ples is required, and the success of the experiment does not depend on the orientation of the apparatus. Furthermore, the combined experiment can be performed with little more difficulty than a single type of neutron experiment. Further research is warranted to investigate the potentialities of this type of experiment more fully and in greater detail under realistic conditions. In particular, the errors and precision involved are not presently known, and these need to be established by suitable laboratory mock-up experiments.

References and Notes

1. A. Palm and R. G. Strom, "Research Report of Elemental Abundances of the Lunar Crust According to Recent Hypotheses," Series No. 3, Issue No. 5 (Space Sciences Laboratory, Univ. of California, Jan. 1962).
2. R. Monaghan, A. H. Youmans, R. A. Bergan, E. C. Hopkinson, *IEEE Inst. Electr. Electron. Eng. Trans. Nucl. Sci.* **10**, No. 1, 183 (1963).
3. J. I. Trombka and E. A. Metzger, *Analysis Instrumentation 1963* (Plenum, New York, 1963), pp. 237–250.
4. C. D. Schrader and R. J. Stinner, *J. Geophys. Res.* **66**, 1951 (1961).
5. M. P. Menon, "An Investigation of Computer-Coupled, Automatic, Remote Activation Analysis for Lunar Surface Analysis," Semiannual Progress Report, May–November 1964 (Activation Analysis Research Laboratory, Texas A&M University, 1964).
6. R. C. Greenwood, J. H. Reed, R. D. Kolar, C. W. Terrell, *Trans. Am. Nucl. Soc.* **6**, 181 (June 1963).
7. W. R. Mills, Jr., L. S. Allen, R. L. Caldwell, G. N. Salaita, T. J. Gray, *Nucl. Sci. Eng.* **21**, 346 (1965).
8. A. H. Youmans, E. C. Hopkinson, R. A. Bergan, H. I. Oshry, *J. Petrol. Technol.* **16**, 319 (March 1964).
9. C. D. Schrader, J. A. Waggoner, J. H. Zenger, R. J. Stinner, *Am. Rocket Soc. J.* **32**, 631 (April 1962).
10. C. D. Schrader, J. A. Waggoner, A. E. Metzger, J. H. Zenger, *Nucleonics* **20**, No. 10, 67 (1962).
11. D. J. Behrens, "Some Notes on the Nature of Experiments, on the Statistics of Counting, and on the Fitting of Exponential Decay Curves to the Results of Counting Experiments," AERE T/R 629 (Atomic Energy Research Establishment, Harwell, Berks., England, 1951).

The Accessory Burrows of Digger Wasps

Like other manifestations of complex behavior, these are best understood through a comparative approach.

Howard E. Evans

Students of solitary wasps have long been intrigued by the varied and elaborate behavior patterns associated with nest closure and concealment. Many ground-nesting species disperse the mound of earth which accumulates at the entrance of the newly constructed nest. The dispersal movements assume many different forms and may be interspersed with digging movements or postponed until after the conclusion of digging. Many species prepare an "initial outer closure," scraping soil into the entrance either before or after leveling of the mound, or in the absence of mound-leveling behavior. Such species must reopen the nest entrance when they return to the nest and must restore the closure each time they leave. Subsequent temporary closures may be less complete than the initial one (for example, in *Bembix*), or they may actually be more complete (for example, in *Ammophila*). Certain wasps also prepare a "temporary inner closure" separating the cell from the burrow. When the nest is fully provisioned, the wasp prepares a "final closure," which characteristically involves filling and packing the entire burrow as well as smoothing off the site of the entrance. Following final closure, some species pick up sticks, leaves, or other objects and place them over the site. Thus, with many digger wasps, the nest is effectively hidden from a human observer at all times when the wasp is not actually working at the nest entrance or entering or leaving (*1*).

It goes without saying that these wasps are able to find their own nests without hesitation, even when hundreds of such nests are scattered over an expanse of bare soil. While some digger wasps apparently require open nest entrances or markers in the immediate vicinity of the nest for orientation, bembicine wasps are able to locate their nests with the aid of points far distant from the nest, including, in some cases, the profile of the horizon as seen from a position facing the nest (*2*). There is no evidence that odor plays a role in nest finding.

A few days in the field suffice to convince one that such terms as *hiding* and *concealment* are not inappropriate —that is, that the biological role of these behavior patterns is in fact concealment from parasites and predators. We know that birds and mammals occasionally dig out the larvae of wasps, but this seems to be a rare occurrence. The major enemies of digger wasps are other insects, particularly members of two groups of flies and of two groups of parasitic wasps. The flies involved are bee flies (Bombyliidae) and miltogrammine flies (Sarcophagidae, Miltogramminae). Flies of both groups have short antennae and very large eyes and are believed to direct their activities with reference to the sight of the wasp or the open burrow. Bee flies, in fact, have been observed depositing their eggs in open holes of many kinds, including holes made with a pencil or, for that matter, eyelets in the shoes of the observer (*3*). The parasitic wasps include cuckoo wasps (Chrysididae) and "velvet ants" (Mutillidae). Members of both groups have well-developed antennae with which they tap the soil constantly during their search for nests of their hosts, and it seems certain that odor plays a role in nest finding in these wasps. However, the tarsal spines in members of these two groups are not nearly as fully developed as those of their hosts, and perhaps the thick closures often prevent these wasps from finding the cells of the nests of their hosts.

The author is curator of insects, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

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Although many observations have been published on the attacks of these parasites (and of others less commonly encountered), very few quantitative data on the incidence of parasitism are available. Thus it is easy to hypothesize that the behavior patterns involved in nest closure and concealment arose in response to parasite pressure, and that differences in nest closure are the result of the relative importance of different groups of parasites in times past (*4*); but completely satisfying proof may be long in coming.

Nature and Distribution of Accessory Burrows

In this article I explore the application of this hypothesis to a still more specialized and relatively uncommon feature of the nesting behavior of digger wasps: the construction of one or more blind "accessory burrows" beside the true burrow. These accessory burrows are invariably left open when the true burrow is closed, and it is worthy of note that they are not known to occur in any of the fairly numerous species of digger wasps which do not normally maintain an outer closure. Descriptions of accessory burrows have, up to now, always been incidental to other studies. I hope to demonstrate that these burrows are of considerable biological interest and deserving of detailed, quantitative studies in their own right.

It has been proposed by several workers independently that accessory burrows serve to dupe parasites into depositing their eggs in an appropriate place or, at the very least, to force the parasites to spend a great deal of time exploring situations where they will not find their hosts (*4–6*). On the other hand, it is possible that these burrows are no more than the fortuitous result of the wasp's taking most of the soil for nest closure from a very limited space.

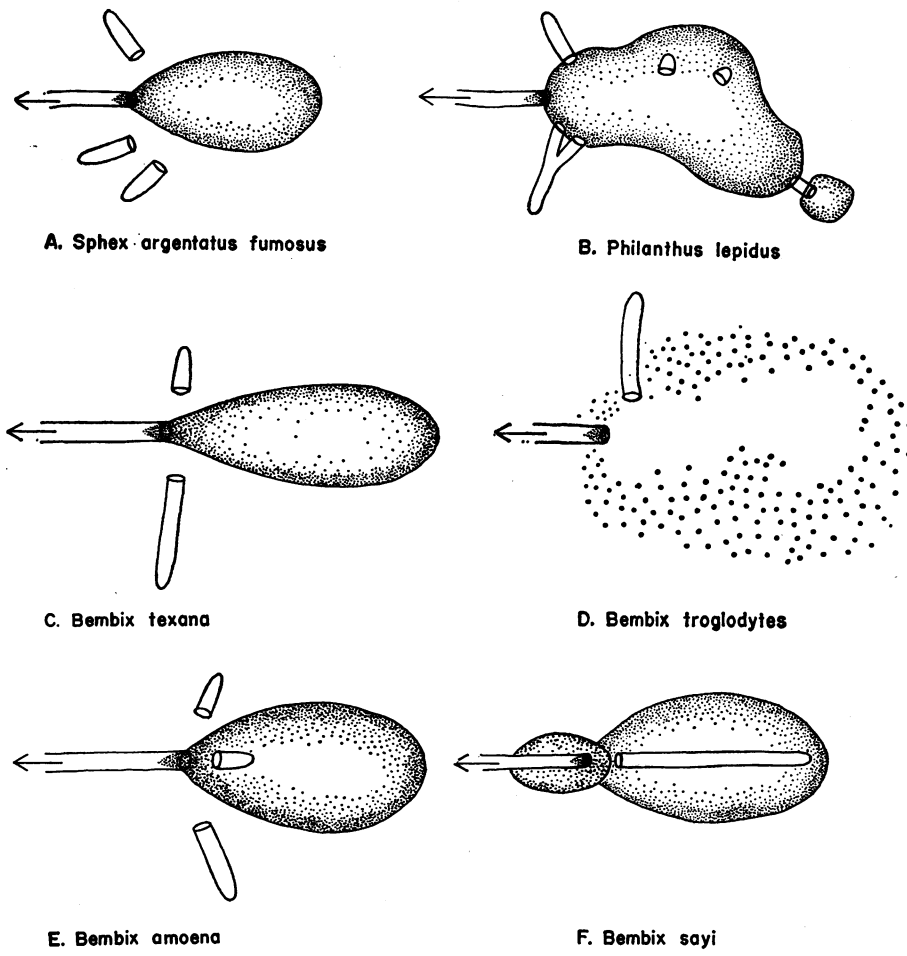

Fig. 1. Schematic drawing of nest entrances of selected species of digger wasps, showing accessory burrows. In each case the course of the true burrow is shown by an arrow. The mound of soil is indicated by stippling; in *D*, the mound has been dispersed. [*A*, after Tsuneki (*6*); *B*, after Evans (*7*)]

As Tsuneki has pointed out (*6*), there is no reason why both these conceptions may not be correct, and why in fact these burrows may not have originated as quarries for soil and later have acquired quite a different biological role. There is no evidence whatever that accessory burrows play an important role in nest finding or that they are used by the wasp for resting or for storing prey, but there is considerable evidence that they do, in fact, divert the attention of parasites.

In previous publications on this subject I have referred to these structures as "false burrows" (*4, 7*). Tsuneki (*8*) objects to this term as implying deceit on the part of the wasps and thus having "a very strong anthropomorphic odour." Although in fact I used the word *false* to mean simply "not true," as it is often used in biology (for example, in *false ribs*, *false scorpions*), it is probably best to avoid this word in studies of behavior, since it has alternate meanings such as "feigned" and "wrong." Tsuneki prefers the term *side holes*, but I feel that this does not distinguish these structures sufficiently from the branches or side burrows of compound nests. These holes are beside (rather than from the side of) the true burrow. I therefore propose to call them accessory burrows and to define them simply as any burrows started from the soil surface in close proximity to the true burrow and made by the same individual.

There is evidence that wasps of many different groups at times take much of the soil for closure from one or a few spots on the periphery of the nest entrance. I have reported such behavior in wasps as diverse as *Poecilopompilus interruptus* (Say) (Pompilidae) (*9*) and *Bembecinus neglectus* (Cresson) (Sphecidae, Stizini) (*10*). Adriaanse (*11*) separated two sibling species of *Ammophila* (Sphecidae, Sphecinae) partly on the basis of the fact that one of them always obtained soil for closure from a quarry beside the nest, while the other did not. Tsuneki and Yasumatsu have independently observed that in *Bembix niponica* Smith (Sphecidae, Bembicini) some females obtain most of their fill for final closure from a hole in front of the entrance, a practice resulting in some cases in "a new tunnel that lies in the opposite direction to [the true burrow]. The wasp carries out the sand from the bottom of her new tunnel and carries it in her old tunnel" (*12*).

In these instances, and many others which might be cited, accessory burrows are made at the time of closure and, in many species, their construction tends to be of irregular occurrence. In contrast, there are several species in which construction of accessory burrows appears to be of regular occurrence; in many of these wasps the burrows are constructed before or after temporary or final closure, thus they clearly do not serve as a source of soil for fill. Furthermore, in some of these wasps the females are known to reenter and "refresh" these burrows from time to time. Some of the first well-documented examples were presented by Tsuneki for the Oriental sphecid wasps *Philanthus coronatus* Fabricius (*13*) and *Stizus pulcherrimus* Smith (*8, 14*). *Philanthus coronatus* was found to prepare a short accessory burrow, 4 to 5 centimeters long, on each side of the entrance, while *S. pulcherrimus* was found to prepare two to four accessory burrows 1 to 5 (usually 3 to 4) centimeters long, "sometimes 2 on one side and none on the other, sometimes 2 on each side, or 1 on one side and 2 on the other." Tsuneki provided sketches of 15 *Stizus* nests studied near Seoul, Korea, all of which had accessory burrows. In a recent comparative study of the nesting biology of 11 species of *Sphex* occurring in eastern Asia, Tsuneki (*6*) found that only one of these species, *S. argentatus fumosus* Mocsary, prepared accessory burrows. However, such burrows occurred in all of the many nests of this species studied; they varied in number from two to three per nest and in depth from 3 to 8 centimeters (Fig. 1*A*). Tsuneki found that they were constructed immediately after the initial temporary closure and that, when destroyed, they were reconstructed. The two or three accessory burrows were dug by wasps going "to and fro between [them], always with intervals of rambling idly around the nest."

In my comparative study of the nesting behavior of North American *Bembix* in 1947 (*4*) I reported accessory burrows in only two of the ten species studied in detail. In one species, *B. troglodytes* Handlirsch, the accessory burrow is dug before the initial closure (Fig. 1*D*), while in the other, *B. pruinosa* Fox, it is constructed after the initial closure. In both species one accessory burrow per nest is the rule, although occasional individuals of *B. troglodytes* make one on each side.

Fig. 2. Female *Bembix amoena* quarrying soil at her nest entrance in coarse geyserite, Yellowstone National Park, Wyoming. The front legs, which are the major digging organs, are in the backstroke and not visible here.

More recently I have reported (*7*) that all individuals in two widely separate colonies of *Philanthus lepidus* Cresson prepared accessory burrows varying in depth from 0.5 centimeter to 9.0 centimeters. In this case, most nests had one or two accessory burrows, but a few had up to five burrows; such nests "presented a confusing picture of holes going in various directions, with the true nest entrance well concealed and discoverable only when the female arrived with prey" (Fig. 1*B*). Four other species of *Philanthus* occurring sympatrically with *P. lepidus* have been studied in some detail and have never been found to construct accessory burrows.

This unusual behavior in a few diverse groups of wasps provides an example of behavioral convergence which one assumes is the result of similar selection pressures acting upon stocks which have evolved separately but which retain certain common traits in their nesting behavior. Such behavior can best be understood if it can be delineated in several species of one stock and found to form one or more ethoclines passing from simple, plastic elements to complex, stereotyped behavior patterns. Studies conducted on the genus *Bembix* since my 1947 report suggest that this genus is admirably suited to such an approach.

Studies of Bembix amoena

During the summers of 1961 and 1964 I was privileged to work at the Jackson Hole Biological Research Station, Moran, Wyoming, which was within commuting distance of several large colonies of *Bembix amoena* Handlirsch in Yellowstone National Park (Fig. 2). I have discussed some of the general aspects of this work else-

where (*15*). Two colonies near the South Entrance were studied intensively in 1961, and a third colony, in the Lower Geyser Basin, a few kilometers south of Madison Junction, was studied for several days during 1964. All three colonies were located in pulverized geyserite in the vicinity of hot springs, but the quality of the soil differed somewhat in the three areas. In colony A, at the South Entrance, the soil was dry and rather hard-packed, but in colony B, only 100 meters away but much closer to the hot springs, the soil was moister and much more friable. The colony in the Lower Geyser Basin occupied soil of intermediate texture; it was relatively friable but dry and contained many large chunks of geyserite. Each of these nesting aggregations contained an estimated 50 to 80 female wasps.

My first impression, obtained in studying colony A, was that most nests had accessory burrows but that these burrows varied remarkably in depth, position, and time of construction. Some females prepared one or two short burrows beside the nest entrance during initial closure; others did not prepare them at this time but added them in the course of later closure; some accessory burrows became accidentally filled in a few days' time, while others were redug and even deepened. These burrows were often very shallow, varying in depth from a fraction of a centimeter to 2 centimeters, rarely to 5 centimeters. At the time of final closure many females obtained most of their fill either from an accessory burrow beside the nest entrance, from a burrow which ran opposite the entrance and passed beneath the mound of earth (in the case of this species, not leveled), or from a trough which passed across the mound. The second and third of these structures were so common and so distinctive that I came to call them "back burrows" and "back furrows," although they are listed as accessory burrows in Table 1. After final closure, a few nests were found to have a back burrow as well as two open side burrows (Fig. 1*D*). As shown in Table 1, about 20 percent of the nests apparently had no accessory burrows at any stage. In the other two colonies accessory burrows appeared to be less frequent, although those that were found resembled the accessory burrows of colony A in every respect. It seemed possible that, in relatively more friable soil, particles for fill could be scraped from the surface more readily, so that it was less often necessary to quarry the soil from one or two points. This is a point worthy of a much more detailed study than I was able to make.

Table 1. Numbers of accessory burrows in three colonies of *Bembix amoena* in Yellowstone National Park, Wyoming.

Colony	Number of nests studied in detail		Estimate of percentage of accessory burrows in all nests observed
	With accessory burrows	With out accessory burrows	
South Entrance (colony A)	31	13	80
Lower Geyser Basin	4	3	45
South Entrance (colony B)	2	6	20

It does seem certain, however, that the accessory burrows of this species are always made in the course of closure and that they do serve as quarries for fill. The great variation observed is very probably related to the wasp's requirement for soil at a particular moment and to the availability of soil at the nest entrance at that moment. Nevertheless, there was a suggestion that, even here, the accessory burrows served a secondary function. In colony A, several species of parasitic miltogrammine flies were abundant, and one of them, *Metopia argyrocephala* (Meigen), was seen entering various open holes in the ground, including one accessory burrow. The chrysidid wasp *Parnopes edwardsii* (Cresson) was also seen entering various holes in colony A, and in the Lower Geyser Basin the bombyliid flies *Villa melasoma* (Wulp) and *Exoprosopa dorcadion* Osten Sacken were very common and were seen ovipositing both in accessory burrows and in open true burrows (outer closure is occasionally omitted by some individuals of this species). I failed to rear any of these insects from the contents of the nests studied, but all are known parasites of bembicine wasps.

Studies of Bembix texana and Bembix sayi

During the spring of 1961 I made a preliminary study of several aspects of the nesting behavior of two species, *Bembix texana* and *B. sayi*, both of which nested in some numbers in and near the Archbold Biological Station, Lake Placid, Florida. Both species make accessory burrows, but the burrows are quite different in the two species and different from the accessory burrows of *B. amoena*. In the case of *B. texana* Cresson, an accessory burrow is dug on each side of the true burrow after completion of the latter and immediately after the initial closure (Fig. 1*C*). The burrows vary in length from 0.1 centimeter to 6.0 centimeters and tend to persist so long as the nest remains active (Fig. 3). I did not observe female wasps entering accessory burrows at any time after they were dug, but on a number of occasions I saw females of the parasitic wingless wasp or "velvet ant" *Dasymutilla pyrrhus* (Fox) entering accessory burrows and digging at the bottom of them (Fig. 4).

Bembix texana tends to be local in distribution and to form large, dense colonies. In contrast, *B. sayi* Cresson is widely dispersed in areas of bare, fine-grained sand, where it tends to form small colonies with widely spaced nests. I have studied many nests of *B. sayi*, not only in Florida but in Kansas, New Mexico, and Colorado, and in no case have I observed accessory burrows during the active nesting cycle. However, following the completion of final closure the female makes an elaborate series of movements away from the nest entrance, scraping sand toward the entrance. As many as 80 such trips (5 to 35 centimeters long) may be made. At the conclusion of this behavior the nest entrance is very well concealed. However, the wasp then begins a burrow in front of the old nest entrance, directed away from the path of the old burrow (occasionally at a right angle to it). This burrow is dug to a considerable depth and then abandoned and left open, the wasp afterward beginning a new true burrow elsewhere (Figs. 1*F* and 5). Measurements of 23 such "back burrows" in Florida showed a range in length of from 4 to 22 centimeters, with a mean of 11 centimeters (the length of true burrows in this area ranged from 22 to 40 centimeters, with a mean of 30.5). One back burrow measured in Colorado was 8 centimeters long; in construction it was very similar to those in Florida. I had no opportunity to observe behavior following final closure in the small Kansas and New Mexico populations studied.

The accessory burrows of *Bembix sayi* are by far the deepest recorded for any digger wasp. Construction of

these deep, blind burrows after elaborate movements for concealing the true nest have been made seems strange indeed. The digging of each of these burrows requires an hour or more of the wasp's time and must inevitably cause wear of the mandibles and leg spines (adult *Bembix* generally live 6 to 8 weeks and show much wear of these parts by the end of that time). These back burrows must play an important role in survival of the species. Only once have I seen parasitic wasps of the genus *Dasymutilla* entering the accessory burrows of *B. sayi*. As is true in the case of virtually all digger wasps, more data on the behavior and incidence of parasites are urgently needed.

Variation in Occurrence

In the case of *Bembix sayi*, I noted the occurrence of back burrows in all nests which were studied following final closure. All individuals of *Philanthus lepidus*, in two widely separated localities, made accessory burrows (*7*). Tsuneki studied *Sphex argentatus fumosus* in four separate localities in Japan and found the digging of accessory burrows to be a fixed component of this species' behavior in all four localities (*6*). However, in the case of *Stizus pulcherrimus*, Tsuneki found accessory burrows in all nests studied in Korea but failed to find such burrows in the one nest studied in eastern Mongolia; he cites this as a case of true geographic variation in behavior (*8*). In my studies of *Bembix pruinosa* I noted the occurrence of accessory burrows in all nests studied in New York State, but in Arkansas only about 85 percent of the nests had accessory burrows, and in Kansas only about 20 percent. I hypothesized that the construction of accessory burrows may have become vestigial in the center of the range due to decreased selection pressure (especially from physical factors), while remaining characteristic of the species on the periphery of its range (*4*). Recent studies of a large colony of this species at Cornish, Utah, revealed the presence of accessory burrows in about 50 percent of the nests. This locality is on the periphery of the range, and the figure 50 percent suggests that the situation is not as simple as I had suggested.

Although I reported accessory burrows in all nests of *Bembix troglodytes* studied in Kansas (*4*), I have more recently studied two nests of this species in New Mexico, both of which lacked accessory burrows. Since New Mexico is close to the center of the range of this species, while Kansas is peripheral, it is possible that the situation is not very different from that for *B. pruinosa*, although obviously a great many more data are required for both species before we can draw firm conclusions.

Bembix texana presents a somewhat different picture. All my studies of this species were conducted in one colony, so I have no data on geographic variation. In this colony, on 5 May 1961, I made notes on 11 nests and found two accessory burrows in ten of them, only one in the remaining nest. But later in the nesting season (17 and 27 May) I studied 15 nests and found two accessory burrows in only seven nests, one accessory burrow in two nests, and none at all in the remaining

Fig. 3. Female *Bembix texana* carrying prey (a bee fly) into her nest. The prey is held by the middle legs, as the front legs are thrust forward in the act of scraping open the nest entrance, which was closed by the wasp when she left on her hunting flight. The opening of an accessory burrow is visible behind and to the left of the wasp, and part of the opening of a second accessory burrow is visible below.

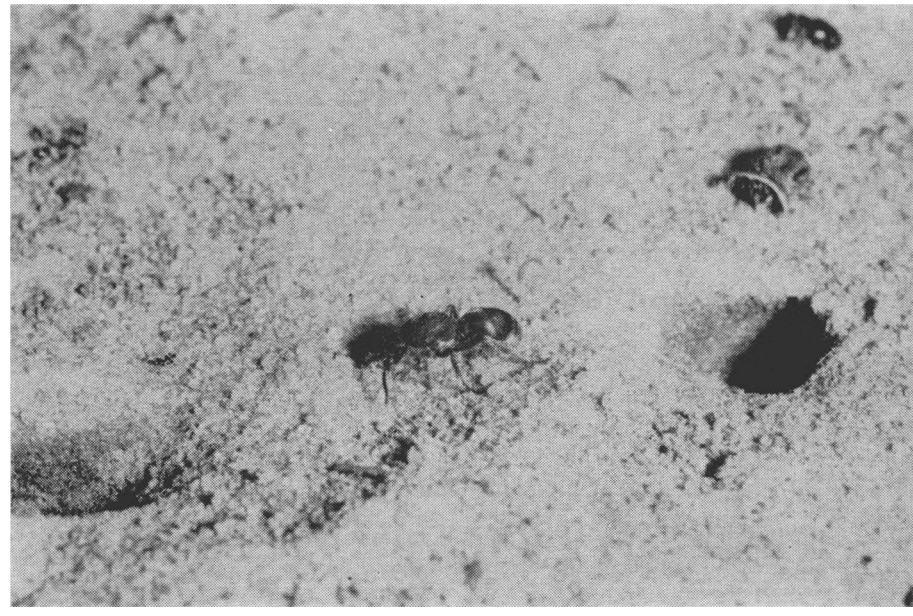

Fig. 4. Female mutillid wasp or "velvet ant" *Dasymutilla pyrrhus* walking from one accessory burrow of *Bembix texana* to another. The parasite is directly over the true nest entrance, which has been thoroughly closed.

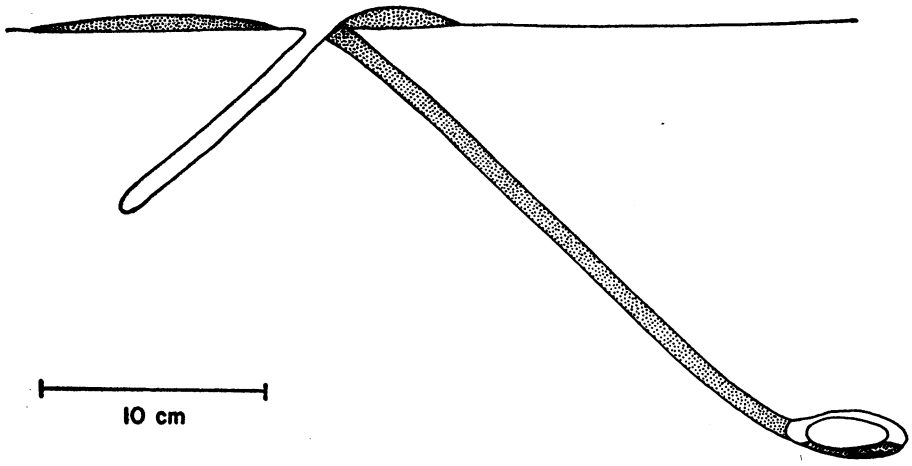

Fig. 5. Schematic drawing of nest of *Bembix sayi* following final closure. The true burrow has been completely filled, and a deep accessory burrow has been dug in the opposite direction. A small, fresh mound from the accessory burrow lies opposite the larger but older mound made when the true burrow was constructed.

six. These figures support the general impression I obtained from scanning the whole colony early in the nesting season and again after a few weeks: accessory burrows are at first a fixed feature of most if not all nests, but later in the season their occurrence is decidedly irregular. This matter should be studied in other colonies of *B. texana*. Needless to say, an ontogenetic change in behavior can seriously complicate data on geographic variation—and no other species have yet been studied over a considerable period. The significance of the apparently declining incidence of accessory burrows during the nesting season of *B. texana* is elusive, but one can think of an intriguing possibility. The accessory burrows of this species are unusually conspicuous, since the soil surface in the nesting area tends to be free of important irregularities. Is it possible that mutillid wasps or other parasites learn to look for the nests in the vicinity of these accessory burrows, or that they learn to wait in the burrows until the arrival of the wasp provides the clue to the true entrance? We have no actual evidence that this occurs, but it would not be out of line with what we know of the learning capacities of wasps. If it does occur, there would be selection pressure for nonconstruction of accessory burrows, more particularly after completion of the first few nests.

Unfortunately this entire subject of variation in accessory burrows (indeed, of natural variation in behavior in general) is in an exceedingly undeveloped state, and at this time one can do no more than suggest some of the problems worthy of study. To point up the importance of studies of behavioral variation, one need only mention the contribution of studies of structural variation to speciation theory and to evolution in general.

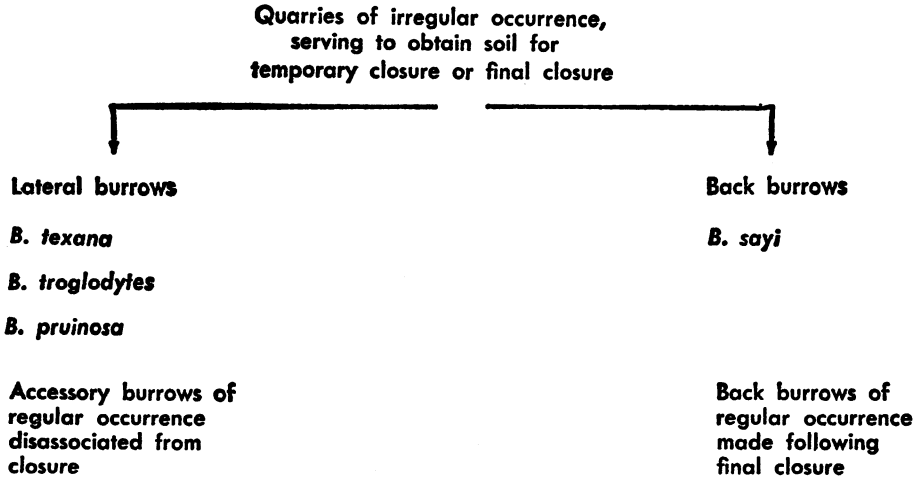

Fig. 6. Diagram showing the probable derivation of the accessory burrows of four species of *Bembix* from the quarries of a species such as *B. amoena*.

Summary of Hypotheses

Evidence suggests that wasps of diverse groups obtain much of the soil used in closing the nest from one or a few shallow quarries near the nest entrance. Such quarries may be dug in response to factors relating to soil texture—that is, wasps may quarry their soil especially when loose soil is not readily available—but the fact that this behavior is reported only for certain species and appears not to occur in other, related species suggests that it has some genetic basis. Quarries are recognizable from the fact that they are prepared at the time of closure (temporary or permanent) and that the soil from them is actually used for filling the burrow. Within a species, quarrying may be of irregular occurrence, as in *Bembecinus neglectus* (Cresson) (*10*), or it may occur with great regularity, as in *Ammophila campestris* Latreille (*11*).

In contrast, a few wasps prepare accessory burrows at times other than during closure, and the soil from these burrows is not used in closure. In these wasps, the building of accessory burrows is a fixed element of behavior, and in some cases the burrows are repaired by the wasps when they are destroyed. In several cases geographic or ontogenetic variation in the incidence of these burrows has been reported, but in other cases such variation is not known. Several persons working with species that build such accessory burrows have independently concluded that they serve to divert parasites into ovipositing in inappropriate places or at least into spending much time exploring blind tunnels (*4–6*).

The genus *Bembix* provides several instructive examples. In *B. amoena* (apparently also in the East Asian *B. niponica*) quarries are of irregular occurrence and are quite definitely associated with either temporary or final closure. From these quarries have presumably evolved the lateral accessory burrows of several other species of *Bembix* and the back burrows of *B. sayi*, as shown in Fig. 6.

We may thus speak of accessory burrow construction by certain more advanced digger wasps as having been ritualized and as having been displaced from its original position in the sequence of behavior patterns and divorced from its original biological role. The new biological role—and the factor which directed this change in behavior—is presumed to be the protection afforded the wasp's progeny by the diversion of parasites. Many more field data are needed before this hypothesis can be confirmed (or refuted).

I have cited examples of parasites attracted to these burrows. I should also mention an entirely different type of accessory burrow found in a few species. These species maintain "sleeping burrows" at some distance from their brood nests. These sleeping burrows are left open during the day and are known to be attractive to parasites, at least in the case of *Microbembex monodonta* (Say) and its bombyliid parasite *Exoprosopa* (*16*). One wonders whether the sleeping burrows of male *Bembix* may serve a similar function (for in this genus the females spend inactive periods in the brood nest).

In his study of the East Asian species of *Sphex*, Tsuneki (*6*) discovered that *S. argentatus fumosus* Mocsary, a species that regularly makes accessory burrows, was less heavily parasitized by flies than the sympatric *S. flammitrichus* Strand, a species that does not make accessory burrows. In two localities the percentages of parasitism of the brood cells of the latter species were 40 and 44 percent, while in a third locality Iwata obtained a figure of 33 percent. The percentages of parasitism in four colonies of *S. argentatus fumosus* studied by Tsuneki were 0, 6, 9, and 21 percent. In these studies one of the localities was the same for the two species, and in this case *S. argentatus fumosus* showed 9 percent parasitism, *S. flammitrichus*, 44 percent. Tsuneki rightfully attached no great importance to these figures, since they are based on relatively limited field data (110 cells of *S. argentatus fumosus* and 45 cells of *S. flammitrichus*). But, as he says, they are suggestive.

Tsuneki points out that many species which lack accessory burrows do in fact survive, and that some of these are among our commonest digger wasps. This point is not really important, however, since species are presumed to have diverged in geographic isolation, often during periods when populations were low and fragmented. The construction of accessory burrows is merely part of the behavioral repertory which evolved under these conditions and under selection pressures then operative. When related, sympatric species are compared, one often finds that each possesses behavioral mechanisms apparently serving to reduce the incidence of parasitism, but that each species has its own devices (*4, 7*). Accessory burrows are only one such device, but a device of special interest since it is so striking and yet has arisen several times independently—inexplicably so, unless one studies this behavior against a broad backdrop of ecological and ethological features. This is only one example among many of the way in which complex behavior can be understood, at least in a tentative and preliminary manner, through a comparative approach (*17*).

Conclusion

Solitary wasps are unpopular subjects for study for several reasons, chief among which is the fact that they cannot be handled effectively in the laboratory. Possibly some day suitable techniques will be found, but even then it will be difficult, if not impossible, to reproduce an entire community. This means that the advantage of working under controlled conditions will be offset by the disadvantage of obtaining partial and sometimes irrelevant answers, for no organism (least of all its behavior) can be fully understood apart from its environment. As William Morton Wheeler said many years ago (*18*), "natural history constitutes the perennial root-stock or stolon of biological science." That this is inevitably so is possibly a nuisance, for nothing is more difficult than working amid the confusion of species and profusion of behaviors occurring in every natural situation.

Unfortunately there is no such thing as an "unimportant" species or as behavior which is "trivial"—or at least we have no a priori basis for concluding that there is. This means that the answer to even relatively simple questions—such as, Why accessory burrows?—may require an incredibly large number of descriptive data, often obtainable only under uncomfortable and frustrating circumstances. That biology has become a more and more highly sophisticated laboratory science is admirable, but that it has become less and less a field science is regrettable. As Konrad Lorenz has said (*19*), "the immense field of observation which is still waiting to be systematically exploited needs whole armies of investigators." There is no draft for the armies Lorenz visualizes, but one hopes that from the current flood of talent there will be many enlistments, and that a few platoons will eventually turn their attention to some of the many problems in wasp behavior, a front now manned by a few ragged militiamen.

References and Notes

1. For a general review of current knowledge of the behavior patterns of solitary wasps, see H. E. Evans, *Ann. Rev. Entomol.* **11**, 123 (1966).
2. J. J. Van Iersel, *Animal Behaviour Suppl.* **1**, 161 (1965).
3. K. E. Frick, *Ann. Entomol. Soc. Amer.* **55**, 13 (1962).
4. H. E. Evans, *Studies on the Comparative Ethology of Digger Wasps of the Genus Bembix* (Comstock, Ithaca, N.Y., 1957), pp. 151, 233.
5. R. J. Llano, *Observaciones Biologicas de Insectos Bonaerenses* (Suplemento, Revista Educacion, Provincia Buenos Aires, La Plata, 1959), p. 89.
6. K. Tsuneki, *Mem. Fac. Liberal Arts Fukui Univ. Ser. II* **13**, 16 (1963).
7. H. E. Evans, *Psyche* **71**, 148 (1964).
8. K. Tsuneki, "Etizenia," *Occasional Publ. Biol. Lab. Fukui Univ. No. 10* (1965), pp. 10–19.
9. H. E. Evans and C. M. Yoshimoto, *Misc. Publ. Entomol. Soc. Amer.* **3**, 94 (1962).
10. H. E. Evans, *Behaviour* **7**, 294 (1955).
11. A. Adriaanse, *ibid.* **1**, 7 (1947).
12. K. Tsuneki, *Mem. Fac. Liberal Arts Fukui Univ. Ser. II* **6**, 115 (1956).
13. ———, *Mushi* **15**, 34 (1943).
14. ———, *ibid.*, p. 37.
15. H. E. Evans, *The Explorer* **4**, 6 (1962).
16. ———, *Wasp Farm* (Natural History Press, Garden City, N.Y., 1963), p. 85.
17. For other good examples, see A. E. Emerson, *Ecol. Monographs* **8**, 247 (1938); M. Lindauer, *Communication Among Social Bees* (Harvard Univ. Press, Cambridge, Mass., 1961), chap. 3; H. E. Evans, *Evolution* **16**, 468 (1963).
18. W. M. Wheeler, *Science* **57**, 61 (1923).
19. K. Z. Lorenz, in *Physiological Mechanisms in Animal Behavior*, J. F. Danielli and R. Brown, Eds. (Academic Press, New York, 1951), p. 240.

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