KARL V. KROMBEIN

Behavioral and Life-History Notes on Three Floridian Solitary Wasps (Hymenoptera: Sphecidae)

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • 1970 NUMBER 46

AUTHENTICATED
U.S. GOVERNMENT
INFORMATION
GPO

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge not strictly professional." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. Each publication is distributed by mailing lists to libraries, laboratories, institutes, and interested specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 46

Karl V. Krombein

Behavioral and Life-History Notes on Three Floridian Solitary Wasps (Hymenoptera: Sphecidae)

SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON
1970

ABSTRACT

Krombein, Karl V. Behavioral and Life-History Notes on Three Floridian Solitary Wasps (Hymenoptera: Sphecidae). *Smithsonian Contributions to Zoology*, 46: 1–26, 1970.—A new trap to attract solitary twig-nesting wasps and bees was developed and tested in Florida. It permits observation and photography of the nesting behavior during nest construction and, subsequently, of the development of the progeny. Observations and photographs were made of the nesting behavior and subsequent development of three sphecid wasps, *Isodontia* (*Murrayella*) *auripes* (Fernald), *Podium rufipes* (Fabricius), and *Trypargilum collinum collinum* (Smith).

Official publication date is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON : 1970

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 - Price 40 cents (paper cover)

Karl V. Krombein

Behavioral and Life-History Notes on Three Floridian Solitary Wasps (Hymenoptera:Sphecidae)

The need to perform field tests on a new type of trap designed to attract solitary wood-nesting wasps and bees provided the incentive for a period of study at the Archbold Biological Station, Lake Placid, Florida, 7–26 April 1969. Normally during this season in south-central Florida there is an abundance of many species of both wood- and ground-nesting wasps and bees. However, populations were abnormally low during my stay, perhaps because the unusually cool wet winter of 1968–69 resulted either in delayed emergence or higher mortality of the overwintering insects. Nevertheless, there was a sufficient number of nesting individuals to determine that the new traps were acceptable as nesting sites to some species, and that they permitted photography of nesting behavior not possible with the kind of trap used in my earlier study (Krombein, 1967).

The traps I used earlier consisted of a hole drilled in a stick of straight-grained white pine. Borings of four different diameters were used: 3.2, 4.8, 6.4, and 12.7 mm. These traps were reasonably satisfactory in my earlier work because I was unable to spend time in the field observing nesting behavior. The prospect that I would be able to make such studies in the near future, however, led me to devise an improved trap to facilitate field observations.

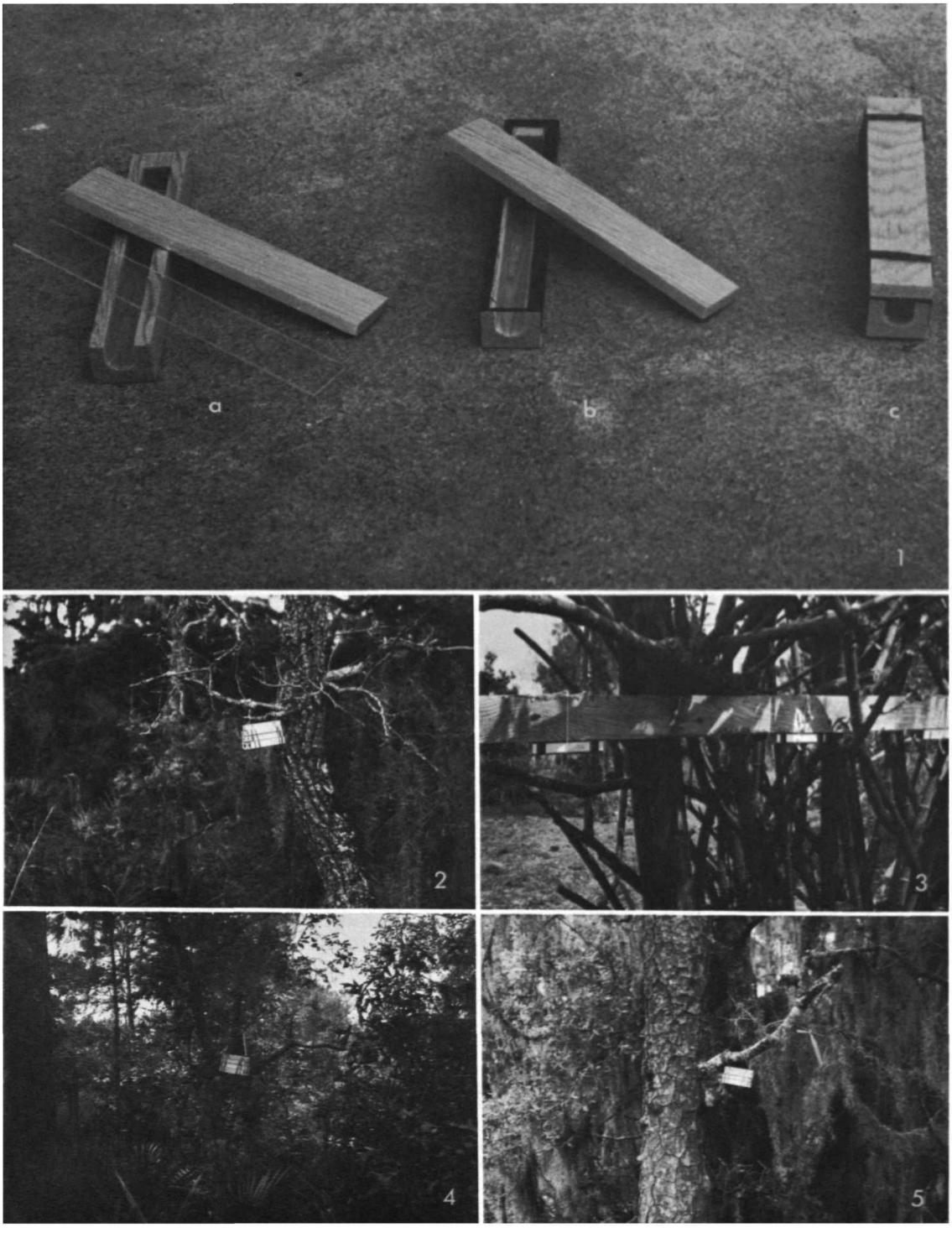
For this pilot study I used cavities of 4.8, 6.4, and 12.7 mm in diameter. The cavities were made by routing out a round-bottomed channel of one of those diameters in a long piece of straight-grained white pine. The channels were routed to the same depth as the channel diameter. The pieces were then cut into 150-mm lengths and one end of the channel plugged with a short piece of wood. The 4.8- and 6.4-mm channels were made in pieces of wood 20 mm wide and the 12.7-mm channels in pieces 25 mm wide. A piece of clear Plexiglas ® $1/16''$ thick and cut to the same size as the strip of wood was then taped against the channel. Finally, a plain strip of wood 6 mm thick and the same length and width as the trap was fastened against the plastic with rubber bands so that the whole assembly presented a light-tight simulated boring. The trap components and their assembly are shown in Figure 1. When used in the field, the plain strip of wood could be readily removed to permit observation and photography of the nesting behavior.

Bundles containing two traps of each diameter cavity were set out at 20 stations. The bundles were suspended from live or dead branches of turkey oak, scrub hickory, or other trees (Figures 2, 4, 5), and a few tied to a wooden frame supporting a *Strophanthus* bush (Figure 3). The traps were inspected periodically to determine when nesting began.

Table 1 presents records for the maximum and minimum temperatures and rainfall at the Archbold Biological Station during the period that nesting was taking place. After the nests were gathered they were held at 72°–74° F in the Station laboratory until the morning of 27 April. From the morning of 28 April until emergence of adult wasps the nests were held at my home in Arlington, Virginia, where the temperatures ranged from maxima of 60°–70° to minima of 50°–60°.

I am most grateful to Richard Archbold and James N. Layne of the Archbold Biological Station for mak-

Karl V. Krombein, Chairman, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.



FIGURES 1–5.—Archbold Biological Station, April 1969. Trap components: 1, 12.7-mm trap; a, grooved wood stick, plexiglas ® strip and plain wood strip: b, plastic taped to grooved stick; c, plain wood strip fastened to grooved stick and plastic to form a light-tight boring. Nesting sites: 2, station 14, nest 107, *Isodontia auripes;* 3, nest 127, *Isodontia auripes;* 4, station 17, nests 32 and 33, *Podium rufipes;* 5, station 10, nests 19 and 59, *Trypargilum collinum collinum.*

TABLE 1.—*Maximum and minimum temperatures and rainfall, Archbold Biological Station, Lake Placid, Florida, 12–26 April 1969, as of 0900 hours on the date of record*

April	Temperatures F°		Rainfall in inches
	Maximum	Minimum	
12	87	59	–
13	89	61	–
14	82	62	–
15	81	58	.04
16	88	65	1.37
17	88	62	.14
18	91	69	–
19	93	70	–
20	82	46	–
21	83	57	–
22	80	57	–
23	85	50	–
24	88	52	–
25	88	58	–
26	82	52	–

ing available the splendid facilities and grounds during my period of residence. I am indebted to the following for identifications of prey used by the wasps and for notes on the ecological niches occupied by the prey: Willis J. Gertsch, Southwestern Research Station, Portal, Arizona, for the spider prey of *Trypargilum c. collinum;* Ashley B. Gurney, U.S. Department of Agriculture, Washington, D.C., for the cockroach prey of *Podium rufipes;* and Thomas J. Walker, University of Florida, Gainesville, for the cricket and katydid prey of *Isodontia auripes*. E. O. Bankmann of the Cabinet Shop, Smithsonian Museum of Natural History, and J. C. Widener of the Plastics Laboratory fabricated the parts for the traps.

Isodontia (Murrayella) auripes (Fernald)

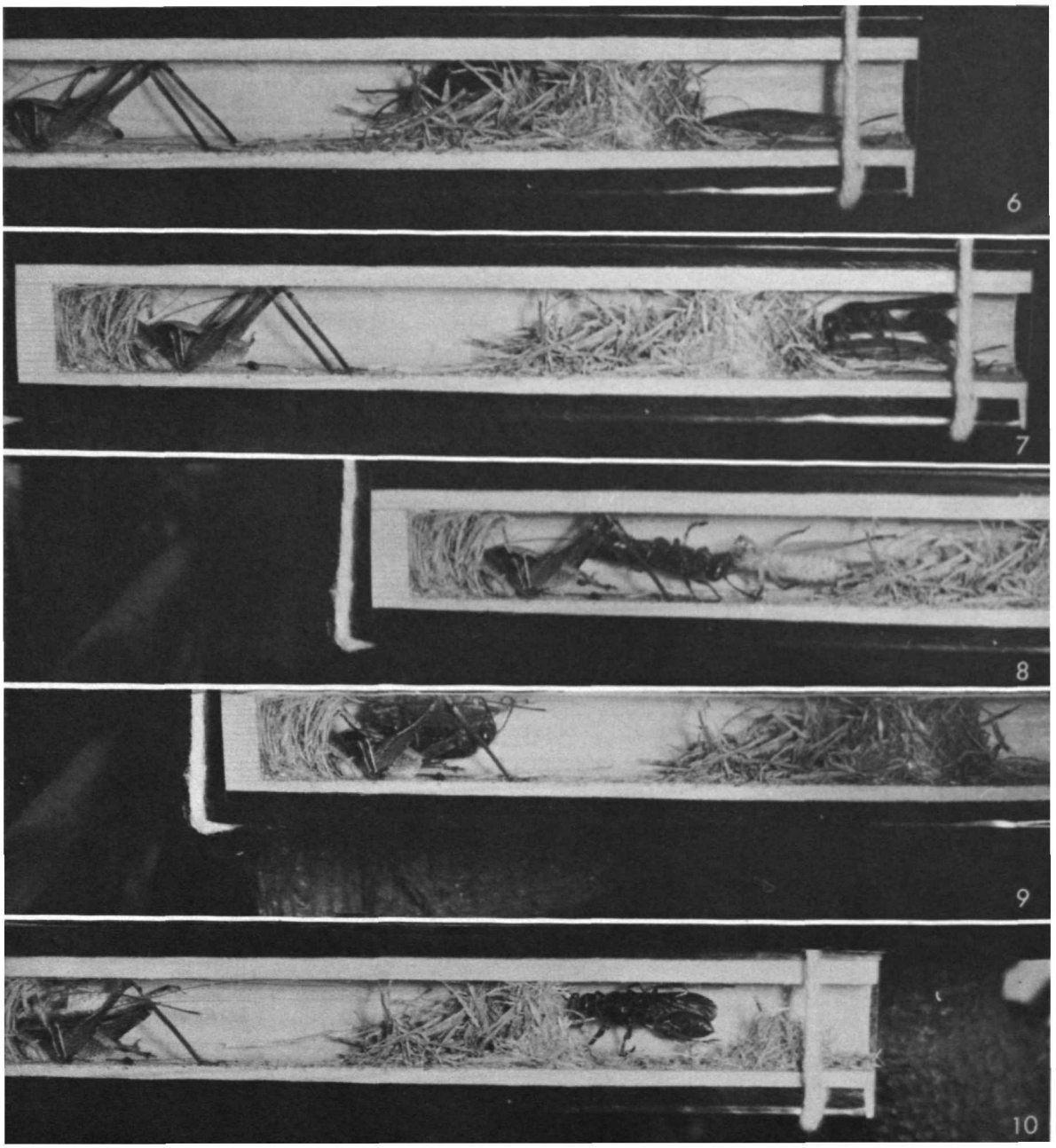
FIGURES 2, 3, 6–39

This sphecine wasp preys primarily on crickets (Gryllidae), but occasionally it also stores one or two shield-backed katydids (Tettigoniidae) in the brood cell. I was able to make observations on the nesting behavior and development in two nests in 12.7-mm traps, numbers 127 and 107. Trap 127 and three others of the same diameter (122, 125, 126) were set out 10 April beneath part of a wooden frame (Figure 3) supporting a *Strophanthus* bush in a cultivated field. I observed carpenter bees, *Xylocopa virginica krombeini* Hurd, emerging from borings in this frame, and I set out only large traps in an attempt to induce nesting by these bees. The other trap was set out 9 April beneath a dead branch of a live scrub hickory (Figure 2) at the edge of a fire lane through the slash pine–turkey oak association in a wooded area quite open to the sun. The traps at both stations were about 1.5 m above the ground.

Nesting Behavior

I checked both of these stations several times a day. The first evidence of *auripes* at either site was at 1145 on 12 April when I noted a female entering and leaving trap 125, flying around for a few seconds, then entering trap 126, and finally leaving the area entirely. Nesting had not begun in any of the traps at this station. At dusk that evening, 1845, this or another female of *auripes* was resting inside trap 122. At 0815 on 14 April the sky was overcast and this female was still in 122. On that same date by 1900 she was resting in 127 where she had brought in some pieces of grass stem and blades. She was still in trap 127 at 0800 on 15 April. At 0925 the wasp was still inside the brood cell and had begun to build up the closing plug. At the already sealed inner end she had earlier constructed a plug of compacted, coiled grass stems; it was 10 mm thick in the middle and 13 mm at the edges. Two hours later I rechecked this trap and found the wasp facing inward near the opening and compacting the materials forming a closing plug by pressing with her head. My examination of her nest disturbed the wasp, so that she turned around and flew out. The brood cell, 80 mm long, contained a paralyzed false-jumping bush cricket (*Orocharis luteolira* T. J. Walker) lying on its belly, head inward next to the plug at the inner end; it bore a pale, yellowish-green wasp egg. The temporary closing plug was 35 mm long and was composed of loosely packed stems and fibers in the inner 25 mm and densely compacted fibers in the outer 10 mm.

My next visit to this station was an hour later, at 1240 on 15 April. During that period *auripes* brought a second paralyzed specimen into the brood cell, a large tettigoniid nymph (*Atlanticus gibbosus* Scudder), which she placed on its belly, head inward next to the bush cricket stored earlier. I removed the plain strip of wood to permit photography through the plastic



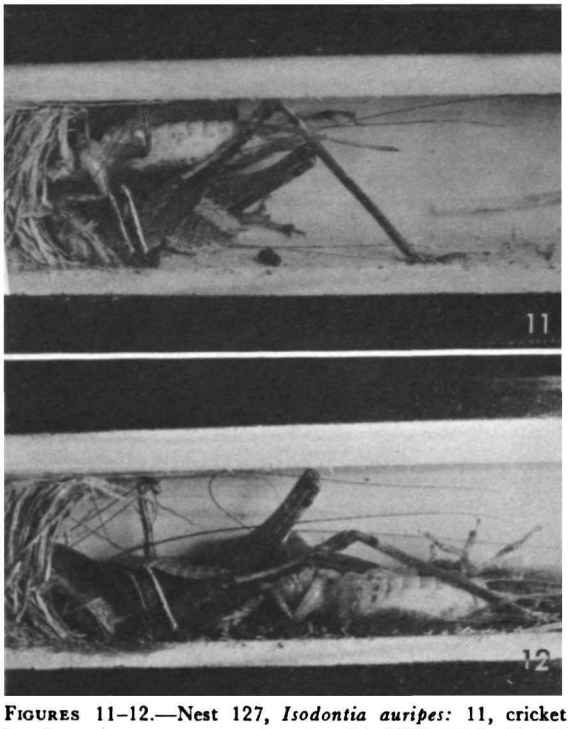
FIGURES 6–10.—Nesting behavior of *Isodontia auripes*, nest 127, 1300–1315, 15 April: 6, paralyzed cricket at outer end of trap, *auripes* making a passage through temporary closure; 7, *auripes* grasping cricket to carry it through temporary closure; 8, *auripes* dragging cricket into brood cell; 9, *auripes* ovipositing on cricket; 10, *auripes* sealing temporary closure.

and could see the abdomen of this tettigoniid pulsating rhythmically. I was unable to see whether it bore a wasp egg. Shortly after 1300 the *auripes* returned with another paralyzed bush cricket, which she left venter down in the outer 30 mm of the trap while she excavated a passage through the closing plug (Figure 6). She entered the brood chamber, pushed the earlier prey closer together, turned around and went out through the closing plug head first. Turning around again, she grasped the head end of the cricket with her mandibles (Figure 7), and carried it venter down through the passage in the closing plug. Once inside the brood chamber, she dropped the cricket, turned around on her back, grasped the head end of the cricket with her mandibles (Figure 8), and dragged it up above the tettigoniid nymph. Then, continuing to lie on her back, she turned the cricket on its side, curled her abdomen upward (Figure 9) and deposited an egg between the fore and mid coxae. Next, she pushed this cricket, now venter up, to the inner end of the brood chamber on top of the first two prey (Figure 11). About 1315 she left the brood chamber, pulled out some fibers from the outer end of the plug, and proceeded to work on the plug to form a tighter closure (Figure 10). At 1327 she flew away, leaving some loose fibers in the outer 40 mm of trap 127. Exposing the nest to light and using the electronic flash for photography did not appear to affect the behavior of the wasp in 127 whatsoever. This *auripes* had not returned by 1335.

Upon my next inspection of nest 127 at 1440 on 15 April, I discovered that the wasp had brought in a fourth cricket. She had also dragged the third cricket down from on top of the tettigoniid nymph and placed it on its back behind that prey. She flew back to the nesting site at this time, apparently not carrying any prey, and flew off in a few seconds without entering the nest. The wasp was not in the nest at 1545, but at 1845 she was resting there for the night, facing outward in the outer end of the boring, with her abdomen against the closing plug. She left the nest before 0830 on the 16th, and sometime during the morning she brought a fifth cricket into the nest (Figure 12). There was no further nesting activity at 1240 or 1330, so I brought the nest into the laboratory for further photography and weighing of the prey. This wasp never began a second nest at this station, even though empty traps were available.

Another female *auripes* began a nest in trap 107, half a kilometer distant from trap 127, during the 3-day period 12–14 April. When I checked Station 14 at 0900 on the 15th, I found that trap 107 contained a plug of compacted Spanish moss strands 5 mm thick at the inner end, an empty brood cell 65 mm long, and a temporary closure of tightly packed Spanish moss about 15 mm thick. Trap 108, adjacent to 107, contained a few short strands of Spanish moss near the inner end; there was no subsequent nesting activity in the former trap, so it is likely that the wasp nesting in 107 may have placed the moss in 108 before or during preliminary nesting activities in 107. While I was examining the traps, a large insect, possibly the *Isodontia,* buzzed around my head and flew off before I could identify it.

The female *auripes* was in the outer end of nest 107 at 1350 on 15 April. She flew off when I shone a flashlight into the trap. At this time the nest contained three paralyzed false-jumping bush crickets lying on



FIGURES 11–12.—Nest 127, *Isodontia auripes:* 11, cricket bearing wasp egg on top of tettigoniid, 1330, 15 April; 12, rearrangement of prey after fifth prey was brought into nest, 1440, 16 April.

FIGURES 13–14.—*Isodontia auripes*, nest 107: 13, 1550, 15 April, showing nest architecture and prey; 14, same as 13 but 1050, 16 April.

their backs, head inward, each bearing a pale yellowish-green wasp egg affixed to the venter of the thorax. I returned to 107 at 1415 and for the next 15 minutes I watched the wasp bringing in plant materials to add to the temporary closure. At 1421 she carried in a piece of grass stem about 5 cm long. It took her 2 minutes to work this into the plug, after which she flew around the immediate vicinity, alighting here and there on dead plants, and trying unsuccessfully to pull off some of the curled, dried leaves. In a few minutes she brought in a piece of Spanish moss about 8 cm long, worked it into the plug for 3 minutes, and then flew out of sight. When I returned at 1551, she flew out of the trap, and I discovered that she had brought in a fourth cricket during the interim and had laid an egg on it (Figure 13). At 1850 that evening she was resting at the outer end of the trap with the tip of her abdomen against the temporary closure; there were still only four bush crickets in the brood cell.

The wasp had already left 107 when I made my first check of that nest at 0820 on 16 April; the nest appeared the same as it had the previous evening. Five minutes later the *auripes* alighted for an instant at the nest entrance and then flew off; she carried neither prey nor vegetation. The wasp flew out of 107 when I returned half an hour later; again, there had been no nesting activity in the interim. The wasp did not return during the next half an hour. However, by 1045 there had been additional nesting activity (Figure 14). One of the earlier prey specimens had been piled on top of the first one at the inner end, another prey had been brought in, and the wasp had left a pile of loose vegetation (Figure 15) at the trap entrance. I checked 107 several times during the afternoon, before removing the nest at 1600, and noted no additional nesting activity. However, subsequent examination in the laboratory disclosed that a sixth prey had been stored during the 16th.

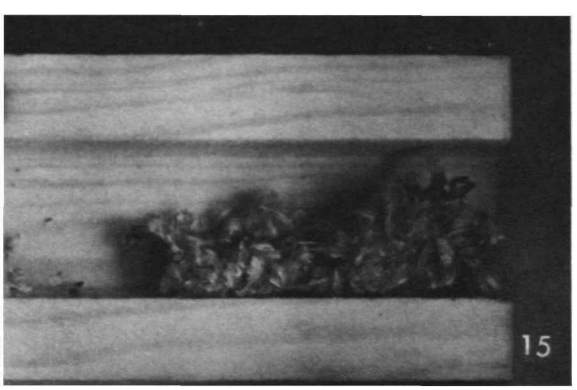


FIGURE 15.—*Isodontia auripes*, nest 107, loose vegetation at nest entrance, 1900, 16 April.

371-049 O—70——2

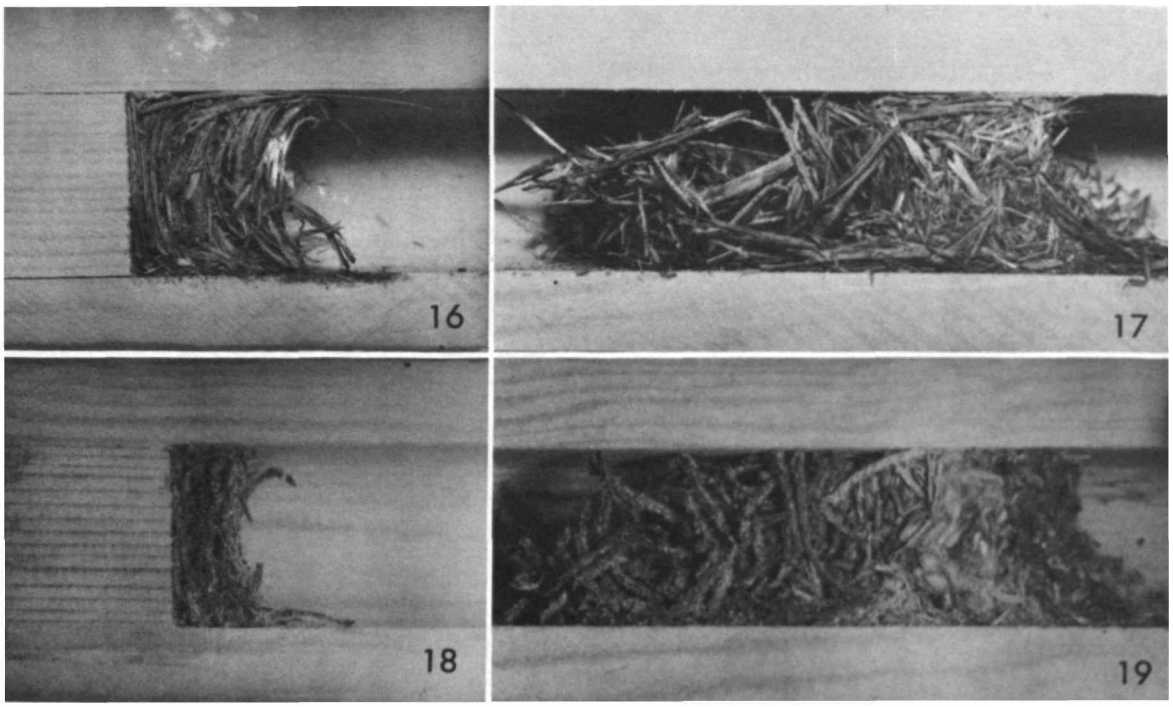
Nest Architecture

Figure 14 shows the architecture of a nearly completed *auripes* nest with a narrow plug of vegetable fibers at the inner end, a brood cell, and a thicker closure of vegetable fibers thoroughly compacted in the outer portion of the plug. It is quite likely that neither of these nests had been completed when I picked them up during the afternoon of 16 April. Normally, when *auripes* makes a final closure, she brings in grass stems and blades which she places along the axis of the boring at the outer end, protruding from the entrance (Krombein, 1967, p. 247).

The plug at the inner end of the boring in 127 was about 12.5 mm thick and consisted of tightly coiled and compressed grass stems and blades (Figure 16); whereas, in 107 the plug was 5 mm thick and made from coiled, compacted strands of Spanish moss (Figure 18). The brood cells were 57 mm long in 127 and 64 mm in 107. The closing plug of 127 was 41 mm thick and was composed of pieces of dried vegetable fiber and grass blades, loosely packed on the inner (left) half and firmly compacted on the outer half (Figure 17). In nest 107 the closing plug was of the same thickness: the inner, loosely packed half was made from strands of Spanish moss, the outer, closely compacted half from small pieces of plant stems having rather long woolly hairs (Figure 19).

Prey

These two individuals of *auripes* preyed principally on the false-jumping bush cricket *Orocharis luteolira* T. J. Walker (Figure 20) and, less frequently, on the shield-backed katydid *Atlanticus gibbosus* Scudder (Figure 21). The wasp in 127 used only adult *Orocharis* and a nymph of *Atlanticus;* whereas, the wasp in 107 used both nymphal and adult *Orocharis* and nymphal *Atlanticus*. Both sexes of *Orocharis* were preyed upon, but only nymphal males of *Atlanticus*. Dr. T. J. Walker, who was able to identify both prey species from fragments remaining in the nests



FIGURES 16–19.—*Isodontia auripes*, details of nest architecture, 16 April: 16, plug at inner end of nest 127; 17, closing plug, nest 127; 18, plug at inner end of nest 107; 19, closing plug, nest 107.

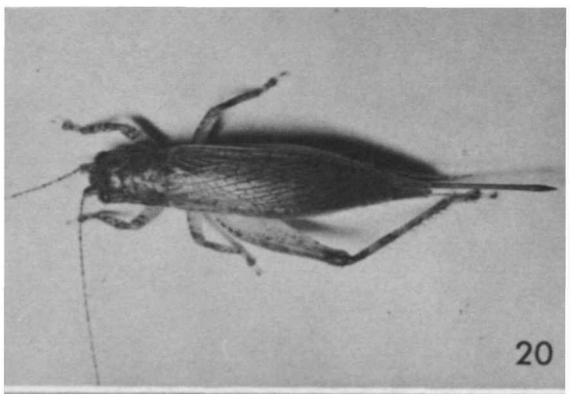
and from photographs, commented that in his experience *Orocharis* never descends to the ground whereas *Atlanticus* nymphs seldom ascend from the ground, especially during the day when *auripes* would be hunting for prey. This suggests that *auripes* exploits several ecological niches while hunting for prey.

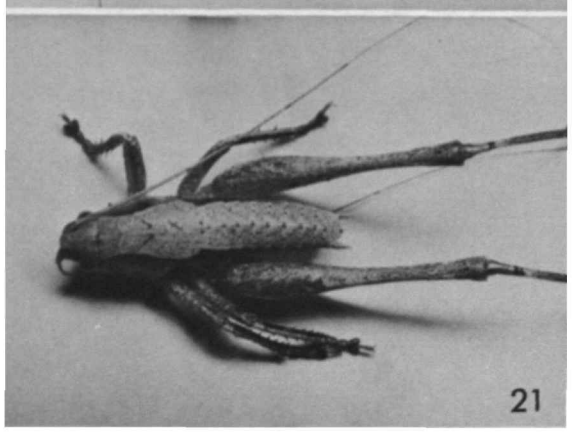
All specimens of prey were thoroughly and permanently paralyzed, and were capable of only weak reflex actions of their antennae, mouthparts, and legs. Feces were voided for a day or two after the prey were stored. In nest 127 each of the crickets lacked a hind leg; these may have been amputated by the wasp.

Table 2 presents information on the prey stored in these nests: their sex, identity, length, and their fresh weight after voiding feces. The specimens are listed in the order in which the wasp arranged them in the nest, 127–1 being the prey at the inner end on the bottom and 127–5 the prey nearest the outer end. It should be remembered, however, that both wasps did some shifting around of specimens subsequent to the prey being brought into the nests. Consequently, it must not be assumed that the order in which I list them is necessarily the order in which they were caught. Prey specimens 127–1, 3, and 5 each bore a wasp egg, as did the

TABLE 2.—*Identity, length, and weight of false-jumping bush crickets and shield-backed katydids stored in nests of* Isodontia auripes (*Fernald*).

Prey number	*Prey identity*	*Length in mm*	*Fresh weight in mg*
127–1	*Orocharis*, adult ♀	17	190
127–2	*Atlanticus*, nymphal ♂	16	290
127–3	*Orocharis*, adult ♂	14	120
127–4	*Orocharis*, adult ♀	17	190
127–5	*Orocharis*, adult ♀	15	140
107–1	*Orocharis*, adult ♂	15	120
107–2	*Orocharis*, nymphal ♀	12	95
107–3	*Orocharis*, adult ♀	17	185
107–4	*Orocharis*, nymphal ♀	11	110
107–5	*Atlanticus*, nymphal ♂	13	115
107–6	*Atlanticus*, nymphal ♂	14	215





FIGURES 20–21.—Prey of *Isodontia auripes*, nest 127, dorsal view: 20, false-jumping bush cricket, *Orocharis luteolira*, adult ♀; 21, shield-backed katydid, *Atlanticus gibbosus*, nymphal ♂.

first five of six prey in 107; these eggs added an infinitesimal amount to the fresh weight of the prey. The mass fresh weight in nest 127 was 930 mg or 310 mg for each wasp egg; similar figures for nest 107 were 840 mg and 168 mg.

I captured a pair of adult *Orocharis luteolira* which had spent the night in two empty traps. The female was 18 mm long, the male 17 mm, and the fresh weights were 239 mg (♀) and 166 (♂) before voiding feces. Each was held for 24 hours, then killed and dried thoroughly in an oven. The resultant dry weights were 67 and 49 mg respectively, a weight loss of a little over 70 percent. Applying that reduction factor to the average weights of prey stored per wasp egg, it is calculated that 93 mg dry weight was provided per egg in nest 127 and 50 per egg in nest 107.

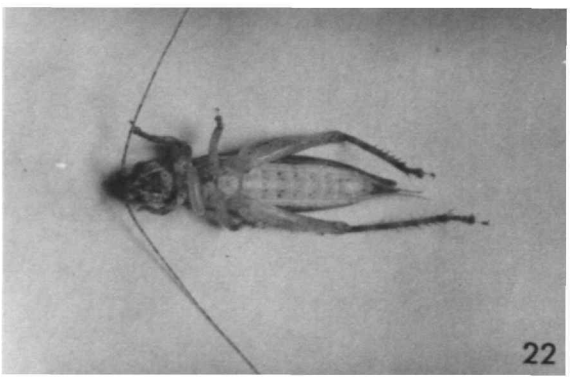


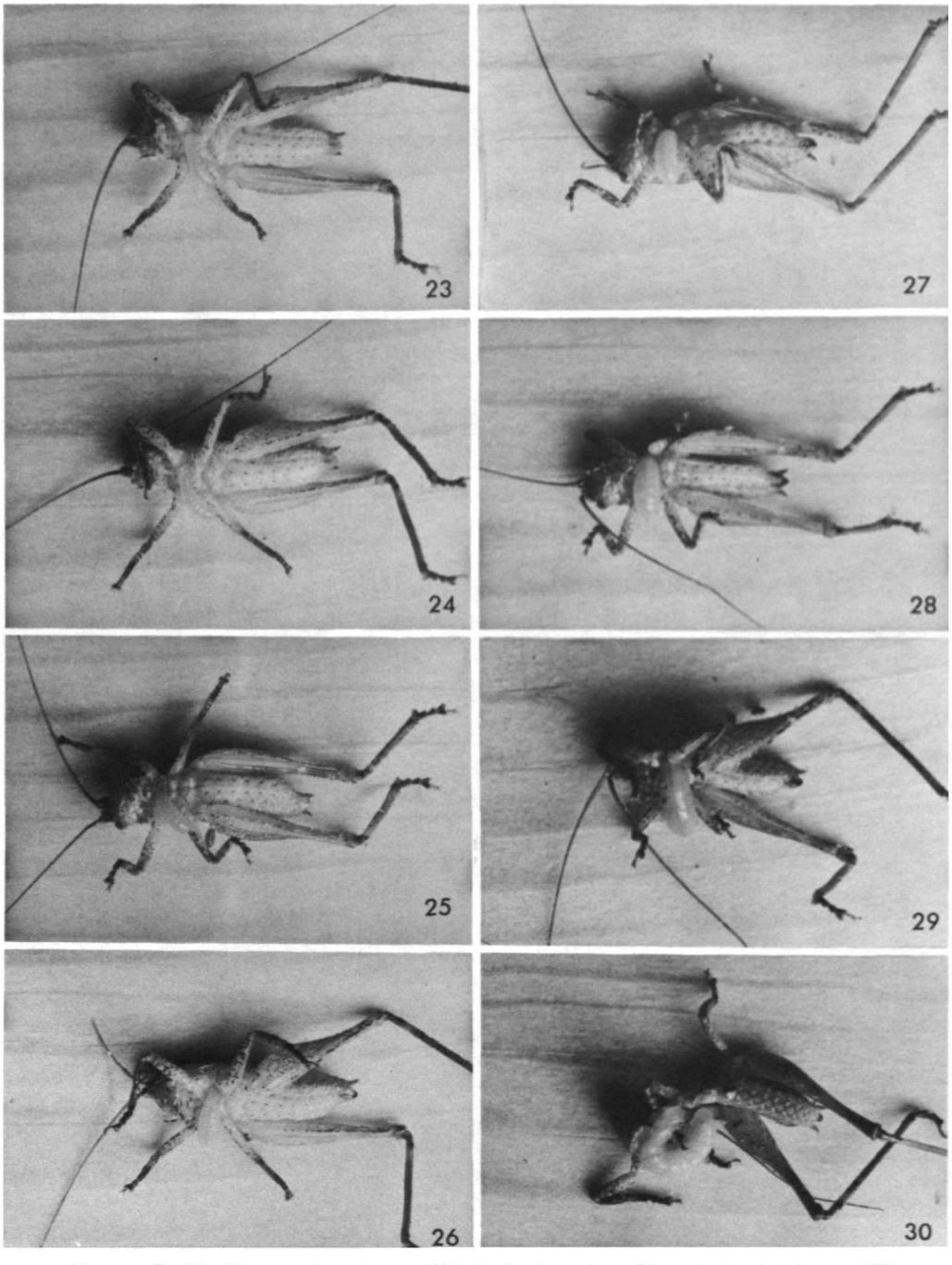
FIGURE 22.—*Isodontia auripes*, egg on adult male, *Orocharis luteolira*, 1600, 16 April.

Adults of *auripes* were so uncommon that I was not able to capture and weigh any of them. However, I did obtain a series of six female and male *Isodontia* (*Isodontia*) *exornata* Fernald, a species of comparable size. These specimens were 17–19 mm long and had fresh weights of 80–123 mg. After thorough drying in the oven, the resultant dry weights were 28–48 mg, a reduction of 61–65 percent.

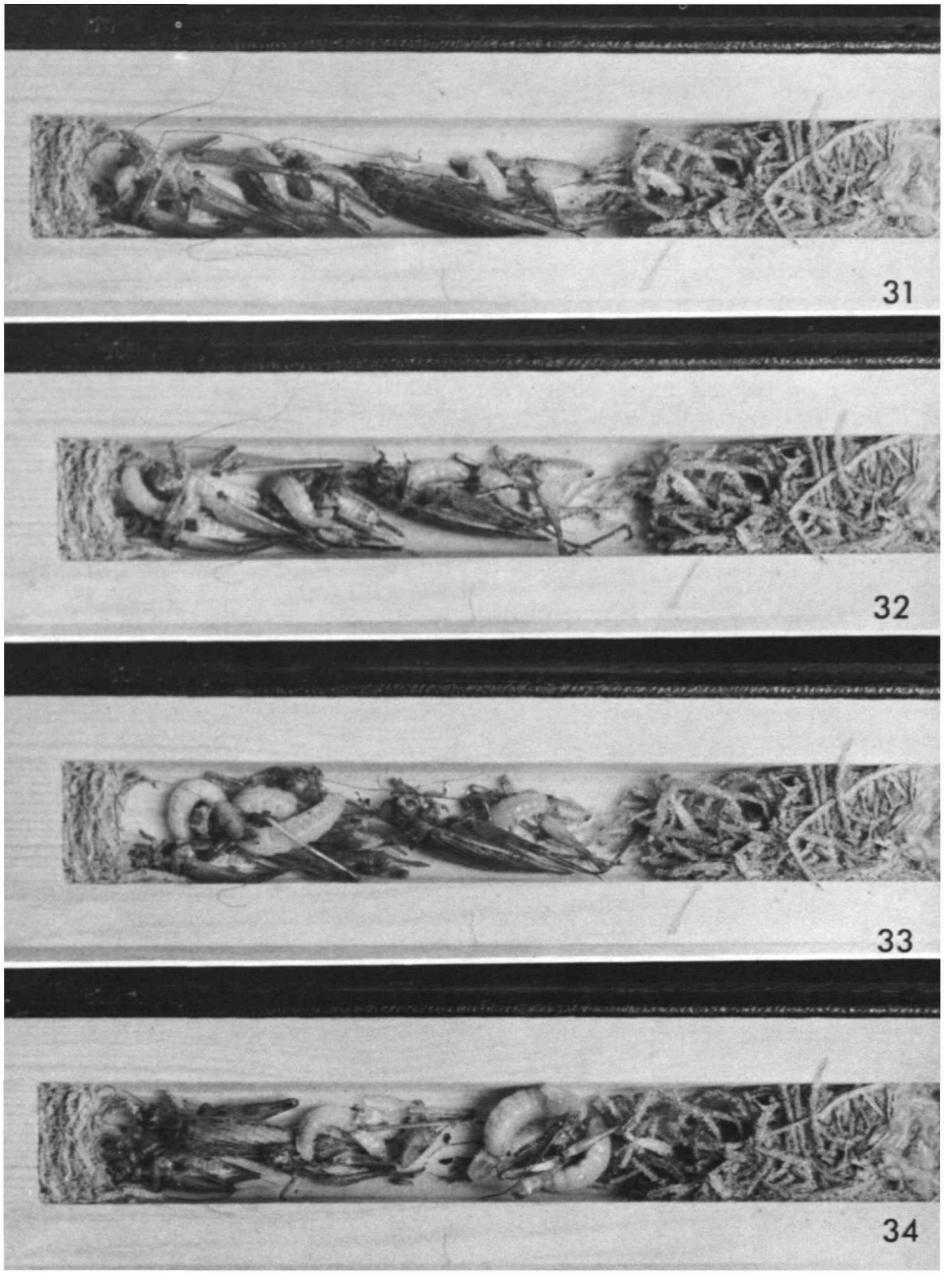
Life History

The sausage-shaped eggs were slightly curved, pale yellowish green, 3.4 mm long and 0.75 mm wide. The anterior end was glued firmly behind the fore coxa and the egg was placed transversely across the sternum so that the posterior end extended beyond the side of the thorax opposite the egg attachment (Figure 22). In nest 127 two of the eggs were attached behind the right fore coxa, one behind the left; in 107 four eggs were attached behind the left fore coxa and only one behind the right.

Larvae hatched from the eggs in 52–54 hours in the five cases where reasonably close information was available on the times of oviposition and hatching. Body segmentation was visible through the chorion for several hours before hatching occurred. The newly hatched larvae began to suck blood at the point of attachment of the egg. Feeding was slow in the younger stages, and the larva required about two days to empty completely the prey on which the egg has been laid. I photographed the development of the youngest larva in nest 107 at periodic intervals over this 2-day period



FIGURES 23–30.—Youngest larva in nest 107, *Isodontia auripes:* 23, newly hatched larva, 1130, 18 April; 24, 1630, 18 April; 25, 2000, 18 April; 26, 0820, 19 April; 27, 1125, 19 April; 28, 1935, 19 April; 29, 0800, 20 April; 30, 1155, 20 April, prey so hollowed out that it broke in two when lifted out of brood cell.



FIGURES 31–34.—Larvae in brood cell, nest 107, *Isodontia auripes:* 31, larvae still feeding inside prey on which eggs were laid, 1225, 20 April; 32, same as 31, but 2000, 20 April; 33, larvae at inner end feeding on prey parts, larva at outer end still feeding internally on original prey, 0800, 21 April; 34, all larvae feeding externally, 2000, 21 April.

(Figures 23–30). The prey had been so thoroughly gutted by the end of the second day that the head and anterior part of the thorax separated from the rest of the body when I removed the specimen from the nest. After emptying the body contents, each wasp larva continued to feed on the exoskeleton, devouring almost all of it but fragments.

When the older larvae finished feeding on the original specimen of prey, they wriggled to one of the untouched prey, if any, and began to feed on it (Figures 31–32). Thus, the two older larvae in 127 finished their original crickets at 0800 on 20 April; by 1155 one of them commenced to feed with its head inside the abdomen of the tettigoniid nymph, and by 1600 both larvae were feeding through the thorax of the two prey specimens which did not originally bear eggs. The larvae in both nests continued to feed on fragments of the exoskeletons for the next day or two (Figures 33–34). On 22 April at 0800 the three larvae remaining in 107 finished feeding and began to pull strands of Spanish moss into the brood cell (Figure 35); they continued to pull Spanish moss into the cell until at least 1600 (Figure 36). The two larger larvae in 127 continued to feed on prey fragments until 0800 on 23 April. By midmorning one of these larvae had caught the anterior end of its body in the hollowed out thorax of the tettigoniid and was unable to extricate itself; it died several days later. The larvae in 107 consumed all of the prey except for parts of the exoskeleton whose dry weight totaled 55 mg; in 127 the larvae left uneaten 108 mg dry weight.

The three larvae in 107 and one larva in 127 began spinning cocoons between 1900 on 23 April and 0800 on 24 April. The cocoons were constructed among pieces of dried plant materials which the larvae pulled from the inner end of the closing plug and among the fragments of the prey (Figures 38–39). The larvae had not been spinning for too lengthy a period by 0800 because they could still be seen through the white silken cocoon walls at that time (Figure 37). By 1915 on 24 April the walls of the white inner cocoons were so dense that the larvae could not be seen through them. On the following morning at 0800 the inner cocoons were light tan, indicating that the larvae had impregnated them, probably with liquid fecal wastes. No information was obtained on the date of pupation because I did not open the cocoons. A male *auripes* emerged from nest 107 on 7 June and a female from nest 127 on 8 June. Thus, the life cycle from egg to adult in these nests was about 54–55 days.

There was a high mortality rate in both nests but very little, if any, was due to cannibalism. In nest 127 where there were three eggs, the youngest egg never hatched and one of the mature larvae died after getting stuck in the hollowed-out thorax of a prey. In nest 107, where there were six eggs, one larva died two days after hatching, the youngest larva (the subject of Figures 23–30) died from lack of food, two larvae died in cocoons, and one adult emerged. The fate of the sixth larva in 107 was not ascertained. It just disappeared one day and may have been cannibalized.

Podium rufipes (Fabricius)

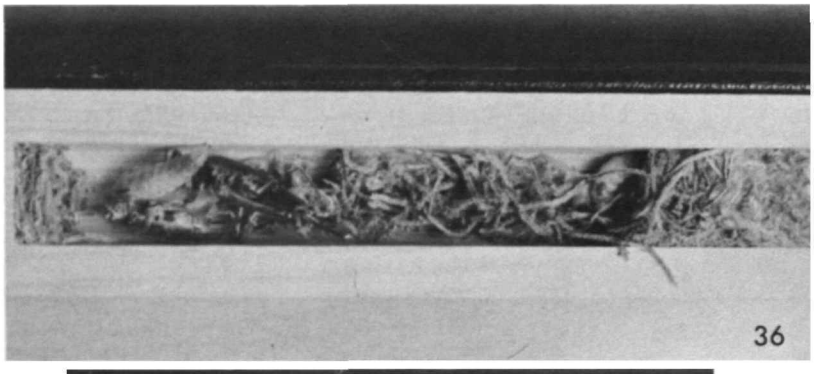
FIGURES 4, 40–61

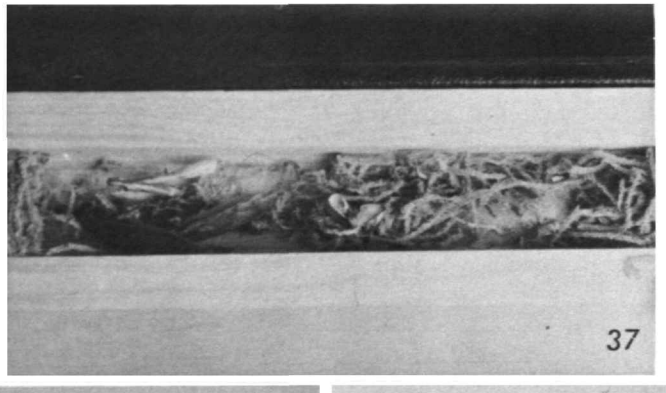
A single female of this cockroach-preying wasp stored two nests (33, 32) in 4.8-mm traps on successive days. The traps were suspended on 9 April beneath the limb of a live scrub hickory (Figure 5) at the edge of a fire lane through slash pine–turkey oak association in a wooded area quite open to the sun. The station (#17) was 1.5 m above the ground with the trap entrances facing northeast.

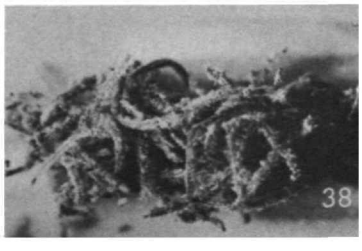
Nesting Behavior

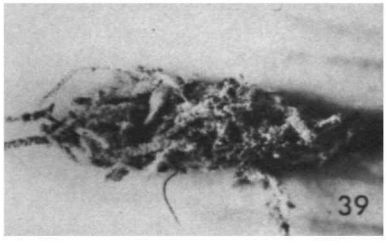
A *rufipes* female was at this station when I inspected the traps at 1035 on 21 April. She did not enter any of the traps while I was there but crawled over them for a few seconds and then flew off. All of the traps were empty at that time. I remained at the station for 20 minutes expecting that she might return for further inspection or with a cockroach, but she did not reappear. I rechecked the traps at 1310 and again at 1640, but no prey had been brought in during the interim periods.

During my next check of this station at 1030 on 22 April, I found that this or another female had placed a paralyzed cockroach nymph at the inner end of trap 33. The cockroach was lying on its back, head inward, and the wasp egg was attached on the midline behind the fore coxae. There was no temporary plug at the nest entrance. Presumably the cockroach had been brought in earlier on the 22nd, inasmuch as the trap was empty at 1640 the previous day. I remained at this station until 1115, but the *Podium* did not return to the nest during that 45-minute period. Upon









FIGURES 35–39.—Larvae in brood cell and cocoons, nest 107, *Isodontia auripes:* 35, larvae pulling moss from closing plug, 0800, 22 April; 36, same as 35, but 1605, 22 April; 37, larvae spinning cocoons, 0800, 24 April; 38, cocoon before removal of pieces of Spanish moss in which it was spun; 39, cocoon after removal of most of Spanish moss.

returning at 1345, I found that the wasp had brought in six more paralyzed cockroaches. The prey were all lying head inward, more or less on their venters, and with the anterior end of each prey resting on the abdomen of the preceding individual.

I removed the plain strip of wood from the trap at 1345 to photograph and observe activities through the plastic. At 1348 the wasp flew onto the set of traps, and ran around on the ends of the sticks in a confused manner, searching for her nest. After a few seconds she recognized the nest, entered head first bearing the cockroach venter down and head first clasped in her mandibles, placed it with the head end on the abdomen of the preceding prey, backed out of the nest, and flew off immediately. At 1355 she returned directly to the traps with another cockroach, began to enter the nest, but was frightened off when I approached closely and took a flash picture. She flew around for a few seconds, then returned and took her prey into the nest. She backed out and flew off at 1358. Twelve minutes later she returned with another cockroach, alighted on the end of the traps, crawled in head first, bearing the prey as described above, deposited the prey, and then backed out and flew off.

Half an hour later, at 1428, she flew back without a cockroach, entered the outer end of the boring for a second, and then flew off. I assumed that she might now be ready to plug the nest for she had amassed nine prey. However, at 1449 and 1529 she returned to the nest, carrying neither debris to construct a plug nor additional prey, peered into the nest for a second or two and then flew off. At 1545, after her fourth such visit, I replaced the plain strip of wood and left the area.

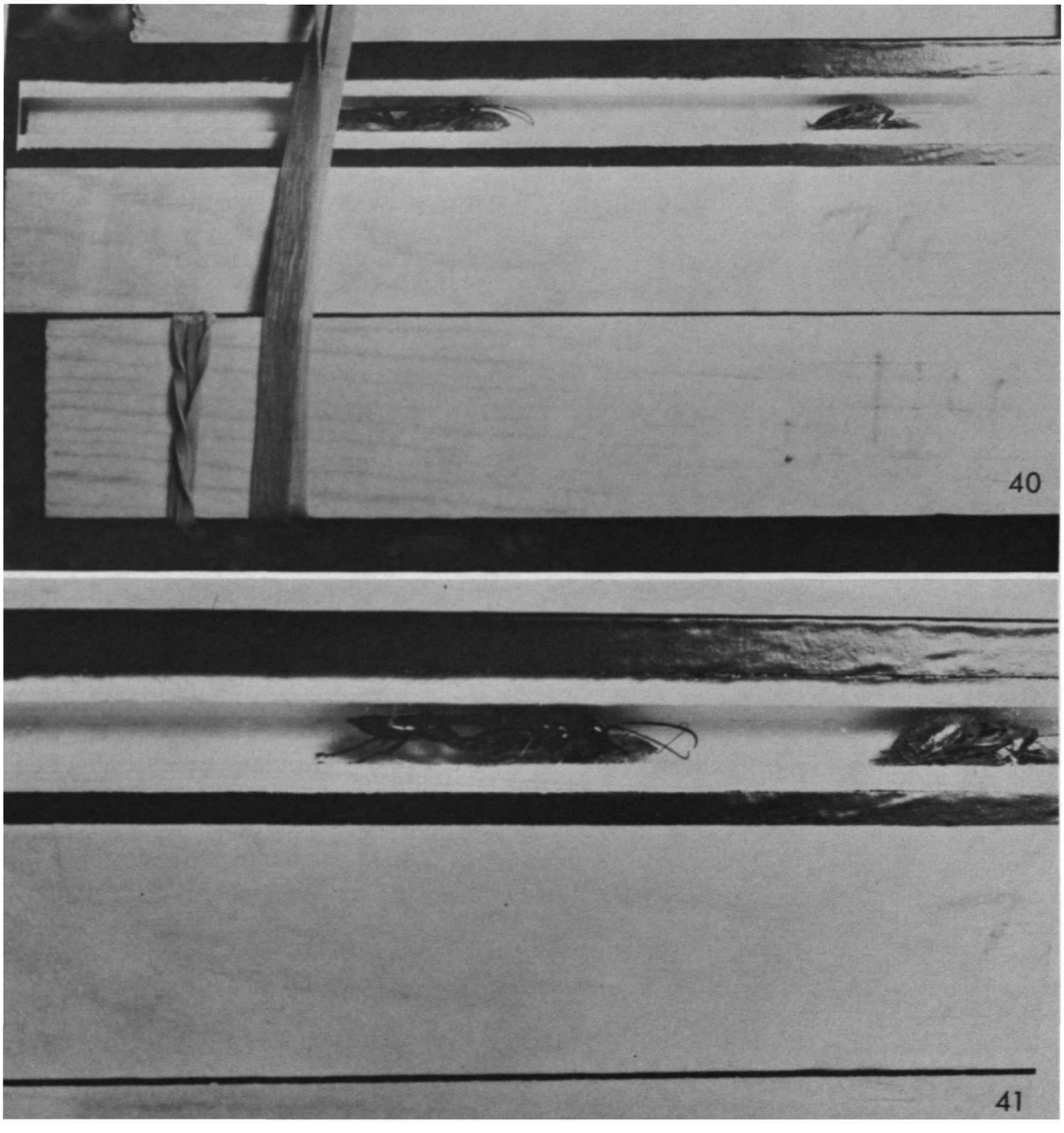
Upon returning to this station at 1900, I found that during the preceding three hours the *rufipes* had brought in two more cockroaches and had constructed the closing plug. Inasmuch as construction of the closing plug is a lengthy process, it is probable that the nest was completed just a short time before 1900. The wasp was not in any of the other traps at this station nor in the immediate vicinity. I removed the completed nest, placed trap 34 in the position occupied by 33, and put an empty trap (32) from an adjacent station in the position occupied earlier by 34.

On the morning of 23 April, I checked all of the other stations before returning to station 17 at 1045. At that time there was a small paralyzed cockroach at the inner end of trap 33, lying on its back, head inward, and bearing the wasp egg behind the right fore coxa. The *rufipes* female, most probably the same individual that constructed nest 32, alighted on the end of the traps at 1100 without a cockroach. She seemed to have difficulty locating her nest, probably because I had removed the strip of wood covering the plastic. In a few seconds, she found the nest, poked her head inside, and then flew off. She did not return by 1130, so I replaced the strip of wood and left the area.

When I returned at 1311, there was a second cockroach in the nest, venter down, head inward, pushed up onto the abdomen of the small cockroach bearing the egg. At 1318 the wasp flew directly to the trap entrances, walked around in some confusion for a few seconds trying to find her nest because I had again removed the plain strip of wood from the plastic. Finally she entered, carrying a cockroach dorsum up beneath her (Figure 40) and pushed the prey up onto the abdomen of the second prey. I could not ascertain how she held the cockroach while she was in flight with it. When she entered the nest, she was definitely pushing it ahead of her, using only her mandibles to manipulate it. She backed out of the nest immediately, downward onto the end of the trap and then flew off.

At 1331 she flew in with another cockroach, but was frightened away when I arose to take a photograph. She flew back several seconds later but was so disoriented that she placed this prey dorsum up and head inward at the inner end of trap 74 rather than in trap 32. After she flew off, I plugged the entrances to the other three traps containing 4.8- or 6.4-mm borings so that she would not make this error again. She alighted on top of the traps at 1348 but was not carrying a cockroach and flew off immediately. At 1355 she returned with another prey and placed it on its belly, head inward next to the third cockroach brought into 32 (Figure 41). The wasp transported the prey within the nest by clutching it with her long, slender, slightly curved mandibles which fitted into the notch on each side of the thorax between the pronotum and mesonotum.

A period of about an hour now ensued during which the wasp without prey visited the nest momentarily at 1405, 1444, 1510, 1527, and 1548. Usually she flew in and alighted directly on the traps, but on one occasion she alighted first on the limb from which the traps were suspended. Upon each of these visits she either put her head inside the entrance and palpated with



FIGURES 40–41.—*Podium rufipes* carrying paralyzed cockroach nymphs into nest 32, 23 April: 40, third prey, *Latiblatella rehni*, 1318; 41, fifth prey, *Chorisoneura* sp., 1355. Note that cockroach is transported by the mandibles only.

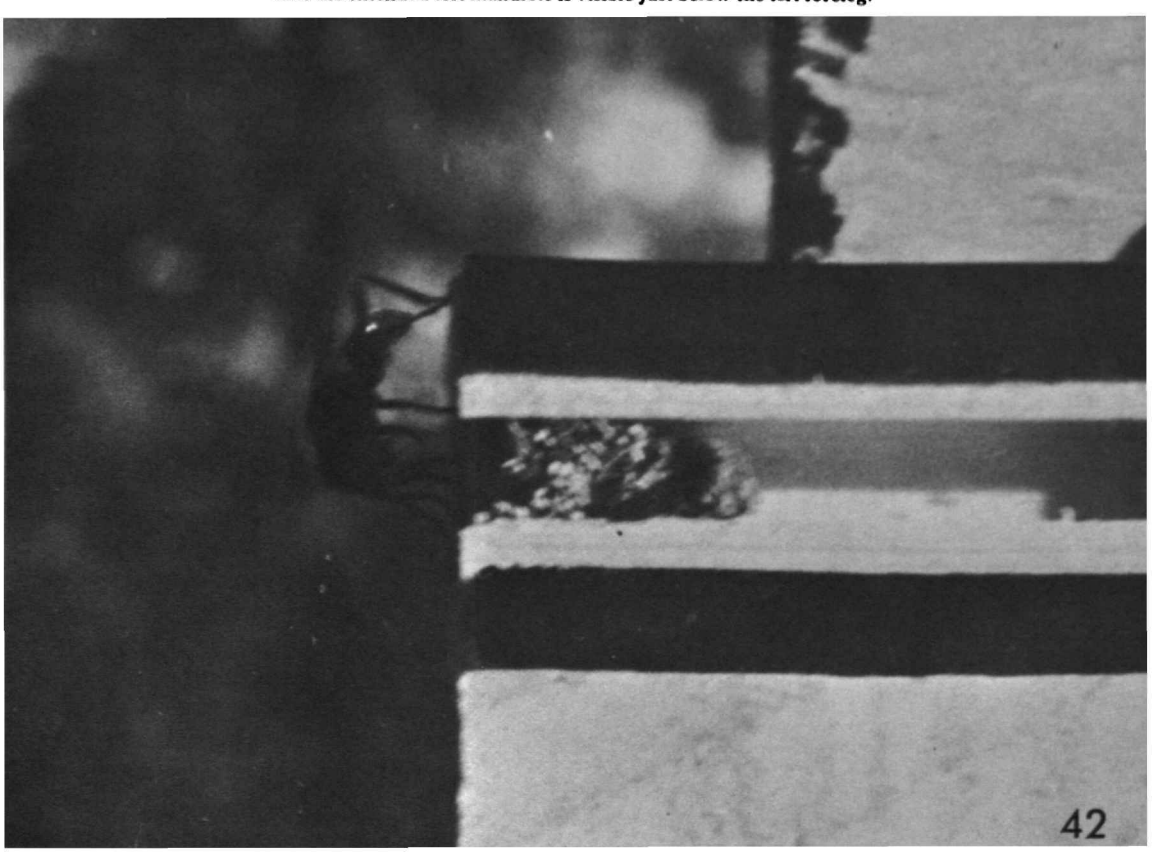
her antennae or went a couple of centimeters into the boring and then flew off.

At 1608 she brought in prey again, but was frightened off three times by my attempts at photography. In the quick glimpses I caught of her at this time, it appeared that she might be carrying the cockroach with her mandibles and forelegs. Finally, she took in the cockroach and left it about 2.5 cm away from the preceding prey. At 1624 she brought in another prey which she placed on the abdomen of the previous specimen. And, at 1636 she flew in with another very large cockroach which she had difficulty stuffing into the boring.

After pushing this last cockroach up against the previous prey, *rufipes* backed out and wandered around on the traps, twice putting her head and antennae into the entrance to nest 32. She flew off after a few seconds and returned at 1639 with a piece of debris which she placed 13 mm inside the entrance. At 1647 she returned without debris, poked her head in for a second and flew off. Then at 1649, 1652, and 1656 she brought in additional loads of debris which she shoved against the first without attempting to compact the mass. At 1659 she alighted on the hickory trunk and in a few seconds flew onto the traps. She did not carry any debris this time and just inspected the plug before flying off again.

At 1702 she returned with a larger load of debris and now she began to compact the various loads. For about half a minute she perched on the end of the trap in various positions, rotating around the entrance and tapping lightly with her mandibles against the mass of debris. At 1705 she was back with another large load which she compacted with the same light pecking

FIGURE 42.—*Podium rufipes* compacting sand in closing plug of nest 32, 1729, 23 April. Note that the extended left mandible is visible just below the left foreleg.



movements for 45 seconds. These latter two larger loads of debris consisted of caterpillar frass spun loosely together with silk. Probably she obtained this mixture of frass and silk from the retreat of a leaf-roller or leaf-tier caterpillar.

The shadows were beginning to lengthen as the sun lowered, and the *rufipes* now began the next step in the construction of the complex closing plug, bringing in her mandibles damp sand which later dried to form a firmly agglutinated layer. The first lump was taken to the nest at 1710 and applied to the surface of the debris carried in earlier. This and successive loads of damp sand were spread over the surface of the plug and tamped in with rapid, light pecking taps with the opened mandibles, the head being held in the normal downward position (Figure 42). To compress the sand evenly the wasp rotated around the entrance. I frightened the wasp away at 1716 when I attempted to photograph her arrival with the next load of sand. She brought in additional lumps of damp sand at 1725, 1729, 1736, 1744, 1751, 1759, and 1804; at 1750 she visited the nest but did not bring in sand. She compacted each load of sand with light blows of the extended mandibles for about a minute, although occasionally the tamping lasted as long as two minutes or as little as 30 seconds. Usually she alighted on the traps and crawled rapidly to the entrance, but occasionally she alighted on the tree trunk and then made a short flight onto the traps.

The final stage in the nest closure began at 1811 when she arrived with a large lump of clear, sticky pine resin in her mandibles. She smeared this over part of the layer of damp sand. She carried in additional lumps of resin at 1815, 1820, 1828, and 1833. These were smeared over the surface of the sand and compacted with more deliberate pecking movements with her opened mandibles for 1–1½ minutes per load. The sun had gone down behind the ridge by 1830, so that it was dusk when she brought in the last few loads of resin. When the wasp did not return by 1841, I picked up the nest, assuming that she had completed the closure.

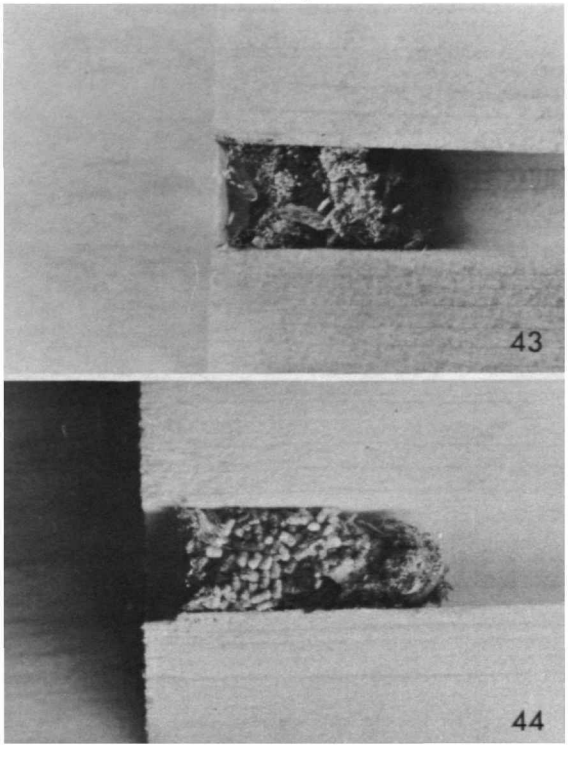
I revisited this station at 0820 on 24 April to set out a replacement trap for nest 32. The wasp apparently had finished the plug on the previous evening, for there was no resin at the entrance to any of the other traps. I checked the traps at this station several times daily through 26 April, but the *rufipes* never returned to begin another nest.

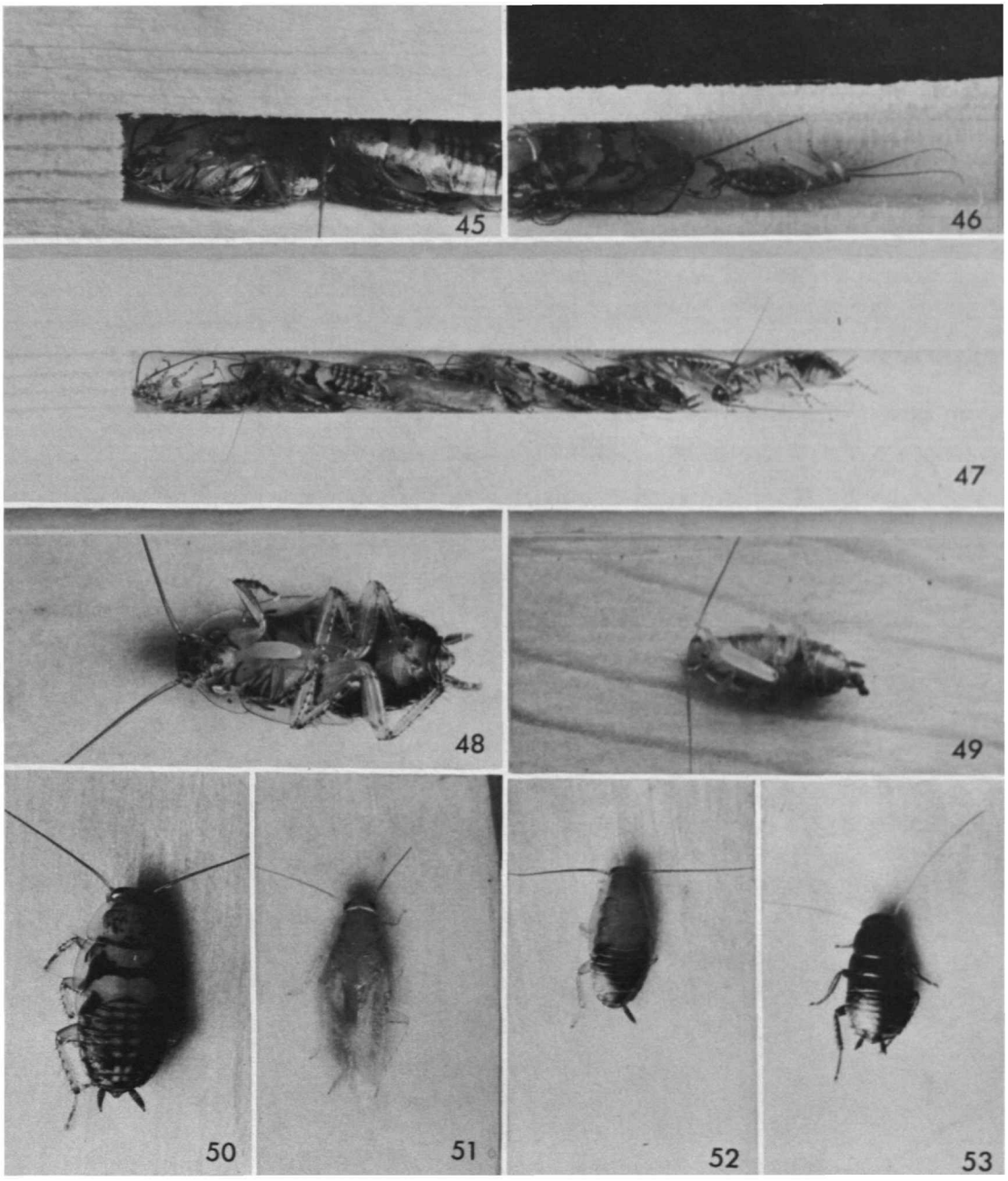
Nest Closures

Nests 33 and 32 were examined and photographed in the laboratory on the evenings of 22 and 23 April respectively. The closing plug of nest 33 (Figure 43) was 10.5 mm thick, the inner debris being capped by a layer of agglutinated sand 0.5 mm thick and an outer layer of clear pine resin 1 mm thick. The debris at the inner end consisted of some dry hollowed-out spider parts, bits of spider web, particles of rotten wood, some fine brown fibrous material and then more rotten wood.

The plug of nest 32 (Figure 44) was 12.5 mm thick, the inner debris being capped by a layer of agglutinated sand 0.5 mm thick and by an outer layer of clear pine resin of the same thickness. The debris at the inner end consisted of some particles of rotten wood, then large clumps of caterpillar frass fastened together with silk, followed by a few more fragments of rotten wood.

FIGURES 43–44.—Closing plugs of *Podium rufipes* nests: 43, nest 33; 44, nest 32.





FIGURES 45–53.—Prey and egg placement, *Podium rufipes:* 45, inner end (at left), nest 33, note egg on innermost cockroach; 46, inner end (at right), nest 32, note egg on innermost cockroach; 47, prey in nest 33, note innermost cockroach lying on its dorsum, the others lying on their venters; 48, egg on *Latiblatella rehni* nymph, nest 33; 49, egg on *Chorisoneura* sp. nymph, nest 32; 50, *Latiblatella rehni* nymph, dorsal, nest 33; 51, *Chorisoneura texensis* adult, dorsal, nest 33; 52, *Chorisoneura* sp. nymph, dorsal, nest 33; 53, *Eurycotis floridana* nymph, dorsal, nest 33.

Prey

The placement of prey in both nests was identical. The first cockroach brought into each trap was placed on its back, head inward at the inner end of the boring, and the wasp egg was laid on it before additional prey were stored (Figures 45–46). Subsequent cockroaches were brought into the nest head first and venter down and stored in that position. Usually the subsequent prey were shingled, so that the head end of one cockroach rested upon the abdominal dorsum of the preceding cockroach (Figure 47). The legs of almost all of the cockroaches were complete, indicating that *rufipes* seldom or never practices amputation.

I did not observe storing of the first cockroach and oviposition. Consequently, it must still be ascertained whether the wasp carries the first cockroach into the nest venter up, or whether the wasp turns this first prey over after placing it at the inner end of the boring. In either case, before ovipositing, the wasp would have to back out of the nest, turn around, and back into it, so that the egg could be placed in the proper position.

Three or possibly four species of prey were stored in the nests as follows: nymphs of *Latiblatella rehni* Hebard (Figure 50), adults of *Chorisoneura texensis* Saussure and Zehntner (Figure 51), nymphs of *Chorisoneura* sp. probably *texensis* (Figure 52), and a nymph of *Eurycotis floridana* (Walker) (Figure 53). I did not observe hunting behavior, but presumably the wasp flushes the cockroaches from their daytime retreats, most likely among fallen leaves or other vegetation on the ground.

Table 3 presents information on the prey stored in these nests: their identity, their length, and their fresh weight. The specimens are listed in the order in which they were placed in the nests, 33–1 being the first cockroach taken into nest 33 and 33–11 the last. The weights of 33–1 and 32–1 include the very infinitesimal weight of the wasp egg which could not be removed without danger of injury. Cockroach 32–4 is the one which was mistakenly placed in trap 74. The mass weight of cockroaches in nest 33 was 347 mg, with an average weight of 32 mg. In nest 32 similar figures were 310 and 34 mg respectively. A male wasp developed in each of these nests.

All of the cockroaches were thoroughly paralyzed and exhibited only relatively weak reflex actions of their antennae, mouthparts, and legs. The prey bearing the egg was no more heavily paralyzed than the other cockroaches. The cockroaches also continued to void feces as may be noted in Figure 54.

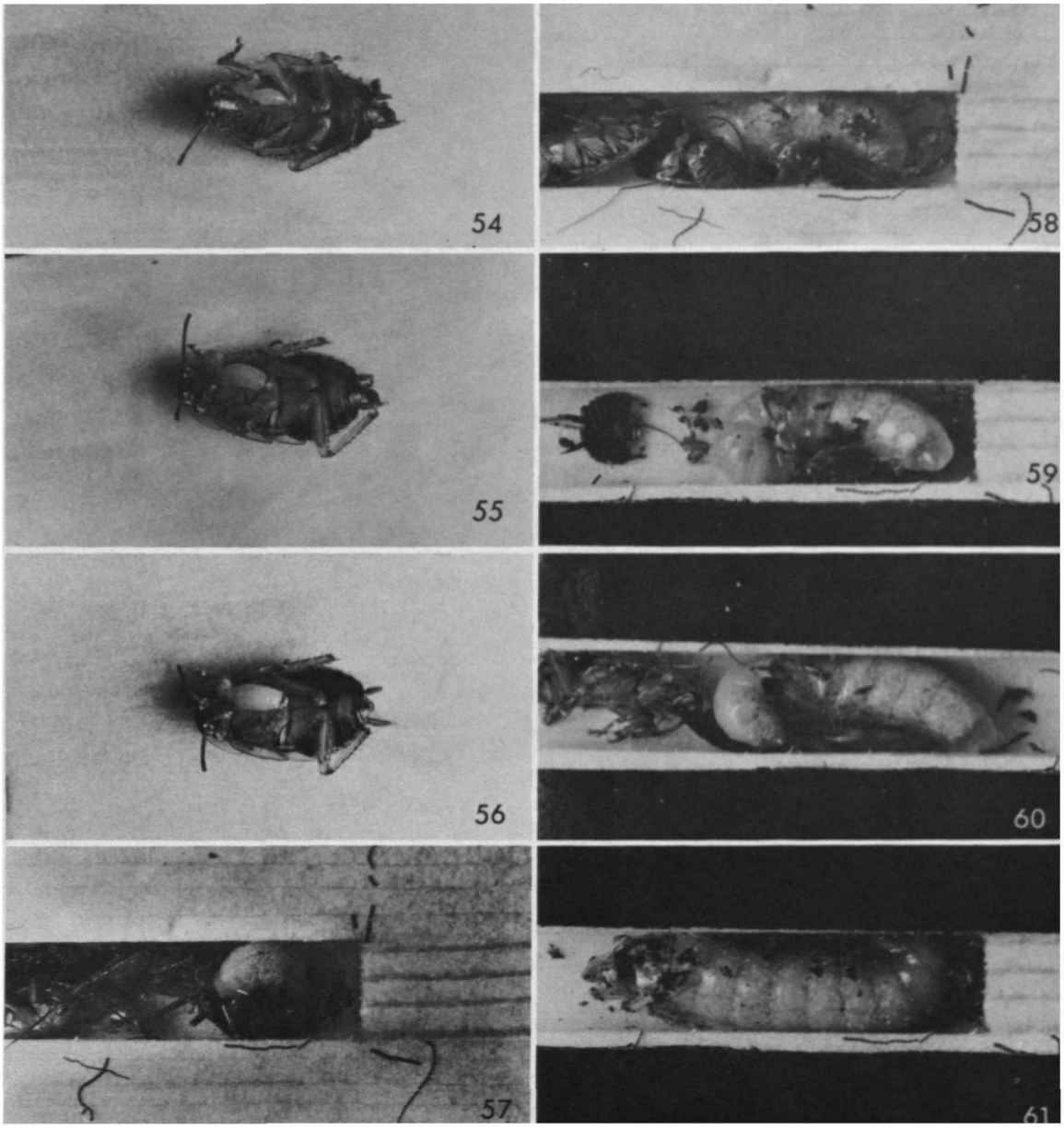
TABLE 3.—*Identity, length, and weight of cockroaches stored in nests of* Podium rufipes (*Fabricius*)

Prey number	*Prey identity*	*Length in mm*	*Fresh weight in mg*
33–1	*Latiblatella* nymph	10.5	52
33–2	*Latiblatella* nymph	8.0	24
33–3	*Latiblatella* nymph	10.5	46
33–4	*Chorisoneura* nymph	7.0	17
33–5	*Chorisoneura* adult	9.0	21
33–6	*Latiblatella* nymph	7.0	19
33–7	*Latiblatella* nymph	10.5	46
33–8	*Eurycotis* nymph	6.0	17
33–9	*Latiblatella* nymph	7.5	25
33–10	*Chorisoneura* adult	9.0	27
33–11	*Latiblatella* nymph	11.0	56
32–1	*Chorisoneura* nymph	6.0	13
32–2	*Chorisoneura* nymph	5.0	8
32–3	*Latiblatella* nymph	11.0	59
32–4	*Latiblatella* nymph	10.5	57
32–5	*Chorisoneura* nymph	8.0	20
32–6	*Chorisoneura* nymph	7.5	20
32–7	*Chorisoneura* nymph	7.0	15
32–8	*Latiblatella* nymph	10.0	59
32–9	*Latiblatella* nymph	11.0	60

Life History

The eggs were sausage shaped, 2.67 mm long and 0.67 mm wide. The head end was glued firmly to the intersegmental membrane just to the left of the midline and behind and somewhat beneath the left fore coxa. The left leg was displaced slightly in a larger cockroach (Figures 45, 48) and rather noticeably in a smaller specimen (Figures 46, 49). The eggs extended backward to the apices of the mid or hind coxae.

The egg in nest 33 hatched between 1930, 24 April, and 0800, 25 April, and that in nest 32 between 1700 and 2030, 25 April. Assuming that the latter egg may have been laid about 1000 on 23 April, we can estimate that egg hatch occurs in 55–56½ hours when it is held at about 80°–88° for 9 hours and at 72°–74° for the remaining time. Judged from the hatching data recorded for the egg in nest 32 and the fact that the



FIGURES 54–61.—Larval development, *Podium rufipes*, nest 33: 54, young larva about 16 (?) hours after hatching, 1150, 25 April; 55, 1150, 26 April; 56, 1930, 26 April; 57, 0930, 28 April; 58, 0700, 29 April; 59, 0720, 30 April; 60, 0645, 1 May; 61, 0720, 2 May.

egg in nest 33 was laid just about 24 hours earlier, we can postulate that egg hatch in nest 33 probably occurred shortly after 1930 on 24 April.

The anterior end of the egg was glued to the intersegmental membrane between the fore and mid coxae. It appeared that the chorion may not be shed until the larva makes some growth, because slight rhythmic contractions were visible posteriorly in the egg in nest 32 at 2030 on 25 April, indicating that feeding had begun. After the larva hatched, it penetrated the cockroach body between the fore and mid coxae and began to suck blood.

The egg-bearing cockroach in nest 32 still exhibited some reflex movements at 0845 on 26 April, a little

more than 12 hours after the larva commenced feeding, but it was quiescent and probably dead by 1915 on that same date. One cockroach in nest 33 exhibited reflex movements as late as 0900 on 28 April, before the wasp larva fed on it and almost 6 days after it was paralyzed.

The newly hatched larvae developed slowly at first (Figures 54–56). If the assumption as to the probable hatching time of the larva in nest 33 is correct, then Figure 54 was taken about 16 hours after hatch; note that the larva is noticeably thicker than the egg (Figure 48), but no longer. Figures 55 and 56 were taken of this same larva 24 and 32 hours after Figure 54; note that the larva has increased in girth during these periods but has not become longer. The larva in nest 33 continued to feed with its head inside the first cockroach until 28 April. By 0900 on that date (Figure 57) it had consumed all of the first cockroach except for the exoskeleton.

Development was now much more rapid. By 0700 on 29 April the larva in nest 33 had gutted the second cockroach in the nest (Figure 58). A day later there were only four whole cockroaches left out of the original eleven (Figure 59). On 1 May at 0645 there was only one untouched cockroach (Figure 60). At 0720 on 2 May the larva was feeding on just exoskeletal remains (Figure 61), which it continued to do until that evening when only very small fragments remained.

Larval feeding in nest 32 followed a similar pattern except that the larva gutted the small first cockroach more quickly and was feeding internally on the second by 0900 on 28 April. There were only two large and one small prey untouched at 0640 on 1 May, and only one large cockroach at 0715 on 2 May. By 1945 that evening there were only exoskeletons remaining, and, except for tiny fragments, these had all been consumed by 0825 on 4 May.

Thus, the larval feeding period was about 8 days in nest 33 and 8½ in nest 32, although 37 mg more of food (the equivalent of one moderate-size cockroach) was provided for the former. The discrepancy is undoubtedly due to the larva in nest 32 being subjected to the cooler Arlington temperatures a day earlier in its developmental cycle.

Regrettably, I was unable to obtain information on the number of larval instars. The manner of feeding during the early stages, with the head buried inside the cockroaches, precluded periodic measurements of the head capsule. I was never fortunate enough to witness the shedding of the cuticle at a molt.

Construction of the cocoon in nest 33 required about 2½ days. By 1800 on 3 May the larva had pulled some of the looser debris from the inner end of the closing plug about 25 mm further into the boring. It had also begun to construct a network of silken threads in which to suspend the cocoon at the inner end of the boring against the plastic and sides of the boring. On the following morning at 0825 there was an opaque, fusiform white cocoon at the inner end; no feces had been voided. Most of the loose debris was now at the extreme inner end of the boring and some was attached to the anterior end of the cocoon. By 1925 the larva had coated the cocoon walls with light-tan liquid feces, and it was still moving inside the cocoon. The next morning at 0705 the cocoon was darker brown, still soft and the larva was still working inside. By 0630 on 6 May the cocoon walls were dry and brittle, and the wasp larva was lying motionless inside. Cocoon construction in nest 32 was done in the same manner and required the same amount of time.

On 8 May at 0645 I removed part of the anterior end of the cocoons in nests 33 and 32. The resting larva in the former was quiescent, but that in the latter wriggled forward out of the cocoon; a little later it wriggled back into the cocoon. Pupation occurred in nest 33 between 0630 and 1830 on 21 May, and between 2200, 22 May, and 0600 on 23 May in nest 32. Eclosion of the adult male wasp occurred 15 June in 33; this adult left the nest 18–19 June. In nest 32 the adult male wasp left the nest 19–20 June.

Discussion

The evidence offered by these observations does not permit a determination as to how a female *rufipes* knows how much prey to store in a nest to bring a larva to maturity. Judged from these data alone, one might speculate that about 9–11 cockroaches are required to bring one larva to maturity. In my earlier lengthy account of this species (Krombein, 1967, pp. 251–255, figs. 62–63), however, I mentioned that nests from North Carolina and Florida contained 3–16 cockroaches. Consequently, it does not appear that the number of prey stored is likely to be the determining factor. An alternative possibility is that the wasp has some sort of internal calculating device to gauge the amount of prey stored by the cumulative weight of the individuals brought into the nest. It will be recalled

that these two nests each contained about a third of a gram fresh weight of cockroaches. Many more observations of freshly stored nests will be needed to determine if provisioning by weight is a plausible hypothesis.

There is another possible explanation concerning the number or weight of prey stored; namely, that the wasp calculates neither the mass nor the number, but that the number of prey stored is entirely dependent upon the success of the wasp in finding cockroaches during a *single* day. It should be recalled that both nests were begun relatively early in the morning, perhaps about 1000, and that the complex closing plug was begun late in the afternoon as the light intensity began to decrease rapidly. One must also remember that the wasp apparently hunted fruitlessly for cockroaches for extended periods during the day, judged from the numerous preyless visits she made to the nest. Can it be that *rufipes* begins each nest early in the day, stores it with as many cockroaches as she can find during the day, and then constructs the closure, regardless of how many prey have been stored, as soon as the decreasing light intensity imposes a requirement for closing the nest? *Podium rufipes* does not spend the night at the nesting site as do many other wasps; this could very well dictate that the nest must be plugged at the end of the day. Again, many more observations will be needed to ascertain the validity of this theory.

Figure 62 in my earlier account of *rufipes* (1967) is a photograph of the prey lying in a nest from North Carolina, showing all of the cockroaches, including the one bearing the wasp egg, lying on their backs head inward. In contrast, in the two Florida nests reported here, only the cockroach bearing the egg was on its back, all of the rest were venter down. Additional field observations are needed to ascertain whether the former method of prey storage is characteristic of the North Carolina population, or whether either manner of prey storage is an individual idiosyncrasy.

I saw no parasites during my lengthy observations at the nest site, and no infestation developed in the nests after they were brought into the laboratory. Actually, *rufipes* is very subject to parasitism by the cuckoo wasp *Neochrysis panamensis* (Cameron). In my account of the latter species (1967, pp. 473–475), I mentioned that it was found in 21 *rufipes* nests from the Archbold Biological Station in Florida, a parasitism rate of 36 percent. Access to the *rufipes* nests is very simple because there is no temporary closure, such as that made by *Isodontia auripes* (Fernald), *q.v.*, and the open, partially stored nest is left unguarded for nearly 8 hours during the day while the wasp hunts for prey.

All of the cockroach species found in these two nests were reported (Krombein, 1967) from earlier nests from the Archbold Biological Station. In addition, *Parcoblatta* (?) and *Cariblatta minima* Hebard were found in one or more of the earlier series of nests.

Trypargilum collinum collinum (Smith)

FIGURES 5, 62–78

The spider-hunting wasp *Trypargilum c. collinum* began nests in traps 19 (4.8-mm diameter) and 59 (6.4-mm diameter) at station 10 (Figure 5). The station was placed 1.5 m above the ground with the trap entrances facing south beneath the limb of a live turkey oak. This tree was in the open sun at the edge of a paved road through the slash pine–turkey oak association. The traps were set out 9 April and checked periodically for nesting activity. The first evidence of nesting was noted at 0845 on the 17th, two days after the previous check at 0800 on the 15th.

Nesting Behavior

These two nests were undoubtedly started on 16 April, because at 0845 on the 17th there was one almost completed cell in nest 59 and there were two completed cells in 19 and two paralyzed spiders in a partially stored third cell. There was no wasp in the former nest, but an adult *collinum*, whose sex I could not determine, flew out of nest 19 when I removed the plain strip of wood. This wasp did not return during the next 15 minutes. There was no further nesting activity in either nest at 1135 and 1600, nor was the wasp in either nest. I removed the nests at 1600 and substituted two others of the same diameters.

At 1035 on 18 April there was a single paralyzed araneid spider at the inner end of trap 20 at this station. The wasp was not in the nest and she had not placed any mud at the inner end. Fifteen minutes later a *Trypargilum* flew toward the nest entrance, but was frightened by my presence and flew off. She must have abandoned the nesting site at this time, because no additional spiders were brought in during the next three days. *Trypargilum collinum* is obviously a much more timid wasp than either of the two species discussed earlier.

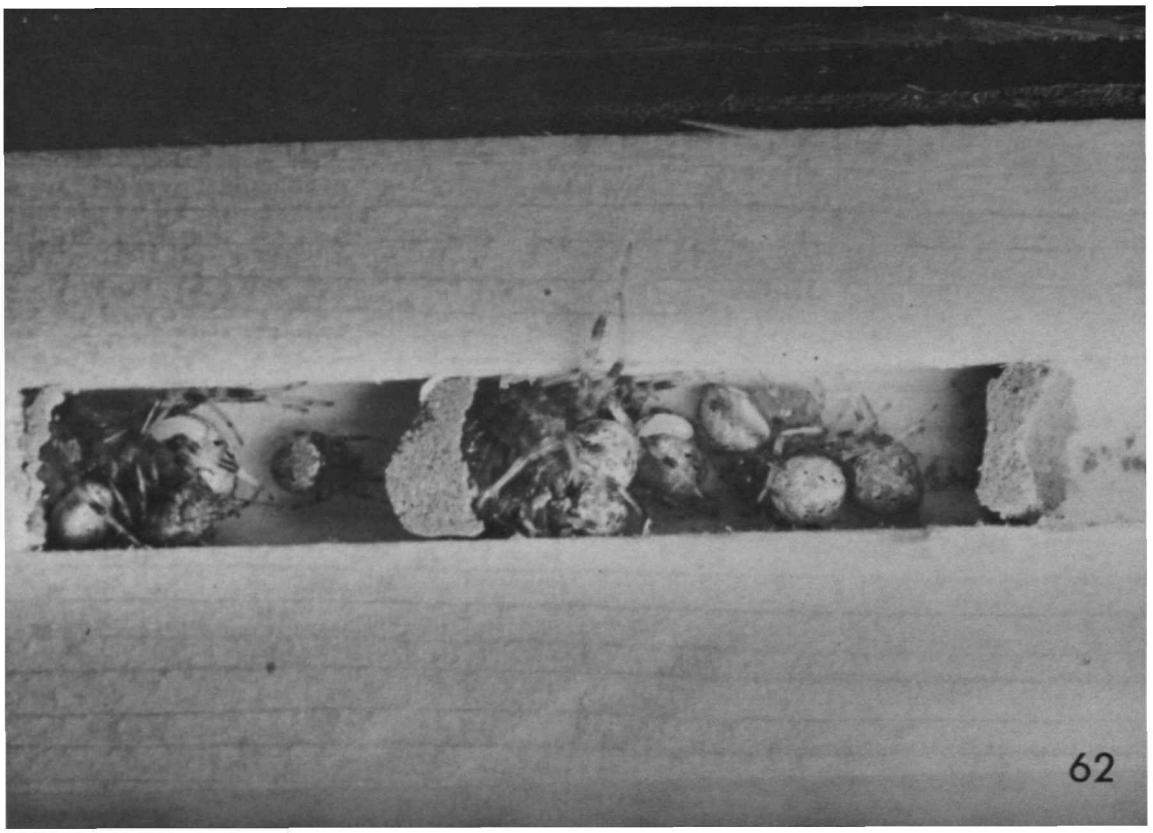


FIGURE 62.—*Trypargilum c. collinum*, cells 1 and 2, nest 19, 1630, 17 April.

Nest Architecture

A small amount of mud was plastered at the inner end of the boring in nests 19 and 59. This mud is very rarely omitted as in nest 20 (see also Krombein, 1967, p. 186). Nest 59 had a single almost completed cell 14 mm long containing 14 paralyzed araneid spiders but no wasp egg. The mud partition closing this cell was about two-thirds complete, suggesting that the egg might not be deposited until the partition is almost finished. Nest 59 may have been started and abandoned by the maker of nest 19, or it may have been that of another female which never returned during the rest of that day.

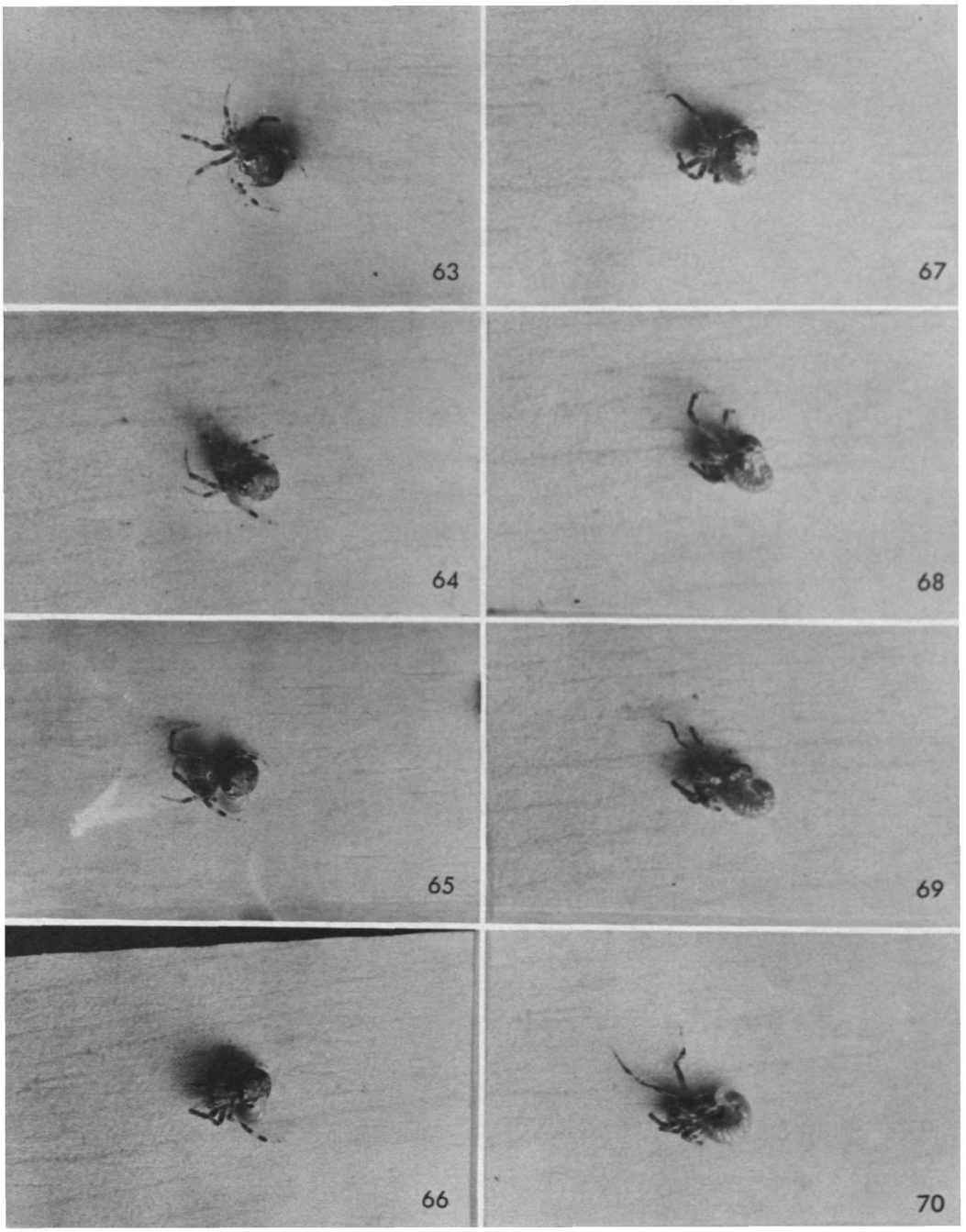
Nest 19 had two completed cells 14 and 18 mm long containing respectively 7 and 11 paralyzed araneid spiders (Figure 62). There were two paralyzed araneid spiders lying at the inner end of what would have become cell 3, but there was no mud annulus at the outer end to delimit this cell. The mud partitions closing cells 1 and 2 were 1.5–2 mm thick.

Prey

Juvenile araneid spiders belonging to a single species of *Neoscona* were used as prey in both nests. They ranged in length from 1.5 to 4.5 mm with a mean of 3 mm. The 7 spiders stored in cell 1 of nest 19 had a fresh weight of 50 mg and the 11 spiders in cell 2 weighed 82 mg.

Life History

The curved, sausage-shaped egg was laid obliquely on the anterolateral portion of the abdomen of one of the



FIGURES 63–70.—Egg and larval development on first spider, cell 2, nest 19, *Trypargilum c. collinum:* 63, egg, 1630, 17 April; 64, recently hatched larva, 0815, 19 April; 65, 1120, 19 April; 66, 2135, 19 April; 67, 0800, 20 April; 68, 2000, 20 April; 69, 0800, 21 April; 70, 1145, 21 April.

FIGURES 71–78.—Later larval development, cell 2, nest 19, *Trypargilum c. collinum:* 71, 1605, 21 April, 4+ hours after Figure 70; 72, 0800, 22 April; 73, 1145, 22 April; 74, 1610, 22 April; 75, 1200, 23 April; 76, 0730, 24 April; 77, 1915, 24 April, start of cocoon spinning; 78, 0800, 25 April, continuation of cocoon spinning.

last spiders stored in each cell (Figure 63). The eggs were 1.9 mm long and 0.58 mm wide. The abdominal segmentation was visible and the eggs were almost ready to hatch at 0045 on 19 April. The larvae were sucking fluid from the abdomen of the spider to which each was attached by 0730 the same day. Assuming that the eggs were laid on 16 April, as is most probable, we can estimate that 57–63 hours elapsed between oviposition and hatching.

The larvae continued to suck fluid from the abdomens of the spiders for about two and a half days (Figures 64–70). At 1400 on the 21st they were still feeding on the abdomens of the original spiders, but by 1600 they had transferred to other spiders and were feeding through the abdomens of those individuals. The growth rate now increased and during the next three days the larvae devoured all of the spiders (Figures 71–76). They were eating the last fragments of spiders at 1400 on 24 April and by 1915 they had begun to spin a few silken threads to form the suspensorium for the cocoon (Figures 77–78).

The spinning of this network of white silk, in which the cocoon proper would be suspended, required about 16 hours. Then the larvae spun the cocoon itself at the inner end of each cell, a process which required nearly two days. The cocoon walls were white and dry until the larva impregnated them with liquid feces about a day and a half after the cocoon was begun; this impregnation turned the walls dark brown and brittle.

The date of pupation was not determined, but a female *collinum* from cell 2 left the nest on 14 June, just 60 days after the nest was begun. The larva in cell 1 died after spinning its cocoon.

Literature Cited

Krombein, K. V.
1967. *Trap-Nesting Wasps and Bees: Life Histories, Nests, and Associates.* Smithsonian Press, vi + 570 pages, 29 plates, 36 tables.

U.S. GOVERNMENT PRINTING OFFICE: 1970 O—371-049

Publication in *Smithsonian Contributions to Zoology*

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy. (An instruction sheet for the preparation of illustrations is available from the Press on request.)

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages of typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date, page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within a taxon, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in or at the end of the taxon. For *references within the text,* use the author-date system: "(Jones, 1910)" or "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910, p. 122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

For *measurements and weights,* use the metric system instead of (or in addition to) the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the individual components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." (For capitalization of titles in foreign languages, follow the national practice of each language.) Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5–9." Spell out such words as "figures" and "plates" (or "pages" when used alone).

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.

SMITHSONIAN INSTITUTION
WASHINGTON, D.C.