because of their moving in a combination of short runs and hops, depending on the substrate. High visual development allows salticids to assess their surroundings and proceed accordingly. All 4 pairs of legs were used by H. agilis in walking, with the palps held clear of the ground. During pauses in walking, the first legs and palpi were alternately or simultaneously waved in the air or tapped on the ground, while the spider turned slowly in a circle or rotated its cephalothorax. The spider then proceeded in the same or a different direction or jumped to a higher position.

H. agilis is able to leap horizontally 8-10 cm. The main force of the jump is provided by the elongated third legs which are bowed under the body in preparation for the jump (Ehlers 1937). This central push and the compact body shape allow the spider to jump forward, somersaulting in the air, to a position directly overhead, or from an upside-down position to a vertical one. Furthermore, the direction can be changed with each jump, making this spider

an exceptionally difficult one to catch. Similar maneuvers can be accomplished while carrying prey. Loss of a third leg results in compensation by the remaining legs, so that the proper direction is maintained. Such handicapped individuals seemed to be equally successful in capturing prey as those with complete sets of legs.

These movements are facilitated by the presence on each tarsus of a scopula, typical of all salticids. This is a cluster of hollow, spatulate hairs, each having numerous minute extensions (Kaestner 1968). Although the precise mechanism of these hairs has been debated, it is most likely that adhesion depends on the film surface tension possessed by most surfaces (Kaestner 1968). But this may be aided by lubrication with maxillary gland secretions when the pretarsi are groomed (Savory 1928). The spiders often stopped to clean the pretarsi, and before each of these groomings, a drop of liquid appeared to exude from the mouth. However, the liquid may assist in removing dirt particles interfering with the surface tension adhesion.

Prey Capture and Feeding

H. agilis, as already mentioned, is endowed with unusual powers of vision and mobility, both of which are basic to a high degree of predatory success and accuracy.

As is typical of all hunting spiders, a small H. agilis 5 mm in length readily attacked a house fly at least 3 mm longer. Such a larger prey, however, required a longer amount of time to be affected by the poison of the spider. One male spider jumped onto the thorax of a house fly and bit it. The fly flew around the bottom of the jar for nearly one minute before the spider released its hold. On the second try, the fly was caught by the leg and

attempted to fly away, but the spider had a firm foothold on a stick and held the fly for about 30 seconds before he let go. The third time, the spider jumped onto the fly as it passed under a twig and was able to hold onto it long enough to let the poison take effect.

When prey was detected and brought into focus by the AME, the spider moved toward it very slowly to a distance of about one centimeter, then quickly pounced. With each succeeding miss, movements became more rapid and more distant leaps were attempted. Inevitably, by stealth or otherwise, the prey would usually be secured. Under natural conditions, a spider's chances of recovering a lost prey are small, therefore they probably only resort to the stealth method.

When prey was secured, most immature spiders moved to a high point where they were able to face down and survey the surrounding area. Presumably this behavior avoided attack while the spider fed. Adults seldom did this, but remained where the prey had been captured and turned in a slow circle while eating. The prey was held by the mouthparts and rotated by the palpi and first 2 pairs of legs. Even while feeding in an inverted position on the ceiling, only the last 2 pairs of legs supported the body, aided by the spinnerets which were tightly clamped around the dragline (Fig. 20).

Age groups vary considerably in the amount of time required to consume prey of approximately equal size. All immatures consumed one Drosophila in an average of 34:27 (min:sec), males 13:52, and females 13:45. Although males and females did not differ in feeding, males were quicker and had somewhat greater success in capturing prey.

Many spiders apparently ignore additional prey while feeding. H. agilis females, however, would fixate for as long as 3 minutes on a potential prey

while consuming another and pursued and captured the second prey immediately after discarding the first. Prey was not dropped prematurely if another was sighted.

One house fly was accepted approximately every other day by adults. Usually, following such a large intake of food, the spider spent the following day inside its cocoon. In the laboratory, where conditions were made as uniform as possible and each spider had a constant supply of food, second and third instars consumed 2 Drosophila a day, fourth instars and up, 3 or more. Males seldom consumed more than 2. Dead flies were often attacked if they were caused to move or vibrate. These were always immediately discarded, followed by grooming.

Following feeding, a spider wandered about, intermittently stopping to groom the eyes, clypeus, chelicerae, and pretarsi.

Cannibalism among adults was nonexistent and among immatures occurred only rarely. Starving third instar individuals, especially shortly after molting, killed and ate smaller instars (Fig. 21), even though Collembola were available. However, if sufficient numbers of Drosophila were supplied daily, the cannibalism stopped.

Sharing of food was observed only once. A female had been eating a house fly for several minutes when a male approached and began feeding on the opposite side of the fly. The female spider turned to fixate her eyes on him then resumed feeding. When she had finished feeding, she walked off slowly and he continued eating.

These examples of nonaggression are rare among spiders and seem to indicate a certain degree of advancement as a species.

Fig. 20. Male Habronattus agilis feeding on Drosophila. The spider is suspended from the ceiling of its container by the third and fourth legs and by a dragline held by the spinnerets. The first 2 pairs of legs encircle the prey and are used to turn and hold the prey in the mouth.

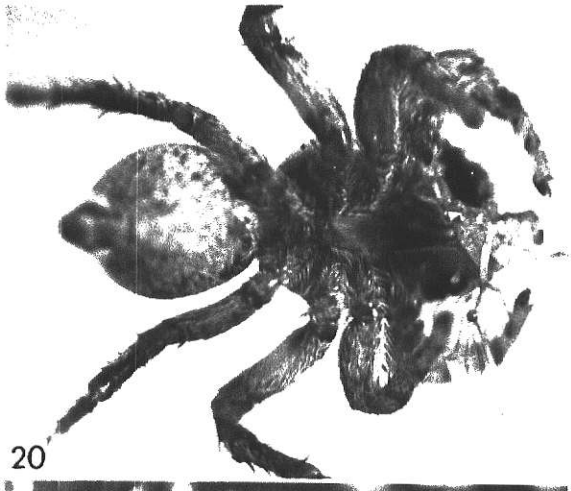
Fig. 21. Immature male H. agilis feeding on a smaller instar. Cannibalism is resorted to only when the spiders are starved. The underfed condition of this spider is shown by the depressed shape of the abdomen, which would normally be full and round.

Fig. 22. Male H. agilis grooming the pretarsus of Leg 1. The leg is pulled around to the mouth without the aid of other legs or palpi.

Fig. 23. Female H. agilis moving Leg 3 toward mouth to be groomed. Legs 1 and 2 help to keep the pretarsus in the mouth, and support of the body is almost completely shifted to the right side.

Fig. 24. Female H. agilis rubbing legs. Leg 2 has just finished rubbing Leg 3, which is now rubbing Leg 4. Body support is shifted to the right side.

Fig. 25. Female H. agilis. The motion of rubbing Legs 3 and 4 is continued posteriorly to the abdomen. Body support has been partially shifted to the left side, as shown by the extended Leg 2.



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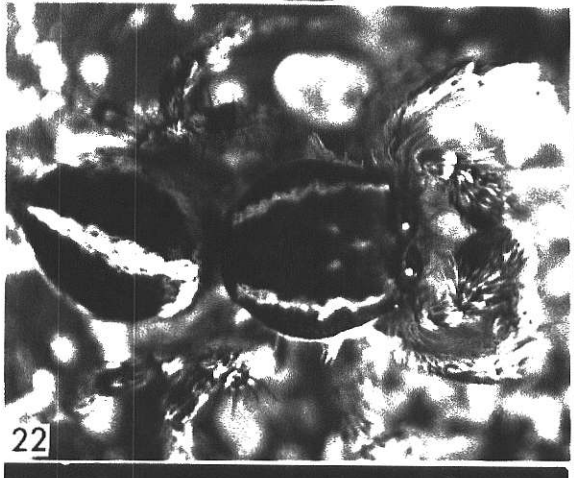

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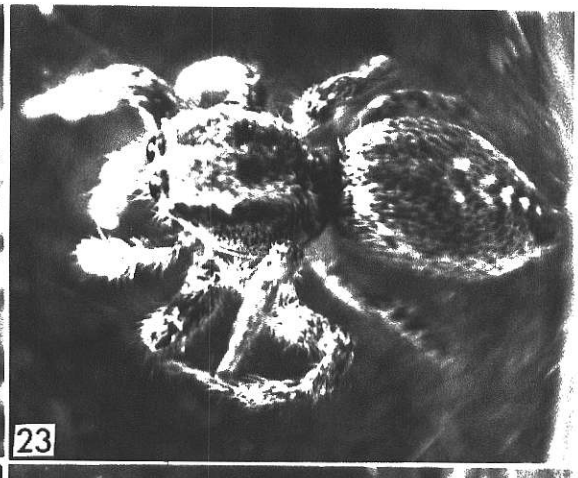

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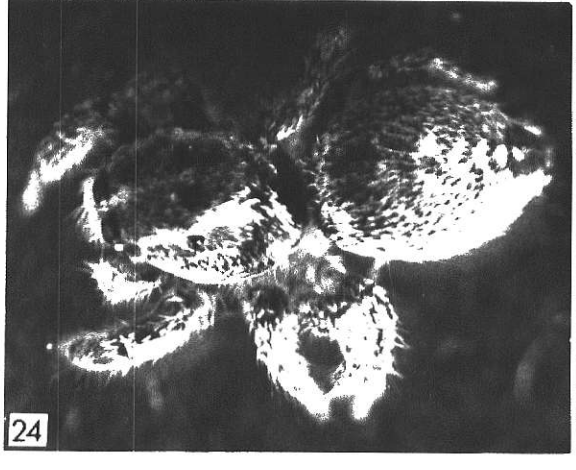

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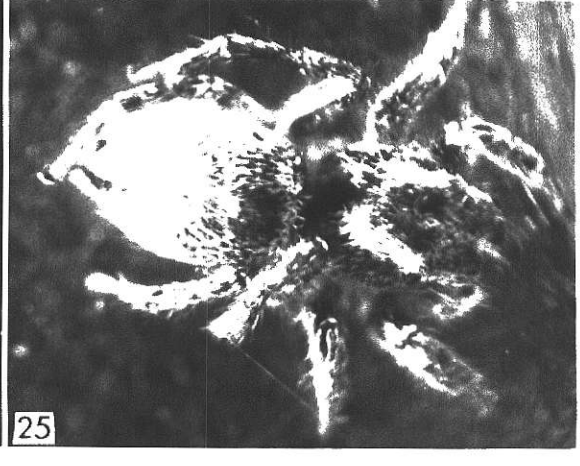

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Grooming

Grooming behavior in H. agilis is similar to that of other salticids in that certain basic motions are consistently repeated. Almost all of these movements involve the first legs and palpi and are confined to the anterior cephalothorax, posterior abdomen, mouthparts, and distal leg segments.

Several types of cephalothoracic grooming occur:

1. Eye and clypeal brushing. The tarsus of the palp bears a brush of stiff hairs on the prolateral surface. The right and left palps are raised above the AME and brought down alternately, brushing across the eyes and the clypeus. This motion is often repeated several times in succession, brushing always occurring on the downstroke.

2. Cheliceral brushing. Eye and clypeal brushing may extend downward to brush the chelicerae, but cheliceral brushing also occurs separately and repeatedly. The palpi are brought to the juncture of the clypeus and chelicerae and brought down across the chelicerae alternately.

3. Palpal grooming. The distal section of the palpal tarsus, especially the hairs thereon, are inserted into the mouth between the fangs and groomed by the maxillae.

4. Ocular quadrangle wiping. The first leg is brought up over the cephalothorax to the PLE then is brought forward across them and the PME to the AME. The motion is generally followed by eye brushing by the palp and is seldom repeated more than once.

Leg grooming can be divided into 2 types.

1. Pretarsal grooming. The pretarsi of Legs 1-4 are inserted, one at a time, into the mouth and lubricated with a secretion, presumably from the maxillary glands, as in palpal grooming. Legs 1 and 3 are most often groomed

(Fig. 22-23).

2. Leg rubbing and stretching. Leg 1 or 2 may begin the motion, stretching posteriorly and rubbing the distal segments against the following leg. The motion is continued to Leg 4 which in turn rubs the abdomen on its lateral edges. This series of movements occurs most frequently prior to molting or jumping (Fig. 24-25).

Any of the above grooming movements was performed separately, but they usually occurred in a series. For example, one of the more common series was: eye wiping and ocular quadrangle wiping followed by clypeal and cheliceral wiping and palpal grooming. Grooming was performed at all times during the daylight. While wandering about, a spider often stopped to perform one or more of the above procedures. Immediately after feeding, the mouthparts were frequently inserted into the mouth and groomed vigorously. Some spiders groomed while feeding, this being confined to eye wiping and leg rubbing. Toward evening, when inside cocoons, spiders spent as long as 20 minutes grooming.

In adult males, the palpal brush is replaced by the copulatory apparatus, yet they retain the motions of eye wiping, clypeal brushing and cheliceral brushing. These movements may serve to loosen any particles adhering to the numerous long hairs projecting around the eyes, or they may by similar to the behavior of a spider with a part of a leg missing. In the latter case, the remaining segments were bent forward to the mouth, and the mouthparts accomplished their usual manipulations, even though the distal segments were gone.

The Sand Cocoon

All salticids make cocoons of silk or of silk combined with substrate materials. The cocoons provide shelter when resting or molting and a place to

lay eggs and protect the brood. The sand cocoon made by Habronattus agilis is the most unusual behavioral characteristic of this species. It is a dome-shaped structure, varying in size with its use and builder, and it is always covered with sand. One, or occassionally 2, entrances are present.

Types

There are 4 types, separated primarily by their use.

1. Resting or overnight cocoon. This type was usually constructed daily by each spider at any time during the day, but most frequently after 3 PM. It was completed in less than 10 minutes, although considerable time may be spent seeking a proper site. In the field, they were often found under sticks and small stones or at the base of plants, all of which provided additional support to the structure as well as protection. Some spiders often occupied cocoons which had already been built rather than build a new one. The size of the cocoon varied with the size of the spider. Second instars constructed resting cocoons which measured 1.2-1.5 times their body length. Third instar and adult cocoons measured 2.0-2.5 times their body length. This type of cocoon usually had only one entrance.

2. Molting cocoon. One to 7 days prior to a molt, the immature spiders built cocoons similar to resting cocoons but with somewhat thicker layers of webbing and 2.2-2.5 times their body length. Inside, the spider occupied the central area until a few hours before molting when it moved to one side of the dome, all the while inverted under the dome. When molting occurred, the spider could stretch the body and legs and draw them free of the exuviae without being cramped for space. After being occupied for an average of 5.2 days, the cocoon was abandoned by the new instar. On a few occassions, the exuviae were removed from the cocoon by the spider and deposited on the outside, leaving the

spider even more room inside.

3. Hibernation cocoon. This was the thickest of all cocoons and had no entrances. During late October or November, the spiders find a suitable place in the sand, about one inch below the surface and weave a cocoon about themselves in which they spend the winter. In the spring, the spiders must make a hole in the cocoon's thick webbing in order to escape. Hibernation cocoons generally measured about the same size as the molt cocoons but had less room inside because of the thickness.

4. Egg cocoon. This type was made by gravid females about to lay eggs and sheltered the spider for 1-2 days before oviposition. Separating the eggs from the female was a sheet of webbing which the female clung to as she guarded them and the first instars. Sometime during the first instar stage, the female left the cocoon through the single opening. The average size of the egg cocoon was 5.8 mm high by 11.3 mm across the base.

Construction

Some cocoons were built above or below old cocoons, using them for extra support, and many were built adjacent to one another, particularly by early instars. When built below an old cocoon, the new cocoon generally lacked a complete dome, the base of the old being incorporated into the new, but often the 2 could be separated into 2 complete cocoons with dome and base. Also, some spiders often spent nights in old cocoons, adding their own layer of webbing to the dome and base. Generally, however, each spider nightly constructed a completely new cocoon away from any support. A proper site was selected by digging in the sand with the first legs and palpi, possibly to test the depth of the sand. After locating a potentially good site, the spider turned in a

small circle, pulling more sand into the center with the first legs and laying a number of strands of webbing. Eventually, all these strands formed a flat sheet of sand shaped like a circle about 6 mm across. Standing on this, the spider grasped one edge with its first legs and, turning upside down, as in a somersault, pulled the sheet over itself (Fig. 26-27). When the sand was deep enough, these steps were omitted, and the spider merely burrowed its cephalothorax into the sand, turned upside down, and weaved the sand grains into a sheet over itself (Fig. 28). With side to side swings of the abdomen, in the approximate shape of a figure-8, webbing was attached to several sand grains outside the edge of the sheet and these sand grains were transferred by the spinnerets to the sheet, gradually increasing its size (Fig. 29). When the sheet completely covered the spider, it was attached to the substrate or other grains of sand and pushed into shape by thrusts of the cephalothorax and first legs until the dome was able to support itself (Fig. 30). The spider rested for 1-2 minutes upside down then turned and wove the floor of the cocoon, occassionally adding reinforcing strands to the dome.

The result was a dome with a floor (Fig. 31), both coated on the outside with sand and on the inside with webbing, and seamed together where they met. These halves could easily be separated at this seam where one or 2,3-4 mm wide holes were left for entrances. The dome was capable of supporting a spider clinging to its inside surface, but removal of only a few grains of sand would result in its collapse.

Other Sand Structures

Exceptions to the daily cocoon construction were common. For reasons unknown, some spiders never built a sand cocoon, but made only a simple webbed structure above the ground. These flat sheets of sand measured from 6-20 mm

Fig. 26. Female Habronattus agilis has woven a sheet of sand grains and has turned upside down onto her back to pull the sheet over herself. Note the draglines from the anterior spinnerets supporting this maneuver.

Fig. 27. Female H. agilis somersaulting over to pull the sheet of sand grains over herself. She has left no draglines.

Fig. 28. Female H. agilis has turned over on her back without weaving a sheet of sand grains and is weaving a cocoon over herself. Such structures are normally built under a supporting object such as a twig or leaf.

Fig. 29. Close-up of spinnerets picking up a cluster of sand grains which have been stuck together with silk. Such clusters are added to the sheet of sand to form the dome of the cocoon.

Fig. 30. A nearly completed dome with the spider still visible beneath.

Fig. 31. Ventral view of 2 immature spiders inside adjacent completed cocoons. When sand is deeper, a bottom is also woven and attached to the dome at its periphery.

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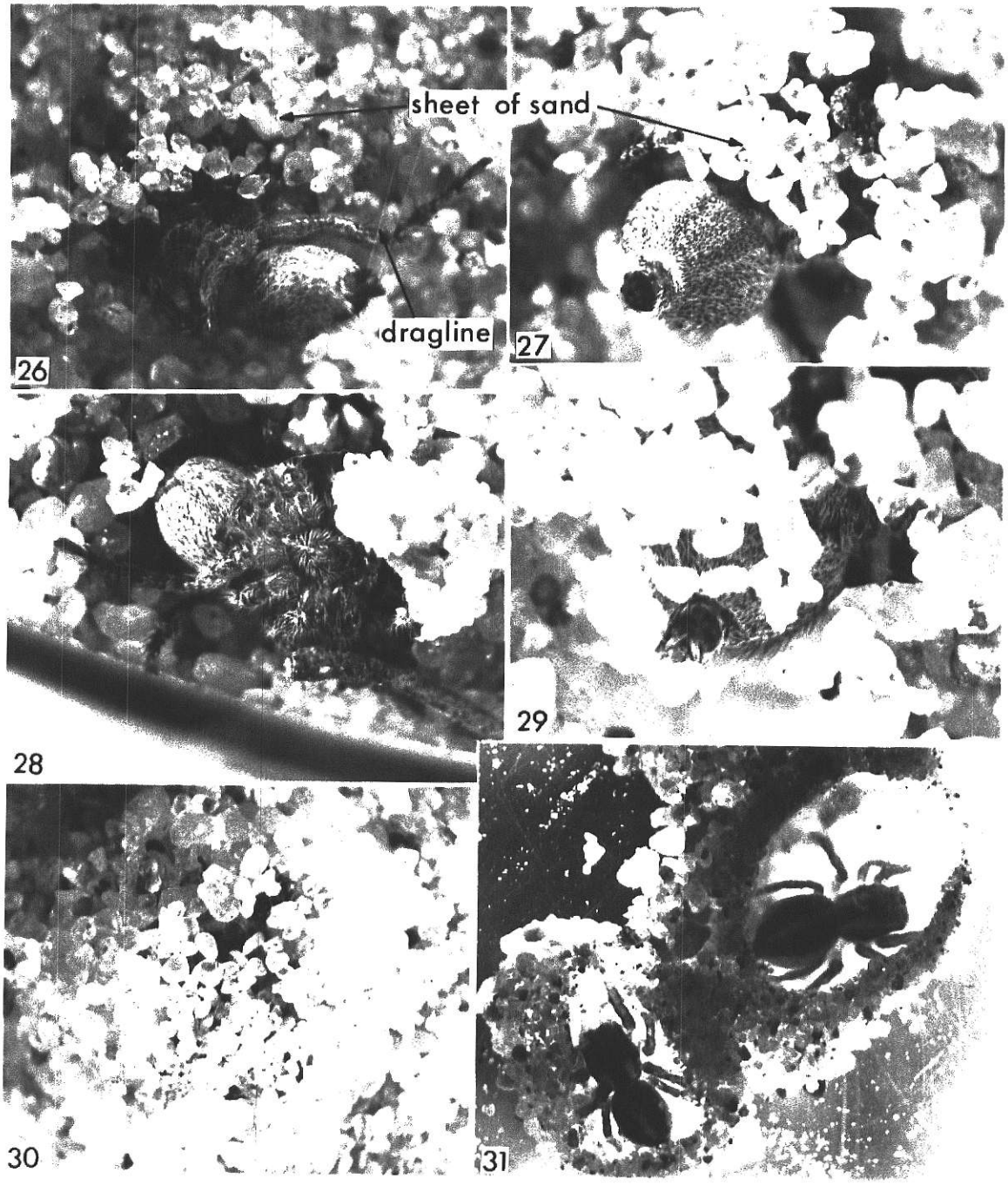
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across, the largest often built by third and fourth instars, and were especially typical of old spiders (second year adults) who built several in one day. The spiders did not rest on top of these at night, preferring a spot on the ceiling of their containers. Perhaps with age they lose the ability to complete the structure. The cycle was begun several times but was never completed beyond the sheet of sand.

A few spiders never incorporated sand into their cocoons but built cocoons in an upper corner of their container, much like most other salticids. The offspring of these spiders were able to construct perfectly normal cocoons, although some would alternate between the 2 types. Two individuals of another species of Habronattus, however, which does not normally construct sand cocoons did incorporate sand into their cocoons when the cocoons had shifted to the sandy bottom of their containers. One of those spiders made a normal cocoon without sand the following night.

Still other spiders sought out old cocoons, spending considerable time testing the sand surface with the first legs and palpi. Actually, the method of locating a cocoon site, mentioned earlier, may have been an attempt to locate an old cocoon, and if one was not found within a certain period of time, a new cocoon was built. However, spiders left in a small container with a previously built cocoon almost always built a new one. In fact some individuals were more prone to the use of an old cocoon than others.

When an old cocoon was located, the spider climbed on top of it and tapped lightly with palpi and tarsi, located the entrance, hesitated there, then turned upside down and entered, pulling the body in by the first legs. If already occupied, the resident spider struck at the intruder with the first legs and remained facing the direction of the disturbance. If further

attempts were made to enter, the resident held down the edges with the first legs. Only extreme disturbances caused the spider to leave its cocoon in a series of long leaps.

Hibernation

Habronattus agilis began hibernation in Kansas in late October as (1) a second year adult maturing the previous spring, (2) a first year adult maturing that fall, or (3) an immature, usually fourth to sixth instar.

The search for hibernating individuals began in early February, to determine the location, depth, and type of hibernation site. It was assumed that they would be no more than 10 cm below the surface, possibly near the roots of plants. On February 28, the first site was found by raking through the top layer of sand. Two centimeters below the surface was a small, sandy, hard-sided pit about 6 cm deep and 15 cm in diameter at the top, covered by dead willow leaves and other loose organic matter mixed with sand. The sandy contents were quite dry, much drier than the frozen sand surrounding it. The pit appeared to have been made by a horse's hoof, and its location amidst a rather dense stand of willow sprouts may have protected it sufficiently from the snow, wind, and frost so that it remained drier than numerous similarly-shaped pockets in the same area that were quite frozen, hard-packed, and lacking in spiders.

The hibernation pit contained 7 cocoons of H. agilis: 3 hibernation cocoons containing adults (2 males, one female), one egg cocoon with first instar exuviae, one cocoon containing exuviae from a male, and 2 empty cocoons, probably used for resting. In addition, there were 3 adult Coleoptera of the families Carabidae and Tenebrionidae, one tenebrionid larva, and several acridid eggs. All were alive. The presence of a molt cocoon and an egg cocoon

indicated that the pit had been used during the preceding summer. It is unlikely that the resting cocoons and these others had been blown into the pit by the wind and remained as intact as they were. It is more likely that such sites are sought by the spiders and used thoughout the year for various purposes because of the protection they offer.

On March 28, a second pit was found, containing one hibernating male and 3 empty resting cocoons. The conditions inside the pit were nearly identical to those of the first pit and the surrounding area was nearly the same.

Four to 5 days after the 4 hibernating adults were brought into the laboratory, they left the cocoons for short periods of time. They did not accept the food and water put into their containers. One male and one female died shortly after, their abdomens greatly shrunken. The remaining 2 spiders accepted food about one week after they had emerged, and in late April, successfully courted and mated.

Social Behavior

Salticids are basically solitary, reacting aggressively toward one another except during courtship. Most spiders will eat any arthropod they can catch within a preferred size range up to slightly larger than themselves. Therefore, each instar is subject to predation by spiders of comparable size or larger, including its siblings. Certain behavior of H. agilis toward one another suggests minimal aggression amd maximal tolerance compared with the behavior of other salticids.

All instars were observed under both natural and laboratory conditions in groups of 2 or more. In the field, 2 or more individuals of any combination of sex, may occupy the same leaf, plant, or stem within a few centimeters of one another, aware of each other, but with no signs of aggression whatever.

Considering the capacities of their vision, and the amount of activity they normally display, the spiders must be able to see one another. In such cases involving 2 or more spiders in close proximity, the spiders normally react by walking away or remaining in the same position but facing another direction, always after noticeably scanning each other.

Males can often be found in groups of 2 or more in low vegetation. In one case, 2 adult males were observed on the upper surfaces of poison ivy leaves, approximately 10 cm apart. The movements of one within the peripheral vision of the other caused the latter to turn until the 2 were facing one another. The reaction of other species of salticids in such cases was to withdraw slightly, with first legs extended outward, palps beating the ground rapidly. The remaining legs appeared tense as the body was lowered in preparation for either attack or rapid retreat. These male H. agilis, however, continued the normal leg and palpal waving which is characteristic of their movement, and within 5 seconds had turned to view another direction. This pattern was repeated several times, the spiders reacting to each sudden motion by turning to view it. They are apparently able to recognize members of their own species by characteristic movements of legs and palpi. One other species of Habronattus, in which the female and her movements are very much like those of agilis, was treated in a similar manner.

Laboratory observations gave comparable results. Nine pairs of H. agilis were kept together for the remaining life span of the spiders, and none was ever killed. Sometimes, from as far as 10 cm, a spider would jump on or toward another spider. The assaulted spider seldom did more than turn to face its attacker before slowly walking away. In all cases, the attacker immediately jumped away from the other spider, and no fighting was observed.

The only times a male retreated from a female was when she was not receptive to courtship. In such cases, the male quickly withdrew as the female moved toward him aggressively, pursued him a short distance, but never captured or killed him.

Courtship and Copulation

H. agilis courted and mated during late April and early May, the only times when the females were receptive to the males. Previous to this time, the females were aggressive and did not tolerate mating attempts in the laboratory, yet after they were fertilized, they reacted almost indifferently, coexisting peacefully with the males.

The value of salticid courtship displays has long been argued, but most investigators agree that vision is the primary recognition factor (Kaston 1936, Crane 1949), with chemoreception and physical contact acting as possible reinforcing stimuli. Whatever factors are involved, the probability of a male courting a female successfully depends on whether she is in a proper physiological condition for mating. A male may begin to court a female he comes across, but her reactions determine how long he continues his efforts (Crane 1949). One such case was observed shortly after all other fertilized females had begun laying eggs. A virgin female was looking out the entrance of her cocoon when a male was added to her container. In his wanderings he passed very near her cocoon several times and each approach caused her to jump halfway out and strike at him with her first legs. Then she quickly withdrew inside and continued to watch him. After several preliminary attempts to build a cocoon, he tried to enter her cocoon. She immediately jumped out and faced him, 2 cm distant. He responded by stretching his first legs out to the side at a 45°

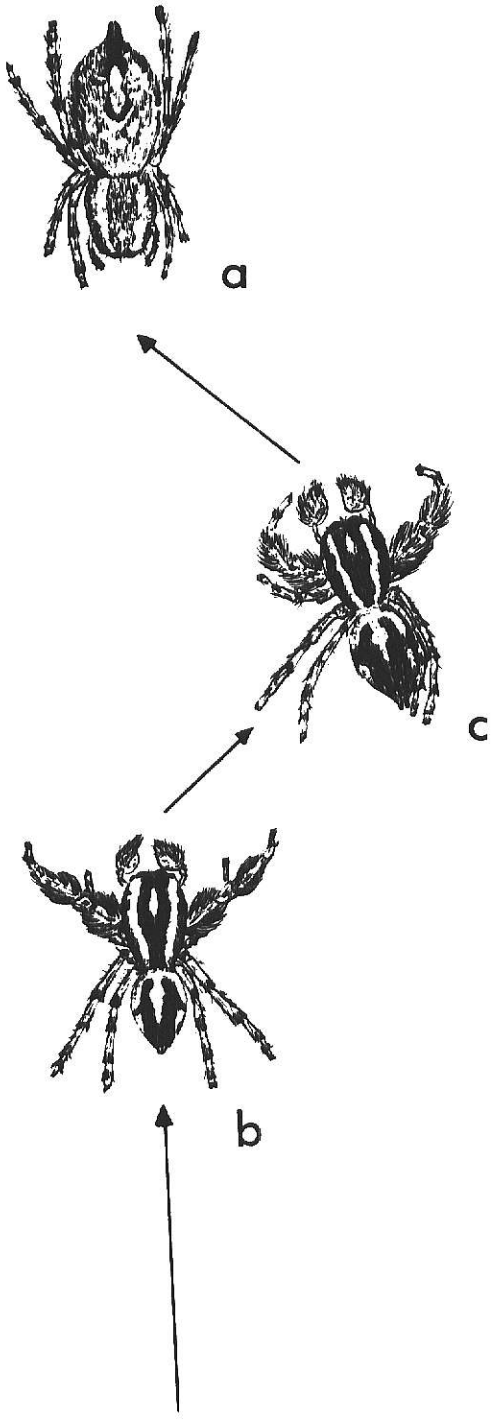
angle above the ground, vibrating them rapidly up and down. She then chased him for 30 seconds before catching and eating a fruit fly. In this case, neither spider was in a proper physiological condition, compounded by the fact that the female was hungry and past the normal mating time. That female lived for 3 months without mating with 3 different males.

More commonly, a nonreceptive female indicated her condition by elevating her carapace and waving her first legs up and down and beating her palpi on the substrate in response to the leg vibrations of the male. The male would then depart and the female would resume her former activities.

When male and female met in the proper physiological state, successful mating occurred. A male was added to the container of a female, and in usual fashion he turned in a slow circle and viewed the surroundings. She was 3 cm away and not moving. The male backed up one centimeter, first legs vibrating up and down, whereupon she crouched low to the substrate. He proceeded forward in a zigzag manner, holding the first legs at a 45^{o} outward angle, but jerking them in and out like tongs, 3-4 times per second, and beating his palpi on the substrate. His abdomen was depressed and rapidly vibrated up and down as frequently as the legs were jerked in and out (Fig. 32). After 2 approaches in this manner, he was able to mount her and copulate. After 1 min, 15 sec, she broke loose and walked slowly away, leaving the male to groom his eyes, clypeus, chelicerae, and palpi while he watched her movements. Each further courtship attempt by the same male resulted in her running off. After 8 tries he reacted only with the up and down leg vibrations.

The same male was introduced several days later to a second female who at the time was eating a fruit fly. He began to court immediately at a distance of one centimeter, but after 5 seconds ran off to a distance of 4 cm, turned

Fig. 32. Courtship of Habronattus agilis. The female (a), if receptive, remains motionless except for turning to watch the male (b) who rapidly vibrates his first legs up and down while standing in one spot. If she remains motionless, he proceeds toward her, zigzagging back and forth (c) 2 or 3 times, whereupon he immediately mounts her and copulates.



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to face her and vibrated his legs and palpi in a vertical plane at a 45° angle, approaching her directly. The female struck at him with her first legs, whereupon he withdrew one centimeter and repeated the vibrations. She struck at him again. After 4 such refusals, he approached her with the zigzag tong jerking movement and was able to immediately mount her and copulate for 5 min, 25 sec. Every 10-15 seconds during copulation, the male, supported on the ceiling of the container by his first 2 pairs of legs, stretched his fourth legs out to the side at right angles to his body and jerked them and his abdomen up and down, once per second. The female broke away suddenly, leaving the male to groom his palpi, eyes, and clypeus as he watched her. After courting once more without success, he groomed all parts of his body for a full 18 minutes, turning in slow circles in normal fashion. She stood 4 cm away and consumed the same fruit fly she had held throughout copulation. Each time she faced him, he vibrated his first legs, resuming his grooming when she turned away. He courted her 6 times more without success, but her reactions were of retreat, not aggression. In fact, she finally fled to the other side of the container.

The success of courtship and copulation depended greatly on the condition of the 2 spiders involved. A male who actively courted one day fled instantly at the sight of a female the following day. The males appeared to be able to tell rather quickly whether or not a female was receptive by her body attitude and movements and tested her with the leg vibrations. A female with body elevated, waving her legs and palpi, evidently was not receptive. On the other hand, if she crouched and remained still, the male continued his courtship, approaching with the leg and abdominal jerking motion. It is strange that the female will pursue a male only when she is nonreceptive during the mating season.

Brood Care

Fertilized females constructed egg cocoons as early as 3 days following copulation. As described in the section on cocooning, the egg cocoon resembles the resting cocoon except for its larger size and thicker weave. With posterior and median spinnerets, the female lined the inside of the dome with figure-8 motions of the abdomen. When complete, she wove a disk 3-4 mm across against the inner surface of the dome. On this she laid 3-25 eggs in less than 30 seconds and then wove a spongy covering over them. All this was covered by another sheet of silk which enclosed the eggs between the dome and itself. The loose webbing between supplied the spiderlings with support.

Due to the normal thickness of the egg cocoon, it was difficult to view the development of the embryos and the behavior of the female. However, when there was only a thin layer of sand, the females built the dome and left the floor open. All observations were made with a 90°prism so that the containers did not have to be inverted and the females were not disturbed.

The female spent most of the time clinging to the outer silk covering below the eggs, or with at least part of her body under them. From time to time she checked the dome and made repairs or added silk. She did not leave the cocoon for food and did not groom. If the cocoon was disturbed she struck at the object with her first legs and fangs, leaving only if the cocoon was torn open or roughly shaken. If the embryos were uncovered, she first covered them with her body, pulling the remaining threads up around them with her tarsi. Then she wove a new covering. All the while she tapped on the embryos with her palpi and tarsi. Damaged eggs were not removed from the cocoon.

When the deutovum stage was passed and the first instars began moving about inside the egg chamber, the female frequently pushed her palpi, tarsi,

and cephalothorax into the webbing, causing the spiderlings to move through the webbing. Some time after this, often immediately after, the female left the cocoon. There were exceptions, however, as one female consistently left her eggs the day after she had laid them. They developed normally. Once she left her cocoon, the female did not return, although she sometimes built a resting cocoon adjacent to it. A new cocoon was built for each brood.

Behavioral Development of the Spiderlings

First instars are capable of only limited movement, the chelicerae move slightly, and tarsi have no scopulae. The retinae of the AME move but do not appear to respond to changes in light intensity. As the spiderlings neared the end of this stadium, their movements became more deliberate and coordinated, and they turned away from disturbances in the webbing of the egg chamber. There was a distinct tendency to move towards the periphery where they eventually molted to the second instar.

Scopulae are present and chelicerae functional in the second instars. The chelicerae were frequently used to bite into the webbing of the egg chamber. Movements became rapid and grooming was often observed, The AME responded to movement of my hand at a maximum of 30 cm. After 2-3 days, when hardening and pigmentation were complete, the first spider made a hole in the egg chamber wall and entered the outer chamber where the female had rested, remaining there usually no more than 24 hours. Over a period of 1-6 days, the spiderlings left the cocoon one by one through the same hole made by the first spider.

Emerged second instars were as well coordinated as later instars. They were able to construct sand cocoons immediately and usually spent the first

2-3 days in them. Upon first contact with the sand, the young spider walked about on it briefly, tapping with tarsi and palpi. Finally, it began turning in a slow circle and wove a flat sheet of sand and completed the cocoon in 3-5 minutes. First cocoons were 1.5-3.5 mm in diameter with one entrance. Often, several spiders built adjacent cocoons.

Collembola were eaten 2-3 days after the spider emerged from the egg cocoon. The spider at first watched them intently, then fixated on one and ran up to within a few millimeters before pouncing. If several Collembola were present, the spider became easily confused and distracted. Following a catch, the spider turned rapidly in all directions, cephalothorax elevated, then climbed to a spot where it faced downward. When groups of spiders were together, they watched each other pursuing and capturing prey. Small spiders often ceased chasing prey when a larger spider pursued the same prey.

Third instars refused Collembola, unless they were very hungry and alone in their containers, But accepted Drosophila readily. All later instars were fed on Drosophila, and adults would eat house flies, even though the flies were larger than the spiders. So long as suitable prey was available, they continued to coexist peacefully, responsive to one another yet nonaggressive.

Time Budget Studies

Time budget studies were conducted to determine the amount of time spent daily by Habronattus agilis in each major activity, whether cycles or sequences in activities occurred, and differences between ages and sexes. Each spider was observed alone for several 30-minute periods, and the duration of each activity was recorded to the second. These times have been summarized in minutes and per cents of time in Table 4. The immature group consisted of all

instars mixed, since there were no obvious differences in the behavior of these groups.

The various behavior categories are listed and described below:

Grooming- any movement wherein the spider rubbed one or more legs or palpi against another part of the body and including the movements of the mouthparts to produce fluids used in grooming.

Locomotion- any form of walking, jumping, or turning in which the position of the spider was altered.

Feeding- the time during which the spider ingested the partially digested prey, identified by rapid pulsations of the abdomen, followed by discard of the empty prey carapace.

Prey Scanning- the time during which a potential prey insect crossed the visual range of the spider followed by fixation of the AME retinae, identified by rapid turning of the spider to face the prey and continued until movement toward or away from the prey occurred. Did not include scanning of objects used for observation (microscope, pencils, etc.).

Prey Pursuit- time when the spider moved toward the prey.

Prey Capture and Hold- the time between capture of the prey and commencement of feeding, when immatures moved to a higher place to feed undisturbed and adults turned in all directions, probably to sight any potential disturbance.

Rest- the times when the spider showed no movement or visual responsiveness.

Cocooning- the time when the spider was constructing a sand cocoon.

Locomotion

H. agilis spiders were almost constantly walking or jumping. Even while

grooming, feeding, or resting, they usually changed position or direction several times, scanning each direction for a few seconds. Grooming, locomotion, and scanning most frequently occurred as the spider wandered about, alternating with this activity. In the laboratory, there were no diurnal cycles of activity, each spider varying from day to day in the amount of activity displayed. Individuals spent up to about half of each day wandering. Some spiders remained inside their cocoons during daylight hours, but none of these was included in the time budget studies. This was most typically observed on rainy or very cloudy days or of old spiders or spiders about to molt or lay eggs. Table 4 gives the per cents of locomotion for each group. Males averaged 52%, females 54%, and immatures 26%. Immatures had a greater tendency to remain in one spot longer, resting during the day. At night, when the spiders were in their cocoons, locomotion was observed as turning, when the spider changed position or direction inside the cocoon. This activity represented only 1% of each group's night activities, occurring most frequently either just after completion of the cocoon or just before emergence from the cocoon.

Grooming

Grooming usually alternated with walking and lasted for about 3 seconds. Concentrated grooming, however, almost always occurred immediately after completion of feeding. This was particularly true of the females which did 46% of their grooming after feeding, but they spent the lowest (11%) total time grooming. Immatures spent 22% of the time grooming, 46% after feeding, and males spent 14% of the time grooming, only 25% occurring after feeding. The remainder of grooming occurred alternately with locomotion, hence males spent more time grooming this way than did females and immatures.

Grooming occurred within the cocoons in the evening, soon after completion of the cocoon. Males spent 4% of the night time hours grooming, females and immatures 3% each.

Prey Scanning, Prey Pursuit, and Prey Capture

Although considerable time was spent in search of prey, the actual process of securing prey required very little of a spider's time. When prey was sighted, the spider fixated on it for an average of 30 seconds, apparently scanning the prey for identity and distance. Scanning time for males averaged 22 sec, females 24 sec, and immatures 43 sec. Thus, immatures reacted much less quickly to prey than adults. It appears that the immatures are less able to recognize prey.

Prey pursuit required less time. Males spent an average of 5 sec, females 23 sec, and immatures 8 sec pursuing prey. Males, moreover, had greater success in securing prey (80%) than females (60%) or third and later instars (25%). Most females caught prey in about 5 sec. However, some females were either slower or more persistent, or more capable of pursuing the same prey for a longer period of time. Immatures required a greater number of attempts to secure prey, possibly requiring a certain amount of experience with various types of prey before they could successfully capture them in one or 2 attempts. Furthermore, they were more easily distracted by a second prey, turning to pursue it instead of following the first prey. Adults were seldom so distracted.

When prey was secured, it was held for a short period of time before feeding began, probably allowing the poison to take effect. Males held prey an average of 20 sec, females 34 sec, and immatures 48 sec. Immatures sought a

high point before starting to feed while adults remained where they had caught the prey.

Feeding

Feeding occurred with equal regularity at all times during the daytime hours. Males spent about the same time feeding (22%) as females (25%) or immatures (27%). However, other observations outside the time budget studies indicated that males and second or third instars consumed half the number of *Drosophila* that females and larger instars consumed.

Resting

A spider often stopped, almost always on the ceiling of its container, pulled its legs close to the body, and remained motionless usually less than 5 minutes, but occassionally up to several hours. Immatures rested this way for longer periods of time (18%) than males or females (4%), and more often (up to 8 times per day) than males or females (2-3 times per day). Time of occurrence of these rest periods varied from spider to spider and from day to day.

Most resting occurred at night inside cocoons. Males spent 95% of their total night hours resting, females and immatures 96%. Small movements occurred rarely during these rests in the form of turns and leg stretching.

Cocoon Formation

Each spider built a cocoon sometime during most days, although occassionally they remained resting throughout the night without a cocoon on the ceiling of the container. Females and immatures spent only 2% of their daytime

Table 4. Total minutes of observation and per cent time for each activity for males, females and immatures[a] of Habronattus agilis.

	Males				Females				Immatures			
	Day		Night[b]		Day		Night		Day		Night	
	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
Locomotion	94	52	10	1	307	54	10	1	176	26	9	1
Grooming	26	14	39	4	62	11	31	3	144	22	30	3
Scanning	4	2			10	2			22	3		
Prey Pursuit	1	1			4	1			3	1		
Prey Capture	4	2			4	1			4	1		
Feeding	40	22			150	25			184	27		
Resting	7	4	456	95	23	4	430	96	123	18	431	96
Cocooning	6	3			10	2			16	2		
Total	182	100	505	100	570	100	471	100	692	100	470	100

[a] Third and later instars

[b] Includes all hours between completion of the resting cocoon and emergence from the cocoon the following day.

hours building a cocoon, while males spent 3%.

SUMMARY

The jumping spider Habronattus agilis (Salticidae) was collected from 2 isolated sandy areas near Manhattan, Kansas and observed in the laboratory from May 1970 to July 1971. The spiders were kept in small plastic boxes. All instars ate Drosophila or Musca except the second instars which ate Collembola and the first instars which did not feed.

Eggs were laid from June 1 to September 9, with a mean interval of 27.6 days between egg masses. Ten females laid 29 egg masses, from 1-4 masses per female, and a mean of 11.3 eggs per mass. The eggs were 0.8-1.0 mm in diameter. Observable development of the embryos began around the ninth day. From Day 9 to Day 12, the palpi and legs developed and the egg membranes gradually lifted away from the body. From Day 11 to Day 13 was the deutovum stage, when retinal pigmentation, chelicerae, and spinnerets began development. Day 14 was the beginning of the first instar, when the spiderlings were able to move around and abdominal coloration began. The parent female left the spiderlings from one to several days later. On Day 25, molting occurred, and on Day 26, the second instars left the egg cocoon.

Instars 1, 3, 4, and 5 were about half (14-20 days) the duration of 2, 6, and 7 (31-42 days). Per cent linear growth rate decreased with each succeeding instar. Both are apparently independent of food prey size in the earlier instars, larger numbers of smaller prey being eaten in place of a few larger prey.

H. agilis is especially dependent on vision, which is highly developed comparable to that of other salticids. Habronattus agilis can leap 8-10 cm

in almost any direction with a high degree of accuracy, with or without prey. The main force of the jump is provided by the third legs which are the longest. Loss of a third leg was compensated for by the remaining legs.

H. agilis was able to capture house flies much larger than itself, but Drosophila were more easily caught without damage to the spider. Adults ate 2-4 Drosophila daily and consumed prey in about half the time (14 min) required by immatures (34 min). Feeding was aided by the first 2 pairs of legs which rotated and held the prey in the mouth. While consuming one fly, some spiders were able to fixate on and eventually capture another.

Grooming was typical of most salticids and was accomplished by the legs and palpi. Types of grooming included: eye and clypeal wiping, cheliceral brushing, palpal grooming, ocular quadrangle wiping, pretarsal grooming, and leg rubbing and stretching. Any of these could be performed alone or in a series, and at all times during the day.

The most unusual behavior of H. agilis was the construction of sand cocoons for resting, molting, hibernating, and brood care. Sand cocoons were built by most spiders every night, but some either did not build one at all, or built one or more other structures of sand. First, the spider wove a flat sheet of webbing over the sand, attaching a number of grains together. The spider then turned upside down under this and lying on its back, added grains of sand to the edges of the sheet. The resultant dome was able to support the spider clinging to the inner layer of silk. Such sand cocoons provided protection and camouflage for resting spiders. The spiders often occupied previously built cocoons.

H. agilis overwinters in dry depressions in the ground as first or second year adults or as immatures (instar 4-6). Two such depressions contained egg

cocoons, resting cocoons, and molt cocoons, indicating that the depressions had been used the preceding summer.

In groups of several individuals of all combinations of age and sex, the spiders were nonaggressive, except when prey was scarce and instars attacked and ate smaller instars.

Courtship occurred only during late April and early May. Before this, the virgin females were nonreceptive and aggressive, but after mating the females were completely tolerant of the males and immatures. When both males and females met in the proper physiological condition, the male first tested her with up and down vibrations of his outstretched first legs. If she crouched low and remained still, he approached her, zigzagging back and forth, jerking his first legs in and out, while his abdomen jerked up and down with the same rapidity.

Females remained with the embryos within the egg cocoons until the first instar stage. While inside, she was constantly clinging beneath the eggs, protecting them and mending the inside of the cocoon. First instars were capable of limited movements, did not feed, had no scopulae, and did not respond to visual stimuli. As soon as the second instars emerged from the egg cocoon, they were able to build sand cocoons, and after 2-3 days, were able to catch and eat Collembola.

A time budget study revealed no distinct periodicity in behavior within daylight hours. During the day, males and females spent about half, and immatures about one fourth of their time wandering. Very little movement occurred in the cocoons in the evening. Grooming alternated with wandering, but also occurred after feeding. About half of the grooming occurred after feeding in females and immatures, one fourth in males. All ages spent an average of 5-10 sec pursuing prey. Males were most successful in securing prey, however, with

80% success. Females were 60% successful, immatures 25%. Immatures responded less quickly to one prey and were more easily distracted by another arthropod. All spent about one fourth of the time feeding, but males and early instars (2-3) consumed half the number of Drosophila as females and later instars. About 95% of all resting occurred during the evening inside the resting cocoons. Immatures spent about 20% of the daylight hours resting outside of cocoons, while adults spent 4% (males) and 8% (females). Cocoon construction required 2-3% of daylight hours in all ages.

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BIOLOGY AND BEHAVIOR OF A JUMPING SPIDER, *HABRONATTUS AGILIS*

by

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Habronattus agilis (Salticidae) from 2 areas of Kansas was studied for 15 months and was found to have certain behavioral patterns unique for salticids.

Ten females laid from 1-4 egg masses per year with an average of 11.3 eggs per mass. Development of the spiders was described from Day 9 to emergence of the second instars on Day 26. Females remained within cocoons with their broods until they were first instars. Duration of instars 1, 3, 4, and 5 were half as long as 2, 6, and 7. Mean growth for each instar was about 0.5 mm, but per cent increase in length decreased with each instar.

H. agilis has highly developed vision and is apparently able to distinguish between prey, enemies, members of its own species, and indifferent objects. Its movements are rapid and well coordinated, allowing the spider to jump in almost any direction from any position.

Adults were observed capturing and eating house flies larger than themselves, but Drosophila were more readily accepted by all instars from 3-7. Females, while feeding on one prey, were able to fixate on a second prey and to pursue and capture it when the first prey was discarded.

The most unusual behavioral characteristic of H. agilis is the construction of sand cocoons for resting, molting, hibernating, and brood care. The spider first tacks webbing over the sand, producing a nearly circular sheet of sand. Then, standing on this, the spider turns upside down to a position underneath the sheet, and lying on its back adds sand grains to the edges until it forms a dome over itself. Later, a floor is added. The resultant dome is lined on the inside with silk and covered on the outside with sand.

H. agilis hibernates from late October to April as a first or second year adult or as a fifth or sixth instar. Hibernation occurs in small sandy bowl-shaped pits, found to contain molting, resting, and egg cocoons from the

previous summer, as well as other hibernating arthropods.

Groups of individuals, especially adults, were nonaggressive toward one another. Exceptions were nonreceptive females during the mating season, and starved younger instars who preyed on smaller individuals.

Courtship occurred in late April and early May. The males tested the females by vibrating the first legs rapidly up and down while holding them nearly straight out to the side. If the female crouched and did not move, the male proceeded toward her, zigzagging back and forth, jerking his first legs in and out and his abdomen up and down, both with the same rapidity. This was immediately followed by a short copulation.

Males and females spent about twice as much time wandering, grooming, and scanning prey during the daytime as immatures. Males were more successful in capturing prey (80%) than females (60%) or immatures (25%). Immatures were easily distracted from one prey by another. They also took twice as long to consume a prey as males and females. About 95% of all resting occurred inside cocoons at night. Immatures spent 18% of the daytime resting, doing so about twice as often as did males and females, and for longer periods of time.