Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined 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." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

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S. Dillon Ripley
Secretary
Smithsonian Institution
Biosystematic Studies of Ceylonese Wasps, XII:
Behavioral and Life History Notes on Some Sphecidae
(Hymenoptera: Sphecoidea)

Karl V. Krombein
ABSTRACT

Krombein, Karl V. Biosystematic Studies of Ceylonese Wasps, XII: Behavioral and Life History Notes on Some Sphecidae (Hymenoptera: Sphecoidea). Smithsonian Contributions to Zoology, number 387, 30 pages, 5 figures, 1984.—The wasps discussed here are solitary, ground-nesting species that construct unicellular nests. Notes are presented insofar as possible on nest construction and architecture, selection and storage of prey, life history, male activity, and associated commensals, predators, and parasites.

Ammophila laevigata Smith stores up to three paralyzed caterpillars per cell for its larva. The prey belong to the Satyridae and Noctuidae.

Ammophila atripes Smith stores a single larger noctuid caterpillar, perhaps that of a cutworm. Sometimes the female acts as a brigand, digging up the caterpillar stored by another female, destroying the egg of that wasp, then reburying the caterpillar in the original nest and laying her own egg upon it.

Sphex obscurs Fabricius preys only upon nymphal or adult tettigoniid grasshoppers belonging to the genus Conocephalus, practices mass provisioning, and provides 4–6 prey per nest.

Sphex sericeus fabrieii Dahlbom also practices mass provisioning; it was observed to have provided four prey in one completed nest. It was unique in that one female made an empty accessory burrow adjacent to the true nest as has been reported for another subspecies of S. sericeus (Fabricius). Most Ceylonese prey records are of Gryllacrididae as in several other subspecies of S. sericeus, but a few Ceylonese females provided Gryllidae or Tettigoniidae.

Sphex subtruncatus krombeini Vecht is a new taxon described by him in the appendix. It differs biologically from the other observed Ceylonese Sphex in that it practices progressive provisioning, that is, the egg is placed on the first prey specimen and additional prey are provided daily after the egg hatches. This wasp preys predominantly upon a wide variety of tettigoniid grasshoppers.
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Biosystematic Studies
of Ceylonese Wasps, XII:
Behavioral and Life History
Notes on Some Sphecidae
(Hymenoptera: Sphecoidea)

Karl V. Krombein

Introduction

The Sphecidae, or thread-waisted wasps as they are commonly called, form a conspicuous element of the Ceylonese wasp fauna. The species are of medium to large size (~12-33 mm long) and are readily recognized by the relatively slender body with an abdominal petiole consisting of one or two segments.

The three subfamilies comprising the Sphecidae all occur in Sri Lanka but only 7 of the 19 genera recognized by Bohart and Menke (1976) have been collected. Eight species of Sceliphroninae have been recorded, two of Chlorion Latreille and three each of Chalybion Dahlbom and Sceliphron Klug. Thirteen species of Sphecinae occur in Sri Lanka, nine of Sphex Linnaeus, and two each of Isodontia Patton and Prionyx Vander Linden. There are three species of Ammophilinae, all belonging to Ammophila Kirby.

The sphecid genera occurring in Sri Lanka are quite diverse in their nesting habits, prey, and other features of their biology. There are also marked behavioral differences at the specific level, as my technicians and I noted in the five species that we observed.

Among the Sceliphroninae, Sceliphron and Chalybion prey upon spiders, but members of the former genus construct mud nests consisting of contiguous cells or tubes, each cell containing one egg and a store of paralyzed spiders. Most species of Chalybion nest in pre-existing cavities or burrows, construct a linear series of cells, each capped by a mud plug and provisioned with one egg each and a store of paralyzed spiders; some species are known to nest in abandoned mud nests of other wasps. Some Chlorion, notably C. lobatum (Fabricius), which occurs in Sri Lanka, paralyse a large subterranean cricket, lay an egg upon it, and sometimes seal it in its own burrow. The cricket recovers from the paralysis and continues a normal existence until it is devoured by the wasp larva. Other extra-limital species of Chlorion are known to mass provision a single cell with a number of crickets, laying an egg on the first prey brought in. These crickets do not recover from the paralysis.

All Sphecinae appear to prey upon Orthoptera. Sphex and Prionyx are ground-nesters. Species of
the former genus prefer Tettigoniidae or occasionally Gryllidae or Gryllacrididae, whereas all species of the latter genus prey upon Locustidae. Most species of *Sphex* make multicellular nests, although some, including the three species we observed in Sri Lanka, make unicellular nests. *Prionyx* usually make unicellular nests, although one species is known to construct a multicellular nest. The species of *Isodontia* nest in pre-existing cavities and provision their cells with Gryllidae or Tettigoniidae. Most Sphecinae are mass provisioners but a few *Sphex*, including the endemic new subspecies *S. subtruncatus krombeini* Vecht, practice progressive provisioning.

The species of *Ammophila* also nest in the ground and usually make unicellular nests. The preferred prey are caterpillars, as we noted for the two Ceylonese species that we observed, but some species have been reported to prey upon sawfly larvae (Hymenoptera) or even occasionally weevil larvae (Coleoptera). Most species are mass provisioning, as are the two Ceylonese species that we observed, but several practice progressive provisioning. Three of the progressive provisioning species maintain several nests at one time.

The 4- and 5-digit numbers with suffixes are the field note numbers. Any specimens (wasps, prey, parasites) taken have been assigned the same number as the field note in which they were discussed.

The field notes and voucher collection of wasps and associated insects are currently in my office in the National Museum of Natural History, Smithsonian Institution. The field notes will be deposited eventually in the Archives of the Smithsonian Institution.

The only abbreviation not defined elsewhere in the paper is USNM (= the former United States National Museum collections now deposited in the National Museum of Natural History, Smithsonian Institution).


Acknowledgments.—My field work in Sri Lanka was funded by Smithsonian Research Foundation Grant SFG-0-6955, and travel was provided in part by grants from the Secretary’s Fluid Research Funds.

Within Sri Lanka I am indebted to Co-Principal Investigator W.T.T.P. Gunawardane, now Director, Department of National Museums, for planning itineraries and arranging accommodations for our field parties. I am particularly grateful to P.B. Karunaratne, former curator of insects at the Colombo Museum, who accompanied me on many of the field trips that resulted in the biological observations reported herein, and for permitting me to include his observations made during my absence on *Sphex sericeus fabricii* Dahlbom and *S. subtruncatus krombeini* Vecht, new subspecies. My Ceylonese technicians P. Fernando, J. Ferdinando, and D. Perera, as well as Karunaratne, helped me make extensive behavioral observations on color-coded females of *S. subtruncatus krombeini* in the Kanneliya section of the Sinharaja Jungle.

I am much obliged to J. van der Vecht, Putten, Netherlands, for identification of the taxa of *Sphex*, advice on nomenclature, and especially for providing the description of *S. subtruncatus krombeini*, new subspecies, that is included as an appendix.

I am indebted to the following specialists of the Systematic Entomology Laboratory, Insect Identification and Beneficial Insect Introduction Institute, U.S. Department of Agriculture, Washington, D.C., for identifications as follows: A.B. Gurney for most of the orthopterous prey of *Sphex*; A.S. Menke for species of *Ammophila* and information on their assignment to species groups; D.A. Nickle for some of the orthopterous prey of *Sphex*; D.M. Weisman for the caterpillar prey of *Ammophila*; and W.W. Wirth for larval Phoridae and information on their host relationships.

I thank Yu. G. Verves, Kiev University, USSR, for identification of Miltogramminae (Sarcophagidae) commensals.

available for study specimens from China identified by O. Piel as *Sphex nigripes* Smith.

G.F. Hevel, Department of Entomology, Smithsonian Institution (SI), prepared specimens of the five taxa of Sphecidae for photography by V.E. Krantz, Photographic Services (SI). G.E. Venable, Department of Entomology (SI), retouched and mounted the illustrations.

I appreciate very much the helpful editorial comments on the manuscript made by my wife, Dorothy, by R.J. McGinley and S.S. Gingras, Department of Entomology (SI), and by F.E. Kurczewski, Syracuse University, and to my wife also for helping correct galley proofs of this article.

**Ammophila laevigata** Smith

*Figure 1*

This small (♀, 14–20 mm long) member of the *sabulosa* Group is the most common and widely distributed taxon of Ceylonese Sphecidae. It occurs in both the Dry Zone and the Wet Zone, though more commonly in the former, at altitudes ranging from sea level to approximately 650 m, and in areas receiving average annual rainfall of 860 to 3900 mm. Bohart and Menke (1976:152) list the species as occurring also in India, Thailand, and Vietnam. Both *A. laevigata* and *A. basalis* Smith are smaller than *A. atripes* Smith (♀, 26–31 mm long). They have clear to lightly infumated wings rather than the yellow (♀) or infuscated (♂) wings of *A. atripes*. The former species differs from *A. basalis* in lacking transverse rugulae on the pronotal dorsum and scutum, and in having a broad patch of appressed silvery vestiture along the posterior margin of the mesopleuron rather than no such patch.

**Collection Locations and Dates.**—**Northern Province.** *Jaffna District:* Kilinochchi, 24–27 Jan; Pooneryn, 24–26 Jan, 7 Nov. *Mannar District:* Ma Villu, Kondachchi, 22–28 Jan, 17–21 Feb, 11–12 Apr, 20 Sep; Marichchukkadi, 26 Jan; 0.5 mi (0.8 km) NE Kokmotte Bungalow, Wilpattu National Park, 22–23 Jan, 25 May; Cheddikulam, 15–16 Jun.


**Western Province.** *Colombo District:* Colombo, 28–31 Jan; Ratmalana near airport, 13 and 19–21 Jan, 6 Jun; Gampaha Botanic Garden, 28 Jan, 27 Sep, 8 Nov; Labugama Reservoir, 2–4 and 16 Feb, 9 May, 11 Jul, 13–14 and 29 Oct.


*Figure 1.—* *Ammophila laevigata* Smith, × 4.
UVA PROVINCE. Badulla District: Badulla, 30 Sep.
Monaragala District: Angunakolapelessa, 21 Jan;
Buttala, 5 Jun; Inginiyagala, 12 Jun, 7–8 Sep.


The dates of activity at such localities as Ma Villu, Udawattakele Sanctuary, Labugama Reservoir, and Gilimale suggest that the species may breed throughout the year in favorable situations. We observed various details in the nesting cycle near Kokmotte Bungalow on 22 Jan, at Trincomalee on 10 Oct, at Ekgal Aru on 20 Feb, 11 Mar, and 10 Jun, at Hasalaka on 17 Feb, at Labugama Reservoir on 16 Feb and 9 May, and at Angunakolapelessa on 21 Jan. I noted a pair in copula (52576 G) at 1400 hrs, 25 May 1976, on a sand bank along an open jungle trail near Kokmotte Bungalow.

FIELD OBSERVATIONS. — *Ammophila laevigata* prefers to nest in flat areas rather open to sunlight and in a substrate ranging from sand to rather densely packed sandy loam, sometimes with intermixed small pebbles. The wasps excavated their burrows at angles ranging from almost vertical to 45° to the horizontal. The excavated soil was removed between the underside of the head and the forelegs. After the wasp backed out of the burrow with a load of soil, she flew forward or backward from half a meter to almost a meter and 5 cm above the ground, dropped the soil, and then flew back to the burrow to continue digging. I was unable to ascertain the time required to dig a complete burrow and cell.

We did not observe temporary closure of the burrow entrance when the wasp completed the nest, nor did we witness the customary orientation flight around the burrow before she departed to hunt for prey. However, we observed prey being brought into the nest several times, and each time the caterpillar was placed on the ground near the entrance while the wasp removed the temporary closure.

I watched the first nesting female (21675 C) at Labugama Reservoir on 16 February at 1448. Her nest was in a path of hard-packed sandy loam interspersed with small pebbles. She carried her paralyzed caterpillar, 14 mm long, head first beneath her and set it on the ground near the nest entrance, removed a larger pebble over the entrance and then reached in and brought out several smaller pebbles. Next she came to the entrance head first, reached out and pulled in the caterpillar head first. Either the burrow or the cell was too small because she came out in about a minute, reached in and pulled out the caterpillar, and then excavated several loads of soil, flying backward half a meter to drop each load. She then entered the burrow head first, turned around, came to the entrance and again pulled in the caterpillar head first. At 1457 she began construction of a temporary plug. She searched for a pebble of the proper size to plug the lumen of the burrow, discarding some as being too small, and finally put one of the desired size 1.3 cm below the surface. Then she scratched sand beneath her into the burrow, pressing it down with the front of her head, but not using a pebble to compact the soil. She occasionally interspersed a few pebbles with the sand. The burrow was filled nearly level at 1502 and she spent the next four minutes scratching and smoothing loose sand over the entrance. She then flew to several plants nearby for nectar and I captured her. The closing plug contained about ten tiny pebbles, each 1.0–1.5 mm in diameter, mixed with sand, and then a larger pebble 4–5 mm in diameter. The burrow was almost vertical, 2.5 cm deep and 4 mm wide, and terminated in a horizontal cell 1 cm long and 8 mm high at right angles to the burrow. The cell had a sand plug 2–3 mm thick, within which was a single satyrid caterpillar bearing the wasp’s egg attached on the right side between the spiracles of the first two abdominal segments. The egg was slightly curved, 2.8 mm long and 0.7 mm wide.

I observed another female (5976 A) at Labugama Reservoir beginning a nest at 1230 on 9 May. When I returned at 1305 she had completed the nest and constructed a temporary closure. I excavated the nest at 1545 and found that no prey had been stored. The entrance was concealed with loose sand, and the temporary closure contained sand and small pebbles to a depth of 4 mm and then a larger pebble. The burrow went
downward for 33 cm at an angle of 75° and terminated in an empty, horizontal subspherical cell about 1 cm in diameter.

On 22 January at 1300 near Kokmotte Bungalow D.W. Balasooriya saw a female (12277 C) flying toward her nest in a sandy path with a light green caterpillar. She alighted near the entrance, set down the caterpillar, removed the temporary closure, entered the burrow head first, turned around, and pulled the caterpillar headfirst into the nest. Balasooriya captured the wasp when she emerged a minute later. The burrow went downward at an angle of 75° and ended in a cell 6.4 cm below the surface. The cell contained a single noctuid caterpillar 18 mm long, bearing the wasp egg on the left side of the third abdominal segment. The egg was slightly curved, 2.7 mm long and 0.7 mm wide.

At Angunakolapelessa P.B. Karunaratne observed on 21 January what was probably storage of the last prey specimen and final closure of the nest (12179 C). At 1400 he noted a paralyzed caterpillar at the entrance of a nest that the wasp had just entered. The nest was in sandy soil in a dry stream bed. The wasp came out of the nest headfirst, grasped the caterpillar at one end and shoved the other end into the burrow. She went into the burrow, shoving the caterpillar ahead of her. A few minutes later she emerged, flew around the entrance in circles, alighted at the entrance, and searched for something to plug the cell. She picked up a piece of charcoal 15 cm from the entrance and carried it into the nest. Then she selected a smaller pellet of hardened earth and pushed it in. She flew around for a minute or two and selected a larger pellet that she carried on the ground to the entrance. It was too large to go into the burrow, so she carried it back to the spot where she had found it. Then she entered the nest headfirst, brought out two pellets of soil, leaving them at the entrance. Probably she removed some obstruction within the nest, for she next flew backward from the entrance, alighted and took the large pellet again. She tried unsuccessfully to place it farther down in the burrow, and brought it back to the surface. She reentered the burrow headfirst, backed out with some soil, and flew backward to drop it. She tried again to get the large pellet into the burrow and was successful in placing it farther down, together with the two smaller pellets removed earlier. Then she removed the larger one again, tried unsuccessfully to place it deeper, and finally carried it away from the nest. Next she placed several more pellets flush with the burrow entrance, and Karunaratne captured her at 1415. The burrow diameter was 6 to 8 mm, and penetrated the ground at an angle of 45° for 2.5 cm. The cell was at right angles to the burrow, 1 cm wide and 2 cm long, and the upper end was only 1 cm below the surface. The charcoal pellet first brought into the nest was at the cell entrance. The cell contained three paralyzed satyrid caterpillars. At the bottom of the cell was a large green one, 16 mm long, bearing the wasp’s egg, then a smaller green one, 13 mm long, on top of the first, and then the larger brown caterpillar, 18 mm long, that had been at the nest entrance at 1400. The egg was damaged in transit, but it had been glued on the right side of the second abdominal segment.

Two rather anomalous behavioral patterns were noted. On 10 June at Ekgal Aru Sanctuary Jungle, Karunaratne caught a female *A. laevigata* (61076 C) as she was digging in her nest. The wasp had been flying backward from the entrance, dropping excavated sandy loam about 0.5 m from the entrance. At the entrance were three paralyzed satyrid caterpillars, 12-20 mm long. Some ants were crawling on and around the prey. He captured the wasp and excavated the nest. The burrow went in at an angle of 45° in sandy loam soil for 3 cm and ended in an empty horizontal cell, 1.8 cm long and 1.3 cm wide. I presume that the caterpillars might have been removed to permit enlargement of the cell. None of the caterpillars bore a wasp egg, and perhaps it might have been removed by the ants before the prey were preserved in alcohol. However, it is also possible that the wasp Karunaratne observed was not the rightful owner, but a second female that had discovered the nest, removed the prey, destroyed the egg, and was about to re-inter the prey, laying her own egg on one of the caterpillars. Tsuneki (1968a:12-13) reported this behav-
ior by two females of the Japanese *A. sabulosa nipponica* Tsuneki, also a member of the *sabulosa* Group. Each wasp excavated the nest of another *A. sabulosa nipponica*, removed the caterpillar, ate the wasp egg, stung the caterpillar, and then replaced it in the nest and oviposited thereon.

The second curious behavior occurred at Ekgal Aru Sanctuary Jungle on 20 February. Balasooriya at 1030 saw a paralyzed caterpillar lying on the ground at the nest entrance just as an *A. laevigata* female (22077 F) returned with another caterpillar. This wasp (A) entered the burrow, turned around, and pulled in one caterpillar just as another *A. laevigata* (B) without prey alighted near the entrance. Wasp A in the nest dragged out the caterpillar it had just carried in and chased off wasp B. Then wasp A returned, flew off into the jungle with one of the caterpillars, and flew back in a few seconds without the prey. She then removed the second caterpillar in the same way and returned without it. She brought a pebble from the ground and pushed it into the burrow, and then brought another pebble and pushed it in. She continued plugging the entrance with loose earth at which time Balasooriya captured her. He excavated the nest, found the two pebbles near the entrance, and the cell at the end of a very steep burrow, 6.4 cm below the surface. The subspheroidal cell was about 0.6 mm in diameter and was completely empty. Wasp B did not return to the nest during this period. Possibly, Balasooriya observed the attempted appropriation of the contents of one nest by another individual, as I suggested above in note 61076 C.

Another possible explanation for the transport of the two caterpillars into the jungle by wasp A might be because she had a second nest to which they were carried. Tsuneki (1968a:9–10) reported a single female of *A. sabulosa nipponica* provisioning four nests simultaneously. These, however, were in close proximity, whereas a second nest of wasp A, if it existed, was some distance removed from the first.

**Discussion.**—There have been no earlier reports of the nesting of *A. laevigata*. In general it is similar in bionomics to *A. sabulosa nipponica* Tsuneki (1968a:3–16) in that the nest is unicellular, several prey are stored in the single cell, and a temporary closure of the burrow entrance is made before the wasp leaves to hunt for prey. Two of my observations suggest that the nest and prey of one wasp might be appropriated by a second, as noted by Tsuneki. I did not observe the use of a pebble to compact earth in the closure as Tsuneki did occasionally, nor did I ascertain that one wasp might have more than one nest. Tsuneki noted that under laboratory conditions the egg hatched in 36–40 hours, that the larva completed feeding in about four days, spun a cocoon, and that the adult emerged about a month after the egg was laid.

**Ammophila atripes Smith**

*Figure 2*

This handsome large species (♀, 26–31 mm long) belongs to the *clavus* Group. It has a wide distribution in Sri Lanka though not so wide as *A. laevigata* Smith, nor is it nearly as common as that taxon. It occurs commonly in the Dry Zone and sparingly in the Wet Zone and ranges from sea level to approximately 650 m in areas receiv-
ing average annual rainfall of 965 to 1950 mm. The Ceylonese population belongs to the typical subspecies that Bohart and Menke (1976:151) recorded from mainland Asia; other subspecies occur in Java, Japan, Korea and southern Manchuria, Taiwan, and the Ryukyu Islands. Typical A. atripes is distinguished from the other two species of Ceylonese Ammophila by its larger size (♀️ only 14–20 mm long in A. laevigata and A. basalis Smith), strongly yellowish (♀️) or infuscated (♂️) wings rather than clear to slightly infumated, and strong transverse ridges on pronotal dorsum, scutum, and propodeal dorsum (present but weak in A. basalis).

Collection Locations and Dates.—northern province. Jaffna District: Kilinochchi, 24–27 Jan. Mannar District: Kondachchi, Ma Villu, 11–12 Apr; Marichchukaddi, 26 Jan; 0.5 mi (0.8 km) NE Kokmotte Bungalow, Wilpattu National Park, 22–23 Jan, 15–16 Feb.


Collecting dates at Padaviya, Trincomalee, and Ekgal Aru suggest that typical A. atripes may breed throughout the year under favorable conditions.

Field Observations.—The following account is based on notes 21675 B and C, 5976 A, 52576 C, 61076 C, 12277 C, 21711 A and J, 22077 F, 101077 A, 12179 C, and 31179 A.

One female initiated burrow construction at 1045 on 23 January across the Moderagam Aru near Kokmotte Bungalow in dry sandy soil containing some humus under the baffle of a small Malaise trap, a site mostly exposed to the sun. She flew forward in several directions with the loads of excavated soil, and dropped them 0.7–1.3 m from the burrow entrance. The burrow was at least 80° to the horizontal, and she stopped when she reached a depth of about 2.5 cm. Apparently she must have come upon an obstruction for she began to scratch sand beneath her into the burrow to fill it, and placed a piece of dry leaf over the entrance when the burrow was filled. She then tried to find a new site in the immediate area, scratching soil here and there, and occasionally flying off about a meter to drop a piece of leaf or twig. Apparently a movement of mine frightened her away, for she disappeared and did not return to the site during my periodic visits throughout the day.

We found a small number of females nesting along a shaded path through the jungle at Uggalkaltota on 24–25 June. The four specimens of prey recovered from nests were large, bulky, dark, unpattered caterpillars, 45–47 mm long, apparently all belonging to the same species of Noctuidae. D.M. Weisman thought that they were nocturnal cutworms or borers because of the dark unpatterened integument. I believe that they were cutworms and that the wasps were hunting for them beneath debris on the ground or in burrows.

P.B. Karunaratne noted the first female (62478 B), 31 mm long, at 1030, 24 June, as she was closing her nest by throwing sand backward beneath her body and into the burrow. Then she grasped a small twig and placed it over the entrance at which time Karunaratne captured her. He was unable to trace the burrow because of the loose soil but he found the paralyzed caterpillar, 4.7 cm long, at a depth of 4.0 cm. The slightly curved wasp egg was 2.8 mm long and 0.9 mm wide, was attached obliquely to the right side of the second abdominal segment, and projected slightly forward.
At 1604 on the same date I found another wasp (62478 C) on this path camouflaging her nest entrance with bits of leaf, rotten wood, twigs, and a lump of mud. She was distributing the debris over a flat area of about 50 cm$^2$. One leaf was 7.5 cm long and some twigs were as long as 10 cm. She worked on the camouflage for 11 minutes before flying off, and I judged from the amount of debris that she had probably worked an equal length of time before I found her. Her paralyzed caterpillar, 4.5 cm long, was beneath 1 cm of loosely packed dirt beneath the debris, and was lying horizontally under dry crumbly soil with interspersed pebbles up to 12 mm in diameter. The egg was $2.5 \times 0.9$ mm, attached on the right side of the third abdominal segment and projected obliquely backward.

Karunaratne noted a third wasp (62478 D) closing a nest on the same morning. He dug up the nest on the 25th, and found a somewhat shriveled, paralyzed caterpillar of the same species in a horizontal cell at a depth of 5.0 cm. It was being attacked by small ants and the egg was already missing.

At 1015 on 25 June I saw a female $A. atripes$ alight on the woodland path, walk around an area of about a square meter, move a few leaves, and then begin to dig into the earth at an angle of 45°. After a minute and a half she had dug a burrow as deep as the length of her head and thorax. She then came out, scratched some loose soil beneath her into the burrow entrance, made a low orientation flight over the area, and flew off into the undergrowth at 1018. At 1025 a male, 20 mm long, alighted on the ground and crawled around the burrow site, presumably attracted by the scent of the female. I watched this area intermittently for several hours during the day, but the female never returned.

My last series of observations demonstrated that a female of $A. atripes$ will exhume the paralyzed caterpillar on which presumably another female has deposited an egg, feed on that egg, reinter the caterpillar, lay her own egg on it, and close the burrow. At 1108 on 25 June I observed a female (62578 B) on the same woodland path at the burrow entrance with a large caterpillar that already bore a wasp egg. She appeared to be struggling to get the caterpillar into the burrow. She abandoned this effort, crawled into the burrow and excavated some soil. She flew forward several times, dropping the soil a meter or so from the burrow, and then fed at the side of the caterpillar, undoubtedly on the egg. She reentered the burrow headfirst at 1112, turned around, came to the entrance headfirst, and pulled in the caterpillar whose rear end was still wriggling. She emerged headfirst half a minute later, flew around the area for a few seconds, returned to the entrance, and apparently pushed the caterpillar farther in. Then she brought small lumps of soil, one at a time, placed them singly in the burrow, and pressed them down with her head. Next she scratched loose earth backward beneath her into the burrow, occasionally entering the burrow to compact the soil with her head. She had filled the burrow almost to the surface by 1130, mostly with soil, but she had also incorporated a round seed about 3 mm in diameter and bits of other debris. I did not capture the wasp, and excavated the nest carefully from the side to expose the profile. The nest was in a gentle slope of dry, crumbly, occasionally firm soil. The burrow was 15 mm in diameter, and went downward at an angle of 75°. The entire burrow was plugged solidly, mostly with earthen fill. The caterpillar was lying on its side in a slightly curled position in a horizontal cell 20 mm below the surface. The cell was 30 mm long and 15 mm high. I did not fill the hole I had dug to expose the nest. Microscopic examination of the caterpillar showed the wasp egg of 62578 B attached on the right side of the third abdominal segment. Firmly attached on the following segment was the shriveled egg of the original wasp that had been sucked dry by 62578 B.

At 1430 I noted either 62578 B or another female digging in several places near that burrow site and I captured her. I watched another female from 1500 to 1520 digging in the area containing my excavation of nest 62578 B. Occasionally she palpated with her antennae the cell from which I had removed the caterpillar. This wasp finally flew from the area at 1537 after digging some 2
cm below the original cell. I noted a third female elsewhere on the path between 1430 and 1500 digging in several places and then partly filling each short excavation.

The impression I received from these latter observations is that some individuals have adopted a parasitic existence. Clearly, the normal female of *A. atripes* hunts for its supposedly subterranean prey by smell. Occasionally, however, a wasp must locate a nest containing the paralyzed caterpillar of another wasp instead of a healthy caterpillar. She then digs it up, destroys the egg of the rightful owner, re-inters the caterpillar, deposits her own egg on it, and closes the nest. I should add that later I examined all of the caterpillars obtained from nests of *A. atripes* and found remains of another egg only on 62578 B.

**Discussion.**—There have been no prior reports of the nesting of typical *A. atripes*. Tsuneki (1968a:36–41), however, observed the Japanese *A. atripes japonica* Kohl (reported as *A. claus japonica*). He found that the Japanese race excavated a nest, made a temporary closure, and camouflaged the entrance. The wasp stored only a single, large (5 cm), brown, noctuid caterpillar per nest. He noted that a pebble was used to compact the soil during the final closure. The burrow was nearly perpendicular and ended in a cell 5 cm below the surface and 25 × 15 × 10 mm in dimensions. He calculated duration of the egg stage at about 36 hours, that the larva completed feeding in about 2½ days, and then spun a cocoon about 25 mm long. He found a nest infested by small ants, and noted another nest being observed by parasitic flies (Miltogramminae ?). He did not observe parasitism of one wasp by another of the same species, although he reported this behavior for *A. sabulosa nipponica* Tsuneki (1968a:12–13).

*Sphex obscurus* (Fabricius)

*Figures 3*

*Sphex hirtipes* Fabricius, 1793, whose type depository is unknown, was listed (Vecht, 1961:32) as a questionable senior synonym of *S. obscurus*. I do not believe, however, that this synonymy is correct because Fabricius described *S. hirtipes* as being as large as *S. ichneumoneus* (Linnaeus), a much larger species than *S. obscurus*.

This is the smallest species of *Sphex* (♀, 12–17 mm long) known from Sri Lanka. In addition to its size, it is easily recognized by the black body and appendages, strongly yellow wings except apices, and the dense, appressed, silvery vestiture on the clypeus and propodeum. It has been collected at only a few localities, mostly in the Dry Zone, although it occurs commonly in the Colombo area in the Wet Zone. It is found in open areas with herbaceous vegetation from sea level to a couple of hundred meters in elevation, and with average annual rainfall of 1500 to 2600 mm. Bohart and Menke (1976:115) noted that it occurs also in India.

**Collection Locations and Dates.**—**North Central Province. Anuradhapura District:** Pada- viya, 18–19 May.


**Western Province. Colombo District:** Colombo, 17–23 Feb, 23 Jun, 8 Jul, 29, 30 Oct; Ratmalana, near airport, 13 and 19–21 Jan, 15–17 Feb, 8 May, 6 Jun, 29 Sep.

Dates of capture in and near Colombo suggest that *S. obscurus* may breed throughout the year.
under favorable conditions. All of our behavioral observations were made during January and February 1975 in a field across the airstrip from the Zoo Farm at Ratmalana.

**Field Observations.**—The soil had areas of both sand and sandy loam and was rather sparsely vegetated. *Bembix orientalis* Handlirsch and *B. borrei* Handlirsch were also nesting commonly in the field. We revisited this site several times in later years and captured a few specimens of *S. obscurus* in May, June, and September. We did not observe any nesting during these visits because the field had become densely overgrown with vegetation.

The following account is based on notes 11975 A, C, E, and F; 12175 A and B; and 21575 B, F, H–M, Q, and R. We observed nesting first on 19 January, excavated two of the nests on that date, and marked two that we dug up two days later. We noted ten nests on 15 February, dug up four of them on that date, and marked six that we dug up two days later.

**Nest Construction:** The nests were begun on bare, flat ground, usually in sand or sandy loam, and frequently adjacent to a grass tuft or small plant. The burrows were constructed at angles ranging from 45° to the horizontal to perpendicular and had a diameter of about 10 mm. The wasp brought the sandy soil to the surface between her head and forelegs, and then scraped it backwards beneath her to form a spoil heap. The spoil heap was low, flat, rounded, and eventually covered an area as much as 5 cm wide and 5 cm long behind the burrow entrance. When a wasp first began a nest she dug in the burrow for only 8–10 seconds before backing out with a load of soil and raking the soil backward over the surface for a few seconds. As the burrow lengthened she spent up to 30 seconds digging and then raked the soil backward beneath her to enlarge the spoil heap.

I was unable to ascertain the time required to dig a burrow and prepare the cell, but it must be lengthy. I saw one female (21575 B) enter a burrow at 0913 on 15 February, emerge a minute later, leave the burrow open, make a brief orientation flight, and then leave. She returned half a minute later, flew around for a few seconds, reentered the burrow and began to excavate, but was disturbed by us and flew off in a few seconds. She returned at 0920, entered the burrow, came out, and then went back inside several seconds later. She then began to excavate sandy loam as detailed above. I spent the next three hours visiting a series of nests, but returned occasionally and noted that 21575 B was still excavating soil at 0937, 0955, 1006, 1100, and 1125. She was not there at 1140 but had left the burrow entrance open, suggesting that the nest had not been completed. At 1200 she returned, entered the nest and then came out, and repeated this sequence several times until I frightened her. The burrow was still open at 1245 and 1355 but the wasp was not there either time. She was completing a final closure of the nest between 1755 and 1815 on 17 February. The fully stocked cell contained a half grown wasp larva and the remains or complete specimens of four prey.

P. Fernando observed another female digging in a burrow at 1100 on 21 January. She continued digging intermittently until 1400, when she flew away leaving the entrance open. We dug up this nest at 1745 and noted that the burrow was perpendicular and ended at a depth of 7.5 cm where the wasp encountered hard-packed soil and abandoned the nest. The lower 5 cm of the burrow was in damp sand. We noted three other burrows that had been abandoned at depths ranging from 2.5 to 10 cm because the wasps came to an impervious stratum. The top 3 cm or so of two burrows had been filled loosely with sand, and the third burrow was left open.

**Temporary Nest Closure:** On 19 January at 1340 I found wasp 11975 C making a temporary closure. She raked sand from the spoil heap backward beneath her into the burrow entrance, then turned around, entered the burrow headfirst presumably to compact the sand with her head. The plug must have been fairly deep for she was out of sight while inside the burrow. She remained inside about 10 seconds, then emerged and spent 5 seconds throwing sand backward into the en-
trance. She continued this sequence for 18 minutes, gradually raking the sand from farther and farther away from the entrance and throwing it in the general direction of the burrow. Then she came closer to the entrance, threw the sand inside and entered the burrow to compact it. At 1358 she left the area, leaving the upper 3.2 cm of the burrow empty. She had not returned to the nest when we excavated it at 1640. The burrow was at an angle of 70°, was 10 cm long, and the bottom 7 cm had been plugged with soil. This was just a temporary closure because the cell contained only two prey and neither bore an egg although one should have been laid on the first prey brought in.

I observed a second female (21575 R) bringing a prey into her nest at 1427 on 15 February. She remained inside the nest with the grasshopper for 20 minutes, emerged headfirst, ran about for a few seconds, re-entered the burrow, came out almost immediately, flew off and returned at 1449 and went inside the burrow. She came out almost immediately and proceeded to make a temporary closure as described above. We dug up this nest at 1530 after the wasp had left and found the upper 25 cm empty, then a plug of mixed dry and wet sand 2.5 cm thick along the vertical axis, and finally a horizontal plug for 7.5 cm to the cell. The latter contained a single prey bearing the wasp egg.

Final Nest Closure: I first saw wasp 21575 Q at 1350 on 15 February when she was filling in her burrow in the manner described in “Temporary Nest Closure” (above). She completed filling the burrow at 1445 after some interruptions, and then began to scrape sand from the shallow depression, 15 cm wide, in which the nest was made in order to make the surface more nearly level. She stopped this process every few minutes to fly onto one of the small adjacent plants to clean her antennae and legs, and perhaps to inspect the area to ascertain whether the nest entrance was adequately concealed. She completed distributing the sand over an area of several square centimeters by 1504, and even dragged in small pebbles and placed them randomly around the entrance. We dug up the nest and found that the entire burrow, 18 cm long, was plugged. The cell had been completely provisioned and contained a large wasp larva, one whole prey, a partly consumed prey, and fragments of two other prey.

P.B. Karunaratne observed final closure of the nest by 21575 B on 17 February. I had noted nest excavation by this female on the 15th. The nest entrance was open at 1630 on the 17th, and still open at 1700. However, by 1755 the burrow had been filled except for a small depression at the top. The wasp returned, filled the depression with loose sand, concealed the entrance with a few bits of dried leaves, and left the area at 1817. The entire length of the burrow was filled with compacted earth to a depth of 17.5 cm. The cell was about 3.7 cm from the burrow axis and contained a half grown wasp larva and four prey (two whole specimens and fragments of two others).

We observed a third female (21575 I) on 15 February making a final closure as described above for 21575 Q. We dug this nest before the wasp had plugged the upper 3.7 cm, and found the burrow firmly plugged with earth to a depth of 15 cm. The cell contained a wasp egg almost ready to hatch and six prey.

On 15 February at 1140 I observed another female (21575 K) excavating her nest. We marked the location and returned on the 17th. There was no trace of a nest at 1645, and the area around the entrance was covered with loose sand and scattered leaf fragments. The burrow was firmly plugged with earth to a depth of 25 cm. The cell contained a wasp egg and four prey.

Nests 21575 I and K described above show clearly that S. obscurus is a mass provisioning wasp, i.e., that an egg is laid on the first prey and that the cell is completely provisioned before the egg hatches. However, mass provisioning is occasionally delayed because of weather, lack of prey, or other reasons, so that the egg hatches and the larva begins feeding before the cell is completely provisioned. It appears that nests 21575 Q and B described above are examples of delayed mass provisioning and not of progressive provisioning as is true in S. subtruncatus krombeini Vecht.
Nest Dimensions: The burrows ranged from perpendicular to an angle of 45° to the horizontal, had a diameter of about 10 mm and varied in length from 10 to 28 cm. Occasionally the burrow curved around a root or other obstruction, but then continued downward along the same axis. Invariably, the cells were in damp sand, horizontal and constructed at the end of the burrow, although occasionally they were made at the end of a short horizontal section of the burrow. The cells were usually ovoidal and 1.3 to 2.5 cm long and 1 cm wide, but occasionally they were almost spherical.

Prey Identification: This population of *Sphex obscurus* preyed upon three species of long-horned grasshoppers, *Conocephalus* (Tettigoniidae, Conocephalinae). They used both sexes of nymphs and adults of *C. maculatus* (Le Guillou) and the brachypterous *C. signatus* Redtenbacher, and only one specimen of *C. longipennis* (Haan). We did not observe prey hunting and capture, but presumably the wasps hunted for their prey in the rather dense herbaceous vegetation surrounding the sparsely vegetated, sandy loam field where nesting occurred.

I observed prey transport and storage only once. The female (21575 R) flew in with her paralyzed prey at 1427 on 15 February. She set the grasshopper on the ground with its head near the entrance, entered the burrow headfirst, came to the entrance headfirst, reached out to grasp the prey and dragged it into the nest.

Fully stored cells contained 4 to 6 prey (average 4.6), usually a mixture of two species and both sexes of nymphs and adults. Altogether we recovered 11 *C. maculatus* (4 nymphs, 5 females, 2 males), 14 *C. signatus* (7 nymphs, 4 females, 3 males), only one female *C. longipennis*, and fragments of one specimen that could be identified only to the genus *Conocephalus*. The prey ranged from 7 to 21 mm in length, but the inedible tegmina extend well beyond the abdomen, so that total body length available to the wasp larva usually did not exceed 11 mm exclusive of the inedible ovipositor.

Immature Stages: Three wasp eggs were recovered from nests of 21575 I, K, and R. Unfortunately none remained attached to the prey. It is presumed that the wasp would have laid the egg transversely on the thoracic sternum of the first prey brought into the cell, with the cephalic end glued between the fore and mid coxae. The eggs were slightly curved, 3.0 mm long, and 0.5–0.6 mm wide. No data were obtained on duration of the egg stage, but presumably the egg hatched within two days after oviposition.

We opened two nests, 11975 C and 12175 B, each of which contained two prey but no egg. It is possible that in each case the egg may have been dislodged during our excavation of the nest for the egg does not seem to be attached firmly to the prey.

We obtained half- to full-grown larvae from a number of cells but did not try to rear any. I presume that the wasp larva reaches maturity within 3 to 4 days after hatching and then spins a cocoon from which an adult will emerge in several weeks.

Male Activity: We observed no activity by males either during nest construction or during prey transport. Perhaps in this species mating precedes any nesting activity by females.

Parasites: The only parasites I noted were three Miltogramminae (Sarcophagidae) on 15 February. The first was a female of *Protomiltogramma seniorwhitei* (Verves), which perched on a grass stem near the burrow while wasp 21575 H was digging its nest at 1025. Later in the afternoon at 1425 wasp 21575 R carrying prey flew toward its nest, followed closely by two miltogrammine flies. I captured one male, 5.5 mm long, as it alighted on the ground near the entrance. It too was a specimen of *P. seniorwhitei*.

Inasmuch as *Sphex obscurus* is not a progressive provisioner as is *S. subtruncatus krombeini* Vecht, it is probable that parasitism of the nest by *P. seniorwhitei* would result in the death of the wasp larva from lack of food. A wasp that practices progressive provisioning would bring in enough prey so that both the wasp and fly larvae would reach maturity as I found in *S. subtruncatus krombeini*.

Discussion.—There have been no published reports on the biology of *S. obscurus*. I had hoped
to obtain additional information, but as noted above we found no wasps nesting on visits during subsequent years.

**Sphex sericeus fabricii** Dahlbom

**FIGURE 4**

This large handsome species (♀, 22–26 mm long) is widely distributed in Sri Lanka in both the Wet Zone and the Dry Zone where it occurs from near sea level to about 700 m, and in areas with average annual rainfall ranging from 1000 to 3900 mm. J. van der Vecht and Krombein (1955:36–37) recorded it also from India. It is the only Ceylonese *Sphex* in which both sexes have about six strong transverse ridges on the propodeal dorsum; such ridges are lacking in all other species. In addition the female has the legs, basal abdominal segments and parts of mesopleuron, scutellum and postscutellum light red.


**CENTRAL PROVINCE.** Kandy District: Udawatta-kele Sanctuary, Kandy, 18–20 Mar, 21–22 Sep; Aruppola, 18 Apr.


**WESTERN PROVINCE.** Colombo District: Colombo, 14 Jan; Nugegoda, Papiliyana, 3–4 May; Gamapaha Botanic Garden, 27 Sep.


**UVA PROVINCE.** Monaragala District: Mau Aru, 24–26 Sep.


Dates of collection in Trincomalee and Sinharaja Jungle suggest that this wasp may be active throughout the year in favorable situations.

**FIELD OBSERVATIONS.**—We made observations of this taxon during 1975 and 1976 under notes 11375 C, 41875 D, 31276 A–C, 31576 B–D, 51676 A, 61276 B, and 62076 A.

P.B. Karunaratne found several females nesting in flat bare ground within the compound of the Padaviya Circuit Bungalow during the period 11–23 March 1976. He watched nesting activities at several sites with several nests being made successively by the same specimen of wasp, but he made no notes on the manner of nest excavation.

Two wasps were digging nests at 1715 on 11 March when Karunaratne reached Padaviya, and he observed also one or two sealed nests in the area. On 12 March at 0930 one female (31276 A) was digging in her nest. At noon the entrance to the nest was open and the wasp was not in the area. At 1415 the wasp flew in with a prey between its legs and mandibles. She alighted near the entrance, dropped the nymphal orthopteran, cleared the entrance after removing a fallen leaf, and entered the nest leaving the prey on the ground. Soon she appeared head first at the entrance, grasped the prey by the palpi, and pulled it into the burrow. A minute later the wasp emerged and immediately re-entered the
nest and Karunaratne heard her buzzing as she plugged the cell for nearly 10 minutes. She came out for a short time at the entrance, then re-entered the burrow, and came out a minute later. Then she made a brief reconnaissance flight over the area and flew off, leaving the nest entrance open. The wasp did not return during the next hour, but when Karunaratne returned at 1530 he found the wasp closing the burrow entrance, a task which she completed in 10 minutes. During this period she walked to the burrow of 31276 B, some 15–20 cm distant, and kicked some earth backward into it. At 1545 this wasp began a new burrow not far from the earlier nest, excavated it for five minutes and then abandoned it, leaving the entrance open. This last behavioral trait is suggestive of the empty accessory burrows that Tsuneki (1963) described for several other species of Sphex. When Karunaratne revisited this nesting site at 1705 he found that the wasp had reopened her nest and was working inside; probably she had just brought in another prey. At 1720 she emerged and began to close the burrow entrance by kicking backward into the burrow the loose excavated soil near the entrance. She had nearly completed this closure at 1745 when the observer left. Karunaratne visited this nest occasionally until 15 March and never saw the wasp reopen the nest.

He had seen wasp 31276 B working on a nest late on 11 March. It was located only about 17 cm from that of 31276 A, and the entrance was open at 0930 on 12 March but the wasp was not in the area. While Karunaratne was watching the nest of 31276 A at 1430, he saw wasp B flying directly to her nest entrance straddling a brown orthopterous nymph. She dropped the prey near the entrance of her nest (B) and then walked to nest A whose entrance was open. She searched around the nest momentarily, then entered the nest and remained for 10 minutes. She came out without prey, walked to her own nest, went inside and then emerged headfirst. She walked to her prey, straddled it and dragged it headfirst to the burrow entrance. She left the prey there, re-entered the burrow, returned immediately to the entrance head first, reached out and tried to pull the prey into the nest by its palpi. The claws of the hind legs of the prey caught on the ground and the wasp had to come out of the burrow, turn the prey on one side and then back into the nest dragging the prey behind her. She remained inside for 10 minutes and Karunaratne could hear her buzzing as she closed the burrow at the cell. After this she emerged, kicked back into the burrow some of the loose earth around the entrance, and then went in and pressed the loose earth firmly with her head. She continued this for 10 minutes by which time the burrow was closed halfway down. She then left the nest for five minutes and returned to close the burrow completely between 1525 and 1530 until there was no trace of the nest opening. Karunaratne observed the nest site occasionally until 15 March and never saw the wasp revisit the nest.

Wasp 31576 B was excavating a nest at 0800 on 15 March. She was still working on this nest from 1220 to 1230 and again from 1400 to 1426 when she started to close the nest. At 1435 this wasp started a new burrow which Karunaratne designated as 31576 D. The wasp dug for an hour and then departed, leaving the entrance open. The entrance to this burrow was closed at 0700 on the 16th. The wasp had returned, was opening the nest at 0735 and was still digging at 0800. The nest entrance was open at 1730 when Karunaratne returned. He noted no further activity at nests 31576 B and D through 22 March. Both nests were empty when he excavated them on the 23rd. I suspect that nest D was actually an empty accessory burrow, not a true nest.

Karunaratne found the last nest (31576 C) at Padaviya early in the morning on 15 March, but he did not see the wasp on several visits during the day. At 1400 while watching 31576 B, he saw wasp C fly in with a brown orthopterous nymph. She left the prey at the nest entrance, went into the nest, reappeared headfirst at the entrance in a minute, grasped the prey by the mouthparts and dragged it into the burrow. The wasp was closing the nest for 15 minutes and left it half closed at 1420. At 1435 she returned and contin-
ued closing the nest until she was captured by the observer at 1445.

**Nest Dimensions:** Measurements were recorded for only three of the nests at Padaviya, 31276 A and B, and 31576 C. The burrow diameter was 10–15 mm and entered the ground at an angle of 35°–45° for 4–7 cm to a depth of 2.5–5 cm. The burrow then turned horizontally for a distance of 3–10 cm. The cell was 20 mm wide and 25–33 mm long. The burrow from the cell to the surface was firmly packed with soil. A fourth nest (51676 A) in compacted soil at China Bay, Trincomalee, had a burrow diameter of 1 cm and went into the ground at an angle of 70°. The cell was on a ledge between two rocks 7 cm below the surface, and was 20 mm wide and 5 mm high. This nest had no accessory burrow.

All observations on nests confirm that this wasp makes a unicellular nest as do *Sphex obscurus* (Fabricius) and *S. subtruncatus krombeini* Vecht, but that it does not practice progressive provisioning as does the latter taxon.

**Prey Identification:** The normal prey of *S. sericeus* appears to be members of the Gryllacrididae, wingless long-horned grasshoppers. Williams recorded *Gryllacris brevispina* Stål as prey of the Philippine *S. s. nigrescens* Vecht and Krombein. The prey in all nests at Padaviya described above were nymphal and adult males, 13–18 mm long, of the gryllacridid, *Melaneremus* sp., probably *M. henryi* Karny. Karunaratne captured a female wasp (41875 D) at Aruppola flying with a paralyzed male of *Gryllacris* sp. However, the single nest at Trincomalee, probably not completely stored, contained the female nymph of a tettigoniid, *Ischnophyllus crassus* Henry, 18 mm long, and two gryllids, *Madasumma marginipennis* (Guérin), a male nymph, 19 mm long, and an adult.

Eggs were found in only two cells, each on the prey at the inner end of the cell. They were slightly curved, sausage-shaped, 4 mm long and 0.8 mm wide. One from Padaviya (31576 C) was attached behind the right forecoxa of the prey and extended obliquely on the sternum to the base of the left hindcoxa. The other from Trincomalee (51676 A) became detached from the prey after being placed in alcohol, but I noted that the egg was attached between the first and second pairs of legs. One nest at Padaviya (31276 A) contained four orthopterous nymphs that exhibited reflex movements of their legs and antennae, but Karunaratne was unable to find an egg or larva on the prey or in the cell.

**Parasites:** This wasp does not seem to be much afflicted by parasites. I noted one wasp (11375 C) alternately flying and perching on vegetation at 1100 on 13 January along a logging road in the Kanneliya section of the Sinharaja Jungle. When it returned preyless at 1130, it was being followed by two miltogrammine flies (Sarcophagidae), of which I captured one, a female of *Metopia (M.) argyrocephala* (Meigen). At Padaviya, Karunaratne observed two small flies with speckled wings trying to enter a burrow (31276 B). The wasp tried to drive away these flies. Later, they entered the nest after the wasp had taken in prey, and he also noticed that they approached the prey lying near the entrance while the wasp was in the burrow.

**Discussion.**—There have been no previously published reports on the biology of *Sphex sericeus fabriici* Dahlbom, which apparently is restricted to the Indian subcontinent. Several authors have contributed notes on two other subspecies, *S. sericeus lineolus* Lepeletier, which occurs from Sumatra and Burma northward to China, Taiwan, and the Ryukyu Islands, and *S. sericeus nigrescens* Vecht and Krombein from the Philippines. Piel (1935:293–294, figs. 19, 20) published on the former subspecies from China under the name *S. (Proterosphex) aurulentus* Fabricius, variety *lepeletierii* Saussure. Tsuneki (in Tsuneki and Iida, 1969:3–4) made brief notes on a Taiwanese population of *S. s. lineolus*. Williams (1919:124–125, fig. 60; 1928:87) contributed some notes on the Philippine subspecies *S. s. nigrescens* under the name *Chlorion aurulentus* (Fabricius), variety *ferrugineus* (Lepeletier).

All authors commented on the preference of *S. sericeus* to nest around or in human habitations in small aggregations as was true of our population.
at the Padaviya location only. Williams found it nesting in dry soil sheltered by eaves or even in the dirt floor of a shed, stall, or outhouse, and sometimes searching for its prey in the walls or ceilings of huts constructed in part from nipa palm fronds. Piel observed it nesting beneath the gutters of a veranda and in the subsoil of basements. Tsuneki noted that it nested “in the ground under the bed-floor or in the corner of the well trodden earth floor” but never in an open field. Tsuneki estimated that a room about 4 m by 3.5 m contained 5–10 wasp nests.

Williams noted that the burrow was oblique and extended two inches below the surface. The terminal enlargement contained a mature female and two nymphs of *Gryllacris*. The smallest nymph had a newly hatched wasp larva feeding between the first and second coxae. A cocoon from another nest was stout, pale brown, and 28 mm long. Piel observed a female flying with an orthopteran that was different from the katydid (*Phaneropterinae*) upon which typical *S. subtruncatus* Dahlbom preyed.

Williams observed prey capture. The preferred prey, *Gryllacris brevispina* Stål, hides during the day in empty leaf-roller nests or among dried leaves. The wasp searches for the prey among the leaves, tries to force it out by unrolling the curled leaf or biting a hole in the leaf through which she can sting the prey.

Both Williams and Piel commented on the habit of *S. sericeus* of roosting in some numbers on bunches of dead leaves, seed pods, or pieces of straw. Williams found as many as 42 wasps congregating nightly on a band of straw about 2.5 cm wide and 30 cm long beneath a nipa house. Piel found only males in his aggregation.

Piel noted the wasps visiting flowers of *Vitex negundo* and *V. japonica* for nectar. None of the authors observed mating.

Reference was made earlier in my description of the nesting activities of 31276 A at Padaviya to the possible construction of an empty accessory burrow. Tsuneki (1963:15–20) and Evans et al. (1982:219–222, fig. 1) described such accessory burrows for the Japanese *S. argentatus fumosus* Mocsár and the Australian *S. cognatus* Smith, respectively. Both authors surmised that these empty accessory burrows might be constructed for deception of parasites. Tsuneki noted that *S. a. fumosus* constructed two or three such burrows around the true nest entrance. Evans et al. discovered that some populations of *S. cognatus* constructed two or three such burrows around the nest entrance, but that other populations made no such burrows. The latter situation may be true also in the Ceylonese *S. s. fabricii* for we found only one nest with such a burrow. Ribi and Ribi (1979) studied two colonies of the Australian *S. cognatus* and noted that no accessory burrows were constructed.

**Sphex subtruncatus krombeini** Vecht, new subspecies

*Figure 5*

This large *Sphex* (♀, 22–27 mm long) is described by J. van der Vecht in the appendix to this contribution. It is found only in the Wet Zone of Sri Lanka where the annual rainfall averages 1950–3900 mm and the altitude ranges from 100 to 600 m. It is easily recognized for it is
the only Ceylonese Sphex having infuscated wings with violaceous reflections. In addition, the female is the only taxon in which the mid- and hind-femora and tibiae are red; the male hind femur is usually red, but occasionally the legs are entirely black in that sex.

**Collection Locations and Dates.**

**CENTRAL PROVINCE.**

**WESTERN PROVINCE.**
Colombo District: Labugama Reservoir Jungle, 14 Jul.

**SABARAGamuWA PROVINCE.**

**SOUTHERN PROVINCE.**

Dates of collection in Gilimale, Weddagala, and Kanneliya suggest that the wasp may be active throughout the year except possibly during periods of little or no rainfall.

**Previous Research.**

*Sphex subtruncatus* Dahlbom is a wide-ranging, polytypic species of the Oriental Region with perhaps as many as a dozen subspecies ranging from the Indian subcontinent through southeastern Asia eastward to Sumba and Flores Islands, Indonesia, and northward into China, Korea, the Philippines, and Taiwan (van der Vecht, in litt.). It does not occur in Japan as stated by Bohart and Menke (1976:117).

Several authors have published biological notes on some of the subspecies. Henry (1932:232-233) contributed brief notes on the prey and nest of *S. subtruncatus krombeini* under the name *S. nigripes* Smith, a synonym of typical *S. subtruncatus*. Tsuneki (1963:41-48, fig. 9, tabs. 7-9) published extensively on the subspecies occurring in Korea and identified the wasp as *S. haemorrhoidalis* Fabricius. Tsuneki (1968b:54) and Tsuneki in Tsuneki and Iida (1969:1-3) published on the Tai-wanese subspecies, calling it the Formosan race of *haemorrhoidalis*. Williams (1919:128-131, figs. 64-66) contributed extensive notes on the Philippine subspecies *S. subtruncatus siamensis* Taschenberg, misidentifying his wasp as *Ammobia mutica* (Kohl).

Piel (1935:289-293, figs. 13-18) published notes on a Chinese wasp that he called *S. haemorrhoidalis* Fabricius, variety *nigripes* Smith. *Sphex nigripes* is a synonym of *S. subtruncatus*, but I am convinced that Piel misidentified his specimen and that it is some other taxon. He observed only a single nesting female that dug a nest on 24 August and stored it completely with four prey on the following day. This is a remarkable behavioral difference from the several subspecies of *S. subtruncatus* that Williams, Tsuneki, and I observed, all of which practiced progressive provisioning. Piel's wasp then began another nest nearby on 25 August and completed it on the next morning. Piel dug up this second nest to observe the architecture. The wasp then began a third nest nearby, completed it, and brought the first prey to it on the morning of the 27th. Adjacent to each of the three nest entrances the wasp prepared one or two empty accessory burrows such as I described earlier for *S. sericeus fabricii* Dahlbom. Furthermore, Vecht (in litt.) stated that the female of *S. subtruncatus* has more slender mandibles than Piel figured for his wasp. Neither Williams, Tsuneki, nor I observed the other subspecies of *S. subtruncatus* making accessory burrows, thereby substantiating the probability that Piel's observations were not made on *S. subtruncatus*. I have examined two pairs identified as "nigripes Smith" from the Piel collection now housed in the Academia Sinica, Beijing, and one pair collected and identified by Piel as "haemorrhoidalis v. nigripes" in the Paris Museum. All are *Sphex subtruncatus* Dahlbom, but one pair is from Ibing, Kiangsu Province, one female from Chenkiang, Kiangsu Province, and the others from Chusan, Chekiang Province. Piel's observations were made on No. 1206, a female from Shanghai, a specimen apparently no longer in existence if Piel did, indeed, collect it. The possi-
bility remains, consequently, that his notes were not made on a specimen of *S. subtruncatus*. Two males from Shanghai in the Paris Museum are *S. subtruncatus* but they were not collected nor identified by Piel.

**FIELD OBSERVATIONS.**—Our most extensive notes on *S. subtruncatus krombeini* were made in the Kanneliya section of the southwestern Sinharaja Jungle and bear code numbers 31272 A, 81472 A-D, 81572 A-G, 10973 A, 11275 A-E and G-J, 11375 D, 11575 A, D, E, H-K, and M, 11775 B, and 18 color-coded wasps during the period 7–12 Oct 1973. We obtained a few notes from Weddagala in the northeastern Sinharaja Jungle coded as 62176 B and 21077 A-C. Some observations were made in the Induruwa Jungle at Gilimale on the southwestern slope of the Adam’s Peak Sanctuary and were coded as 61776 E-G, 61976 E, 2777 A, and 31479 A. P.B. Karunaratne observed an aggregation in Udawattekele Sanctuary, Kandy, and code numbers 41875 A-C, 41975 A-G, and 51175 A-F were assigned to these wasps. Finally, we obtained one prey and nest record, 71478 D, in Labugama Reservoir Jungle.

The color-coded wasps were identified by letter and number, e.g., YT 3, GTW 5, standing respectively for the third wasp bearing a yellow spot on the thorax and the fifth wasp bearing a green spot on the thorax and wing.

My first extended observations on this wasp were made on 14 and 15 August 1972 along the edge of a logging road in Kanneliya. Two of the nests that we excavated, 81572 F and G, established conclusively that *S. s. krombeini* practices progressive provisioning. This behavioral trait is characterized by the wasp preparing a nest, capturing a prey, putting it in the cell and laying an egg upon it. After the egg hatches the wasp brings in additional prey on a day-to-day basis as more food is needed. Occasionally, several prey may be brought in before egg hatch, but in any case the wasp brings in additional prey after the larva begins feeding on the first prey. Nest F contained a small wasp larva, 5 mm long and 1.8 mm wide at the middle, feeding on the first prey brought into the nest, a katydid nymph, 15 mm long, *Hexacentrus unicolor* (Serville), and seven other katydid nymphs, five of a species of *Phaneropterinae*, 9–15 mm long, one of a species of *Xiphidiopsis* or related genus, 10 mm long, and another *H. unicolor*, 20 mm long. Wasp F returned to the nest while we were digging it but she carried no prey on this trip. Nest G contained two *H. unicolor* nymphs, each 8 mm long, one of them bearing a small wasp larva only 1.5 mm wide at the middle; the wasp flew in with a third *H. unicolor* nymph, 10 mm long, just as I finished digging the nest. Both Williams and Tsuneki independently established that the Philippine, Korean, and Taiwanese subspecies practiced progressive provisioning, although Williams did not recognize that he was witnessing true progressive provisioning.

The leisurely pace of provisioning of a few wasps in 1972 suggested the possibility that a wasp might be provisioning two or more nests simultaneously such as has been recorded for several species of *Ammophila*. Accordingly, on my next trip to Kanneliya, 7–12 Oct 1973, we color-coded a number of wasps with acrylic colors. There were several small aggregations scattered along several kilometers of a logging road, and four Ceylonese technicians and I spent many hours of the six days watching a number of marked individuals. We found no evidence whatsoever of a wasp maintaining more than a single nest, but we obtained a great deal of information on nest construction and architecture, temporary and final closures, orientation flights, and prey transport and placement in nest.

**Nesting Sites:** Almost all of the nesting sites at Kanneliya were located on relatively steep banks of 45° to 80° cut along logging roads in the rain forest. Usually the wasp selected a small, more or less level area of a few square centimeters on the bank to serve as a platform from which she could dig into the steep slope. A few wasps at Kanneliya nested on more gently sloping ground above a low cut. The ground here was a heavy, damp, light brown, clayey soil containing rocks. The few wasps observed at Weddagala selected similar sites for their nests, but here the soil was a damp
sandy loam with quite a high sand content.

At Gilimale and Udawattakele the wasps nested in relatively level ground, although steep roadside banks were available at the latter locality similar to those preferred at Kanneliya and Weddagala. The nests at Udawattakele were on a level area of a former carriage road where the soil was a red clay mixed with coarse grains of quartz from deteriorated sandstone. All nests at Gilimale were on level or sloping jungle trails with compacted earth due to the constant foot traffic, or occasionally in sandy loam. Nests at Kitulgala were also in compacted earth along jungle trails but we did not excavate any of them.

It appears that *S. subtruncatus* normally nests in bare, level, or slightly sloping areas. Henry saw nests of the Ceylonese subspecies at Kitulgala along a jungle trail. Williams and Tsuneki found that the Philippine, Korean, and Taiwanese subspecies nested in flat areas on paths, along roads, or in sparsely vegetated fields. The atypical nesting sites at Kanneliya and Weddagala may have been an adaptation to avoid nesting at the bottom of the slope where there would have been frequent runoff from the rains. The level road surfaces at these two localities were not available because the logging lorries often churned much of it into a sticky mud.

*Nest Construction:* When the wasp selects a suitable site for a nest, she starts to bite out pieces of the heavy earth with her mandibles, buzzing loudly as she does so. As the burrow deepens she carries out the excavated soil in the basket formed with her forelegs and mandibles, and throws it backward beneath her body to form a spoil heap. Usually she brings out a load of soil at intervals of 15 to 50 seconds. Frequently she pauses on the ground to clean her antennae after dropping a load. Occasionally, she rakes the spoil heap backward to level it and spread it over a wider area. If she is nesting on a steep bank, much of the excavated soil falls to the bottom of the bank, but if she nests on level ground the spoil heap is low and elliptical, about 12.5 cm long and 7.5 cm wide.

The time required for the wasp to dig the burrow and the cell varies with the type of soil, sometimes with external factors such as humans or vehicles interrupting the work, or commensal flies lurking near the entrance, and, perhaps, occasionally when a wasp is less industrious than others in the nesting aggregation.

Wasp RT 1 began a burrow at noon and by 1205 the burrow was 12 mm deep. She was frightened off for periods of 8 and 27 minutes by my approaching too closely, and once she left the area for 2 minutes for an unknown reason. At 1425 she began to make a temporary closure at the burrow entrance, so actual digging of this nest required about 1¾ hours.

We found wasp 81472 D digging a burrow at 0830. She must have been working no longer than 15 minutes for the burrow was only about 6 mm deep. We did not keep her under periodic observation, but sometime before 1400 she had made a temporary closure at the nest entrance and had left the area.

Wasp YT 1 began a new nest at 1010 after completing the old one nearby. She left the nest some time thereafter and returned at 1100 and resumed digging. She was not watched during the period 1145 to 1235, but at 1238 she completed the nest and began to make a temporary closure.

Commensal sarcophagid flies belonging to the Miltogramminae sometimes frustrate completion of a nest. We saw wasp RT 6 beginning a nest at 0850 on 10 October. She was observed digging at 0925 and 1012 but had left the nest before 1030. She returned to digging at 1035 and continued until at least 1155, but had left the nest before 1222. By 1321 she was back at her nest but had not resumed digging because two Miltogrammini were hovering or alighting near the entrance. She continued to guard the nest until at least 1525, but had left it by 1555 and had not returned by 1630. The nest entrance had a temporary closure at 0830 on 11 October but the wasp was not there, nor was she at the nest at 0845, 0910, 1015, and 1050-1110. At 1115 she was digging until 1130 when she began to close the entrance. She was still guarding the entrance at 1148 and
at 1220, and there were miltogrammine flies hovering around a nest lower on the bank. The wasp had left by 1300 and was not seen at the nest during our six subsequent visits ending at 1605. The wasp was not at the closed nest at 0815 on 12 October but she was working at the entrance at 0837 and left at 0840; there were no flies there during that period. When we dug up the closed nest later that day, we found only a burrow 6 cm long and the wasp had not constructed a cell.

Tsuneki and Williams found the same kind of nest construction for the Korean and Philippine subspecies. Tsuneki commented on the loud buzzing ("dzi dzi" sounds) made by the wasp while digging.

The Ceylonese wasp occasionally uses an old burrow rather than digging a new one. Presumably a newly emerged female sometimes (always?) uses the nest from which she emerged for her first nest. We observed wasp 11775 B digging in a nest in a 20° slope of gravelly loam. There was an empty cocoon near the entrance and we presumed that she was cleaning out an old nest. Later on the same date but at a different nesting area on slightly sloping area on slightly sloping gravelly loam we saw 8-10 emergence holes with remains of cocoons on the surface adjacent to some holes, suggesting that these nests were being cleaned out for re-use. Tsuneki considered that the Korean subspecies also utilized the old cell in which they were born.

Upon rare occasions we observed females fighting when two nest entrances were close to each other. This happened when one female apparently could not locate her own sealed nest entrance and tried to open the closed burrow of another. If the rightful owner returned during this event, she would dash at the other and the two would fly around each other in tight circles buzzing loudly until the interloper flew away.

Abortive Burrows: We noted at Kanneliya the occasional occurrence of empty burrows without closing plugs on the sloping banks in which most aggregations nested. We dug up 13 of the burrows without closing plugs and found that most had been abandoned after running into a rock. These burrows were 1.5-7.0 cm long and none terminated in a cell. We watched some of the wasps excavating the abortive burrows, and found that in some instances the wasps were simply frightened off by passing vehicles or humans and immediately began another burrow on the bank a few meters away.

Also at Kanneliya we obtained an anomalous abortive burrow. Wasp RT 1 began a permanent closure of a nest at midday on 9 October. She was not at the nest at 0900 on the 10th, but she was working on the closure by 0942 until 1000. She then flew about 2 m distant to another burrow that already was about 2.5 cm deep. Three minutes later she returned to the first nest and worked on the closing plug for half a minute and then flew off. She returned to the nesting site at 1025, flew to each burrow but did not work on either, and left the area at 1029. She flew back to the first nest at 1111, stayed there half a minute but did not work on the plug. She then rested motionless on the bank halfway between the two nests, and at 1116 began to make a temporary closure in the second nest about 2 cm from the entrance. She was frightened from the area by a passing lorry at 1120. At 1140 she flew back to the first nest and worked on that closure again. At 1150 she flew to the second nest and started to make a closure about 1.2 cm from the entrance. By 1159 she had compacted so much earth into the burrow that only a shallow rounded depression marked the burrow entrance. Immediately she flew to a spot halfway between the first and second burrows and started to dig a third burrow. At 1205 this burrow was 1.2 cm deep and she began to fill it with excavated earth from the spoil heap. She made an orientation flight around the area at 1207 and left. She returned at 1246, opened the third burrow, and soon was so deep inside that she could not be seen while she deepened the burrow. She was frightened off at 1254 and returned to resume digging in the third burrow at 1302. She continued digging until 1325 when she started to make a closure about 2.5 cm from the entrance. I frightened her away at 1327 by approaching too closely but she returned to resume digging at 1354, left for 2 minutes at 1356, and then continued digging. At 1425 she began a temporary closure and finished it at 1430. When
we excavated the three closed nests of RT 1 on 12 October, we found a newly spun cocoon in the first nest, were astonished to find just a burrow 6.4 cm long without a cell in the second, and a burrow 7.5 cm long ending in an oblique ovoid cell without prey in the third nest. The second nest was obviously an abortive burrow although it did not terminate at a rock. It is puzzling that the wasp made a closure rather than leaving it open as was done in all other abortive burrows.

Tsuneki found some open abortive burrows without cells from 1 to 10 cm long in the Taiwanese subspecies of *S. subtruncatus*, but neither he nor Williams noted such burrows in the Korean and Philippine subspecies. Foot traffic may have disturbed Tsuneki’s wasps and caused their inability to relocate the burrow, because he did not mention finding an obstruction at the end of any burrow. It is possible that some abortive burrows are abandoned because the wasp has not yet made an orientation flight to memorize the precise location of the burrow.

**Nest Dimensions:** The burrows were cylindrical at all localities and 12–13 mm in diameter. Tsuneki noted “10 mm or so” as the burrow diameter in the Korean subspecies; that taxon is as large as the Ceylonese subspecies. In nests constructed in level or gently sloping soil (Gilimale, Udawattakele) the burrows usually went into the soil at quite a steep angle ranging from 45° to 80° (average 67° for 15 nests). However, in nests constructed in a slope of 20° to almost vertical (Kanneliya, Weddagala) the burrows penetrated the soil at a more shallow angle ranging from 15° to 75° (average 41° for 20 nests).

Normally the burrows penetrated in a straight line to the cell that sometimes was just a widened terminal section along the burrow axis, and sometimes was placed at an angle to the axis. There was a significant difference in length of the straight burrows, those in level or gently sloping soil being longer (7.4 cm, range 3.8–10.0 cm in 14 nests) than those in banks of 45° or greater slope (5.4 cm, range 3.2–10.8 cm, in 15 nests).

Tsuneki’s nests in Korea and Taiwan were on level ground and the burrows penetrated the soil at a steep angle, usually 70°–80° but occasionally as much as 90° or as little at 60°. The burrows in the Korean nests were straight for 6–8 cm and then turned gradually toward a horizontal position to terminate in the cell. The burrows in the Taiwanese nests were 7–10 cm long (average 9.6 cm for 8 nests). Williams found that in the Philippine subspecies “the burrow is at first vertical, or nearly so, to a depth of about three inches, when it extends horizontally for about two or three inches more, the terminal portion being somewhat enlarged to form a cell.”

Two nests at Kanneliya were anomalous in that the burrow made an angle before terminating in the cell. One went downward at 30° for 2.5 cm and then horizontally for 4.3 cm before the cell. The other went in at 35° for 2.5 cm, then turned at 30° and continued downward for 1.3 cm to the cell. Three nests at Udawattakele had burrows with an angulation before reaching the cell. Two burrows went downward at 80° for 5.1 cm, and one then angled at 60° for 5.1 cm, the other at 45° for 5.7 cm. The third was almost vertical for 3.8 cm and then horizontal for 2.5 cm. Such angulations in burrows of the Ceylonese subspecies may be caused by an obstruction, but I noted in the second Kanneliya nest that there was no obstruction at the angulation.

The cell is elongate ellipsoidal and in 20 nests it averaged 35.0 mm long (range 25.5–51) and 16.0 mm in diameter (range 13–28). In two of these nests the width was 19 mm and the height 13 mm, and this is the usual proportion, i.e., that width is slightly greater than height. Two nests at Kanneliya were unusual in that they were spherical with a diameter of 19 mm, and both contained a single prey with attached egg. It is unlikely that a wasp could develop successfully in so small a cell, so perhaps each of these females might have lengthened the cell as the larva increased in size. In steep banks the cell was just an enlargement at the end of the burrow along the same axis in 16 nests but at an angle to the burrow in 13 nests. In the latter group five cells were at an oblique angle to the burrow axis and sometimes at a lesser downward angle and sometimes horizontal. Eight cells were at right angles to the end of the burrow with the burrow some-
times at one end of the cell and sometimes in the middle. Of 10 nests in level or gently sloping soil the cell continued along the burrow axis in only one nest, and was at an angle to the burrow in the others. In two of the latter nine the cell was at right angles to the burrow, and horizontal or at a lesser downward angle in the remaining seven nests. Four cells at Udawattakele in level ground were 5.0–7.5 cm beneath the surface (average 6.0 cm).

Tsuneki (1963:44) noted that the cells in Korean nests averaged 40 mm long (range 35–55), 23 mm wide (range 17–28) and 20 mm high (range 15–25), but that the width always exceeded the height. Usually the burrow curved more or less toward the horizontal and terminated in a cell along the burrow axis, but he found that occasionally the cell was at an angle of 70°–90° to the burrow axis. The top of the cell was 3–13 cm below the surface (average 6.2 cm for 26 nests). In the Taiwanese subspecies Tsuneki found that five cells averaged 40 mm long (range 35–45), 27 mm wide (range 25–40) and 20 mm high (range 15–25). Three of these cells were 7–9 cm below the surface (average 7.7). Williams gave no dimensions for cells of the Philippine subspecies.

It should be noted that each wasp we observed making multiple nests constructed the second and later nests near the first nest, usually at distances not greater than 0.75–1.5 m.

First Temporary Closure: After the cell has been excavated the wasp makes the distinctive first temporary closure. Usually she constructs a thin mud plug about 12 mm from the burrow entrance. If there is a spoil heap of excavated earth beneath the burrow entrance, she scratches some of the loose soil backward beneath her body with her forelegs into the burrow and compacts the particles by pressing with her head, while buzzing loudly. Occasionally while compressing the earth, the wasp rotates around so that she is sometimes lying on her side or back. If the nest is on a steep bank and there is no spoil heap, she bites pellets of earth from above the burrow entrance or even from the upper end of the burrow, rotating within the burrow to maintain its cylindrical shape. These pellets are then compacted by pressing with her head. Within five minutes she usually completes the closure by raking loose particles beneath her into the mouth of the burrow and scraping some around over the surface to conceal the entrance. One female (B1472 C) behaved abnormally in making her first nest closure. She began the closure at 1153 in the manner noted above but interrupted closing activities frequently for no apparent reason. During the next 19 minutes she stopped closing activities a dozen times for periods ranging from a few seconds to 35 seconds, and once flew off into the jungle for as long as five minutes, perhaps to visit flowers for nectar. During the shorter absences she made brief irregular flights along the bank near the burrow or perched on vegetation nearby. She terminated the closure at 1212 in the usual manner by scratching some loose soil backward beneath her to fill the burrow and conceal the entrance. She returned three times to the burrow vicinity for a few seconds by 1258 but did not carry on further closure activities, and made an orientation flight only after the first visit.

Orientation Flights: We observed two initial orientation flights made by females just after excavation of a nest and construction of the first temporary closure. Each nest was the second and third, respectively, that we had seen each wasp construct. The first wasp began a series of short, low, irregular orientation flights along the bank on each side of and above the nest entrance. After each flight she alighted near the entrance for a few seconds before starting the next flight. Then she sat at the entrance for 15 minutes alternately flicking her wings and grooming herself, and then made three more brief flights. She was still sitting at the entrance when I left for another nesting site 10 minutes later.

The second wasp completed the first temporary closure at 1430 and spent the next minute making a series of irregular flights low over the bank. The flights began in the area about a meter around the entrance and gradually lengthened to a distance of 2.0–2.5 m on either side of the entrance. She then flew into the jungle at 1431, returned
preyless at 1537, alighted briefly near the entrance, flew off and had not returned when I left at 1608.

Later orientation flights were basically the same except that there were fewer of them after provisioning was in progress and the wasp became more familiar with the precise location of the nest. Sometimes the flights were omitted when the wasp was thoroughly familiar with the area.

Usually wasps had no difficulty finding their nests. However, we confused some females by inserting a small twig in the entrance plug or covering the entrance with a bit of leaf so that we could determine whether the wasp had entered during our absence. Usually the wasp located the nest after a little searching, and sometimes she removed the marker with a loud buzz.

Subsequent Temporary Closures: After provisioning has begun later closures of the nest are different from the initial closure in that the wasp makes no attempt to conceal the burrow entrance by scattering mud pellets over a wider area. The upper part of the burrow is filled with compacted earth but this plug may end as much as 12 mm from the surface or it may fill so much of the burrow that only a dimpled depression is visible to mark the burrow entrance. Occasionally when the plug does not nearly fill the burrow, the wasp may place loose pellets of earth in the upper end.

Tsuneki reported that temporary nest closures in the Korean and Taiwanese subspecies were made of compacted earth and that the burrows were not filled flush with the surface. He did not mention that loose pellets of earth were placed in the upper end of the burrow in any of these nests. He stated that the closure made immediately after nest construction was the same as later closures, i.e., that the burrow entrance was not concealed by loose pellets of earth scattered around the area.

Final Nest Closure: We never observed a wasp making a final closure, but we dug up three nests that contained either a cocoon or a full-grown larva. It is clear from these nests that the final closure differs from the temporary closures. The wasp does not construct a mud plug either at the anterior end of the cell or about 12 mm from the entrance. Instead she fills the burrow with loose earth pellets and then constructs a firm but thin mud plug flush with the surface or not more than 5 mm below the surface. She does not place any loose pellets of earth above this plug. It is noteworthy that in these three nests there were scarcely any inedible prey remains such as tegmina, legs, or other heavily sclerotized parts. Apparently the wasp cleans such debris out of the nest before proceeding with the final closure.

Prey Transport and Provisioning: We were never so fortunate as to witness a wasp capturing prey, and neither Williams nor Tsuneki saw this aspect of wasp behavior. All of the wasps we observed flew off into the jungle after completion of the first temporary burrow closures and orientation flights. Most prey that we recovered from nests or captured with wasps were predominantly nymphs of Tettigoniidae (long-horned grasshoppers) although some adults were found. However, we recovered from one nest a paralyzed adult female cricket (Gryllidae) and five Tettigoniidae, and in another nest we found two adult females and a dismembered nymph of Tettigoniidae, and a dismembered adult male probably belonging to Gryllacrididae. Williams and Tsuneki reported that the prey of the Philippine, Korean, and Taiwanese subspecies were mostly nymphal Tettigoniidae (Williams called them by the incorrect name Locustidae), but Tsuneki said that some adults were used later in the season in Korea.

Only once were we able to ascertain the length of time that elapsed between completion of the first temporary closure and bringing the first prey to the nest. This wasp completed the closure at 1153 and returned with her first prey at 1345.

The wasp flies to the burrow with her first prey held beneath her, venter up and head forward. She alights near the burrow entrance, leaves the prey on the ground venter up, rapidly chews through the mud plug sealing the burrow, and scatters the loose earth beneath and behind her. Then she backs out of the burrow, turns around, grasps the prey by the head end and backs into the burrow dragging the prey in after her. If the
nest is on a steep bank, the prey frequently falls to the bottom of the slope. After opening the burrow, the wasp searches for the prey, flying up and down facing the bank until she finds it. Then, she either flies back to the burrow with it and pulls it inside, or drags the prey backward on foot up the bank until she reaches the burrow and pulls in the prey.

The wasp places the prey on its back, head inward at the posterior end of the cell as we had ascertained by digging up 10 nests that contained only the first prey and egg. The wasp remains in the nest a few seconds, during which period she lays the egg. Then she emerges and makes the closure as described above (see "Subsequent Temporary Closures"). Tsuneki noted the same placement of the first prey in nests of the Korean and Taiwanese subspecies, but said that occasionally this prey was placed on its side rather than on its back.

In progressive provisioning the wasp normally opens the burrow occasionally after storing the first prey. This is to ascertain when the egg is about to hatch or has hatched. She then provides another prey, followed by additional prey at more frequent intervals as the wasp larva becomes larger and eats more voraciously. I presume that this is the normal sequence in _Sphex subtruncatus krombeini_, although our team could not obtain substantiating data by watching color-coded females. It is possible that the second prey is brought in before the egg hatches, for we dug up one nest that contained two prey, one of them bearing the wasp's egg. Perhaps we may have dug up the 10 nests that contained only a single prey before the wasp had time to supply a second. Tsuneki reported that six nests of the Korean subspecies contained only a single prey with egg, but that one nest contained four prey with an egg upon one.

Prey provisioning proceeds more rapidly after the wasp larva has grown some, probably to at least the second instar. In working with color-coded wasps we frequently inserted a small twig or grass stem into the closing plug. This marker would be removed when the wasp opened the nest to add another prey, although we noted that sometimes a preyless wasp would remove the marker if she visited but did not open the nest. For example, we found wasp No. 10 at her nest at 0845 on 11 October, placed a marker there at 0910, and this had been removed by 1015 when we revisited the area. We placed another marker, which the wasp removed when she brought a small nymph at 1120, closed the nest and left at 1130. Another new marker was gone by 1300, and still other new markers by 1340 and 1416. A final new marker on that date was still in place when we left the area at 1605. On 12 October we dug up the nest at 1115 and found a wasp larva about a third grown and whole specimens or remains of eight Tettigoniidae (five nymphs and three adult males), 10-14 mm long. Another wasp, GT 5, was noted closing her burrow at 0855 on 8 October after bringing in a tettigoniid nymph. This may have been her first prey because she continued to bring in prey and remove markers through 11 October. We saw her bring in a prey on 9 October and she removed three markers on that date. On 10 October we saw her bring in another prey, and she also removed three markers by 1630. We did not see her bring in prey on 11 October but she removed four markers. She did not visit the nest during the morning of 12 October and we excavated the nest early that afternoon. It contained a half-grown wasp larva, nine dismembered or whole tettigoniids, (five nymphs, two adult females and two adult males), 10-30 mm long, and an adult female gryllid, 10 mm long.

The prey never recover from the paralysis of the wasp's sting. Most uneaten prey found in the cells or captured with the wasps were capable of weak reflex movements of the palpi, antennae, and tarsal segments, and of excretion, respiration, and circulation as was noted also by Tsuneki for prey of the Korean subspecies.

It was not possible to ascertain the total number of prey stored per cell because the wasp removed most inedible fragments either before or at the time of final closure. Also, there was frequent considerable variation in size of prey within
a single cell which would have affected the total number stored. In five cells, none of them completely stored, the range in length of prey was 10-14, 10-16, 10-18, 10-30, and 15-30 mm. The largest number of dismembered and whole prey found was 10 in the nest of GT 5 as summarized two paragraphs above.

**Prey Identification:** Listed below are the species of prey obtained from nests or wasps. Also included are the number of specimens, stage and sex where known, and the range in size. Measurements were taken from the head to the apex of the abdomen excluding the tegmina. The latter in adults may extend well beyond the tip of the abdomen but are not consumed by the larva. Including the tegmina in the length would give an erroneous impression of the bulk of the prey available for consumption. A number of prey from cells were too dismembered or fragmentary for positive identification and are not included in the tally. The prey were pale green or light brown according to the species except for the strikingly marked *Gonatacanthus werneri* Karny. This species is black with light yellow clypeus, labrum, and palpi, and a scarlet abdominal venter. All adult prey were fully winged except for *G. werneri*, which is flightless with very abbreviated tegmina.

**Family Tettigoniidae**

**Agryphinae**

*Ischnophylius viridipennis* Redtenbacher: 9 nymphs, 10-14 mm long; 6♂, 14-17 mm; 3♀, 12-14 mm

*Ischnophylius* sp. or spp.: 6 nymphs, 10-15 mm; 3♀, 13-19 mm; fragment of 1 adult

*Gonatacanthus werneri* Karny: 18 nymphs, 8-22 mm; 7♀, 25-30 mm; 1♂, 27 mm; fragments of 2 adults

*Scytoceroides ceylonensis* Henry: 1 possible nymph, 18 mm; 3♀, 25-30 mm

Sp. or spp.: 6 nymphs, 10-15 mm

**Listroscelinae**

*Hexacentrus unicolor* (Serville): 4 nymphs, 8-15 mm; fragments of 2♂ adults

*Hexacentrus* sp., spp., or genus near: 13 nymphs, 8-29 mm; 1♀, 17 mm; fragments of 2♂ adults

*Xiphidiopsis* sp., spp., or genus near: 5 nymphs, 10-21 mm

*Decolya* sp. near *splendens* Henry: 1♂, 17 mm

**Meconematinae**

*Nicaihora* sp., spp., or genus near: 2 nymphs, 10-11 mm; 1♀, 16 mm

**Mecopodinae**

*Mecopoda platyphoea* Walker: 6 nymph, 20 mm

**Phaneropterinae**

*Molpa bilineolata* Walker: 1 nymphal fragment; 2♀, 19-24 mm

Sp. or spp.: 15 nymphs, 9-21 mm

**Pseudophyllinae**

Sp.: 1 nymph, 23 mm

Family *Geryllacrididae*

Sp. probably in this family: 1 dismembered ♀

Family *Geryllidae*

**Podoscirtinae**

*Madasumma* sp.: 1♀ 10 mm

The wasps exhibited no prey specificity other than restricting themselves almost entirely to Tettigoniidae. Undoubtedly they were merely exploiting the particular ecological niche(s) preferred by the tettigoniids. The prey in eight nests that contained more than three specimens usually belonged to two subfamilies, although one of these nests had representatives of three subfamilies and another contained six nymphs of *G. werneri* only.

There were differences in the prey stored in Udawattakele and at Kanneliya that probably reflected the relative abundance of particular tettigoniids in the two areas. The wasps at Udawattakele used predominantly *G. werneri* whereas that species was used only once at Kanneliya. The other prey in Udawattakele included only the single specimen of *Decolya*, fragments of two Phaneropterinae, and two specimens of *M. bilineolata*. A much wider prey spectrum was used at Kanneliya that included all of the other species listed above.

Henry recorded 1 male, 1 female, and 1 nymph of *G. werneri* and 1 male and 2 females of *I. viridipennis* as prey of the Ceylonese subspecies. Tsuneki reported the following as prey of the Korean subspecies: 4 adults and 25 nymphs of *Hexacentrus japonicus* Karny; 2 adults and 9 nymphs of *Conocephalus maculatus* Le Guillou; 4 nymphs of *Phaneroptera nigraantennata* Brunner; and 1 adult and 2 nymphs of *Homorocoryphus lineosus* Walker. Tsuneki stated that the Taiwanese subspecies preyed mostly on nymphs of
Hexacentrus unicolor (Serville) but that two nymphs of Homorocoryphus lineosus were also included. Williams did not provide specific identifications for prey of the Philippine subspecies.

**Life Cycle:** The sausage-shaped egg is creamy white and is glued by the anterior end between the fore- and midcoxae of the first prey, usually on the right side of the mesosternum. It extends transversely across the sternum beyond the opposite side of the thorax. Eleven eggs ranged from 4.5 mm long by 0.7 mm wide to 5.4 by 1.2 mm (average 5.0 × 1.0).

Tsuneki noted that two eggs of the Korean subspecies were 5.3 × 0.9 mm and 5.8 × 1.0 mm, and that the egg was placed slightly posterior to and slightly inside one of the forelegs, crossed the thorax obliquely and extended beyond the front of the midcoxa on the other side. He also stated that on a laterally compressed prey such as Phaenoptera the egg was attached to the side of the thorax and extended downward without crossing the sternum. He estimated that the duration of the egg stage was 17–20 hours.

We were astonished to excavate one nest and find a single prey at the inner end of the cell but no egg upon it. Tsuneki (1969) reported finding a nest in Taiwan with two prey each bearing a wasp egg. He ascribed this to a second wasp mistakenly placing her first prey in the nest of another wasp and laying an egg upon it even though this cell already contained the first prey and egg of another wasp.

We did not observe duration of the larval stage. Tsuneki estimated that in the Korean subspecies the time from egg hatch to spinning of the cocoon was 3.0–3.5 days.

The cocoon is fusiform in shape with the anterior end bluntly rounded, the posterior end tapering gradually to a narrow, nipple-like tip, and with the greatest width about a quarter of the length from the anterior end. Six cocoons were 30–37 mm long (average 34 mm) and 10–15 mm wide (average 13 mm). The cocoon is light brown and is composed of two layers. The outer layer is a soft, relatively loosely spun silken sheath, whereas the inner layer is more closely spun, tougher, and lined on the inner surface with a dark brown varnished material. The latter material is probably derived from the larval excrement that is not voided until the whole cocoon has been spun. The adult wasp emerges by cutting off the cocoon cap about 6 mm from the anterior end. Williams and Tsuneki described similar cocoons for the Philippine and Korean subspecies, and Williams stated that the cocoons were about 39 mm long and 14.5 mm wide.

We reared one female from a cocoon dug out of nest YT 1 at Kanneliya on 12 October. This nest had been completed during the late afternoon of 7 October or early morning of the 8th. We kept the cocoon at the Colombo Museum in a depression in a tin of soil that was moistened occasionally. The adult female emerged on 14 November so apparently about five weeks elapse between completion of larval feeding and emergence of the adult. Williams tried to rear adults in Hawaii from three cocoons obtained in the Philippines during August-September. Two of the occupants were moldy by the end of the following May. The third transformed to a pupa 27 mm long on 31 May but was subsequently killed by mites.

**Male Activity:** Males are quite uncommon and my impression is that the sex ratio is strongly skewed toward females. One of my technicians observed a pair flying in copula on 13 January at Kanneliya but he was unable to capture them. Apparently males emerge before the females and patrol the nesting site awaiting emergence of females. On 15 January at 0915 I watched two males for several hours. They were patrolling about 10 m of a sloping mud bank. Neither seemed interested in a specific burrow and I noted no nesting females in the area. Occasionally one would chase the other in a wild figure-8 flight along the bank. They alternated rapid flights with perching alertly on foliage near the bank or more frequently on dead branches. Both left the area several times for as long as 15 minutes and I finally captured one to confirm the sex.

During another visit we observed a female bring prey into the nest on 10 October. On the following day we saw a male trying to mate with her as she was closing the burrow entrance. The
male hovered around the female but she drove him away. She completed the closure and departed 10 minutes later.

We collected several males on flowers of bowitla (Osbeckia aspera (Linnaeus), Melastomaceae) and podi-sinna-maram (Eupatorium riparium (Regel), Compositae).

Tsuneki noted that males of the Korean subspecies patrolled the nesting site and that females were chased so violently and tackled by the contending males that the females soon flew away.

Commensals, Predators, and Parasites: We frequently observed adult female flies belonging to the Miltogramminae (Sarcophagidae) around wasp nests. The flies perched on vegetation near the entrance and watched the female wasps digging or closing their nests. Occasionally, when the wasp was not around, the fly might investigate the sealed burrow entrance. I never witnessed larviposition by the flies but presumably the maggots are deposited on the prey lying near the burrow entrance while the wasp is opening the nest. The maggots do not harm the wasp larva but feed on some of the prey provided for it. Inasmuch as the wasp practices progressive provisioning, enough prey are provided for both the wasp larva and its maggot cellmates to reach maturity. I collected five female flies around wasp nests and they were identified as Senotainia (Sphinxapata) albifrons (Rondani) from Weddagala; Metopia (Metopia) argyrocephala (Meigen) from Kanneliya and Gilimale; and Metopia (Australoanicia) nudibasis (Malloch) from Gilimale.

Four nests at Kanneliya contained miltogrammine maggots or puparia. There were two maggots or puparia in two nests. A third nest contained a number of maggots on 12 October, four of which pupated on the 15th, and two females and two males of S. albifrons emerged on the 24th. The fourth nest contained 13 maggots, some of which formed puparia within a day or two, and one puparium. These puparia appeared to be identical with those of S. albifrons.

Tsuneki observed in Korea that miltogrammine maggots infested several nests but that they acted only as commensals and did not harm the wasp larva. He found three maggots in one cell with a nearly full grown wasp larva, and two and three puparia respectively in two other nests already containing cocoons of the wasp.

A wasp egg from a nest at Gilimale had on its surface three maggots, 0.78 mm long and 0.18 mm wide at the posterior end. These were identified as a species of Phoridae and were very similar to larvae of Megselia. Robinson (1971) recorded several species of Megselia as having been reared from grasshopper egg pods and larvae of various insects, as well as developing as commensals on dead insects, snails, and other invertebrates. A single species might behave as either a parasite or as a commensal. The occurrence of these larvae on the wasp egg suggest that they would have penetrated the egg, fed on the contents, and then continued their development on the paralyzed prey.

Small red ants were troublesome in several nests in Kanneliya and acted as predators. One wasp brought in a prey at 0920 and ants twice attempted to gain access to the nest while she was completing a temporary closure. The wasp lunged at the ants, buzzing her wings, and drove them off each time. Another wasp without prey opened her burrow, presumably to check on the condition of the larva and prey, and some of the small red ants around the nest entrance took this opportunity to enter the nest and carry off an orthopterous leg. A third nest was abandoned by the wasp, perhaps because it may have been invaded by ants. The burrow was open and we found in the cell only a few tettigonid antennae and some prey excreta.

Williams stated that during heavy rains in the Philippines armies of small Phidole hypax ants were forced to leave their nests and invaded the wasp nests, causing their abandonment and destruction of the contents. He also found that Polyrhachis ants sometimes fell into the wasp burrows from their nests in the foliage above. The ants were not aggressive and were chased out of the wasp nest or carried out in the wasp’s mandibles.
Appendix

A New Subspecies of Sphex subtruncatus Dahlbom

by J. van der Vecht

Sphex subtruncatus krombeini, new subspecies


Sphex haemorrhoidalis Fabricius.—Turner, 1912:369 (“in specimens from Ceylon the wings are fusco-violaceous as in the African form.”) [misidentification of S. haemorrhoidalis Fabricius].

Sphex nigripes var. siamensis Taschenberg.—Strand, 1915:89-90 (♀, Kandy, Ceylon) [misidentification of S. siamensis Taschenberg].

Sphex nigripes var. erythropoda Cameron.—Berland, 1928:329 (Kandy, Ceylon) [misidentification of S. erythropoda Cameron. Berland was probably misled by Kohl (1890:422) who erroneously described the yellow-winged Sphex erythropoda Cameron as having “Flügel braun, mit violettem Glanze.”]

The dark-winged Ceylonese form of Sphex subtruncatus Dahlbom (Vecht, 1973:350-351) appears to have been misidentified by all previous authors. The female is very similar to specimens from some other localities at the margin of the area of distribution, but the discovery of the male by Dr. K.V. Krombein showed that this form deserves subspecific rank.

FEMALE.—Length, 23-26 mm (one abnormally small specimen measures only 20 mm). Wings brown, with violet reflections. Legs black, femora and tibiae I more or less extensively red (almost entirely red in ♀ from Kitulgala, with only the femora slightly reddish beneath in some ♀ from Kanneliya Jungle), femora and tibiae II and III red; in some specimens apex of tibiae II, or of II and III, more or less fuscous.

MALE.—Length, 21-25 mm. Wings as in ♀, or slightly darker, with similar reflections. Legs black, femora III mainly red (base and a line on dorsal side black in allotype), varying to slightly reddish on ventral side only or entirely black; femora I with small reddish spot at base of ventral side.

Antennal segments 5-10 with well-defined flat median sensory area (“placoid”), which is nearly as wide as the segment and covers its entire length.

HOLOTYPE AND ALLOTYPE.—♀ and ♂ respectively from Kanneliya Jungle, 13-16 Aug 1972 (USNM Type 74056). The other specimens recorded below (except 1♂ without antennae from Kandy in Institut für Pflanzenschutzforschung, Eberswalde = IPE) are paratypes.

SPECIMENS EXAMINED.—♀, Ceylon, from Staudinger (Leiden Museum); 1♀, Kandy (Museum of Comparative Zoology, Harvard University); 1♀, Kandy, May 1901, P.L.G. Benoit (Institut Royal des Sciences Naturelles de Belgique, Brussels); 2♀, Kandy (nigripes var. siamensis, det. Strand) (IPE); 1♂ (without antennae), Kandy (nigripes var. muticus Kohl, det. Strand) (IPE); 2♀, Kandy, Rosenau, Jun 1953; 1♀, Kitulgala, Kegalla Province, Oct 1953, F. Keiser (Basel Museum); 1♀ (Leiden Museum); 2♀, Galle District, Kanneliya Jungle, Hiniduma, 500 ft (152 m), 11-12 Mar 1972, K.V. Krombein (USNM, Leiden Museum); 9♀, 5♂, Kanneliya Jungle, 300 ft (91 m), 13-16 Aug 1972, K.V. Krombein and P.B. Karunaratne (USNM; 2♀, 1♂, Leiden Museum; 1♀, 1♂, British Museum); 3♀, same locality, 500 ft (152 m) 21-22 Apr 1973, at black light, Baumann & Cross (USNM; 1♀ Leiden Museum; 1♀, same

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locality, 300 ft (91 m), 28 Jul 1973, G. Ekis (USNM).


Also, I was able to examine the *Sphex* collection of the Colombo Museum. The subspecies proved to be represented by 21♀ and 5♂ specimens collected since 1907 in the periods Apr-Jun and Sep-Jan in several localities: Kandy, Labugama, Ratnapura, Urugala, Kitulgala, Balangoda, Deniyaya, Bulutota, and Hanwella. These specimens also are not included in the type series.
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Williams, F.X.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantial review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼ margins. Submissions as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: title page with only title and author and no other information; abstract page with author, title, series, etc., following the established format; table of contents with indents reflecting the hierarchy of heads in the paper; also, foreword and/or preface, if appropriate.

First page of text should carry the title and author at the top of the page; second page should have only the author’s name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under “Literature Cited.” For botany, the long form (taxon, abbreviated journal or book title, volume, page, year, with no reference in “Literature Cited”) is optional.

Text-reference system (author, year:page used within the text, with full citation in “Literature Cited” at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series. (Jones, 1910:122)” or “… Jones (1910:122).” If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed “Literature Cited,” “References,” or “Bibliography.” Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume(number):pagination: “10(2):5–9.” For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press.

All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed Figures and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: “Figure 9b.” Illustrations that are intended to follow the printed text may be termed Plates, and any components should be similarly lettered and referenced: “Plate 9b.” Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as “mm, ft, USNM, NNE.” Spell out numbers “one” through “nine” in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: “9 April 1976.” For months in tabular listings or data sections, use three-letter abbreviations with no periods: “Jan, Mar, Jun,” etc. Omit space between initials of a personal name: “J.B. Jones.”

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.