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ADAPTATION OF A

CLOSING HER NEST, female *Bembix pruinosa* bends forelegs inward so that the long spines on the tarsi scrape the sand backward beneath the body. Since adult opens nest entrance only to enter or to leave, parasites cannot attack the larva.

SAND WASP

By Howard E. Evans

THERE IS SCARCELY a place on the face of the earth more sterile and uninviting than the central part of an active sand dune. The slightest wind picks up handfuls of sand particles and drives them along. The sun pours down torrents of heat and the bright surface hurls it harshly back. Any rain that falls percolates so rapidly through the sand that it leaves no impression at all. Temperatures often rise to 90–100° F. by day, and the sand surface commonly measures as much as 125° F., or even more. Studies have shown that physical conditions in sand dunes are very much the same the world over, whether it be in the Sahara or in Aweme, Manitoba. Even a plant sturdy enough to withstand the heat and dryness soon has the sand blown out from under its roots or piled in drifts over its branches. Little wonder that such places are so devoid of life!

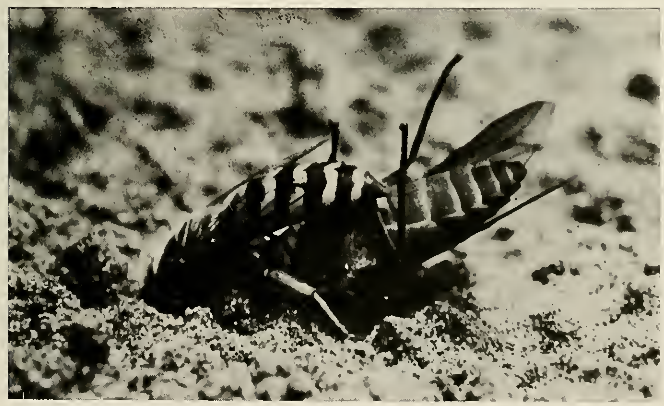
But visit a sand dune—not in the cool of evening or of winter or spring. but in the hottest part of the day and in the hottest part of the year—and you may find it teeming with a particular insect, which, in fact, occurs nowhere else. This is the sand wasp *Bembix pruinosa*, an insect that is over half an inch in length and is brightly patterned with pale, yellow-green markings. At the proper season, one rarely finds a sand dune east of the Rocky Mountains that lacks a thriving colony of these wasps. Along with the wasps often occur some of their parasites—certain species of flies and hairy, wingless wasps known as velvet ants. But that is very nearly all; the wasps and their parasites make up almost the entire diurnal fauna of the dunes.

ONLY a remarkable insect can thrive in this habitat. It must be able to adjust to or avoid the extremes of temperature and aridity, not only for itself, but also for its more delicate eggs and larvae. It must be able to rear its progeny where they will not be exposed or buried deeply by blowing sand. It must be able, without fail, to find its nest in a vast expanse of shifting sand. And it must be able to survive in spite of numerous parasites. It so happens that many of the parasites of sand wasps are not host-specific—they are not restricted to one host, but attack a variety of different wasps in different situations. Here *Bembix pruinosa* is at a distinct disadvantage: the parasites are wide-ranging and ever-present, but the wasps are restricted to suitable parts of active sand dunes. Ordinarily, when parasites cause the decline of a population, they bring about their own decline, too. since they create a shortage of suitable hosts. But not so here: if *Bembix* declines, the parasites continue to live on other hosts in surrounding areas, areas that *Bembix* is unable to invade. Only by "outwitting" its parasites can this species maintain its numbers.

Digging with forelegs, *Bembix* raises its abdomen to allow a passage for sand.

By various and often unique behavioral devices, the pruinose *Bembix* is able to accomplish all these things. It is interesting, for purposes of comparison, to note that there are many other species of *Bembix* besides *pruinosa*—most of them living in more congenial situations and not nearly so restricted to one particular ecological niche. The behavior of many of these more "ordinary" sand wasps is simplicity itself. For example, *Bembix spinolae*, which occurs all over eastern North America, digs its burrow in sandy gardens, waste places, sand pits, beaches, and the periphery of dunes. At the end of this simple burrow, the bottom of which is only three to six inches deep, the egg is laid in a small, oval cell. In a day or two, after the egg hatches, the wasp captures and stings a number of flies and presents them to the larva. When the larva is small, two or three flies a day suffice, but after a few days the larva requires many more flies a day, as many as twenty. The larva feeds only upon the soft parts of these flies, leaving a mass of wings and hollowed-out bodies, which eventually form a mat on the bottom of the cell. After about six days the larva begins to spin its cocoon, and the female wasp fills up the burrow and begins a new one nearby.

Bembix spinolae has many parasites. Some of them attack the larva directly—such as the bee flies, which drop their eggs into the nest entrance, and the velvet ants, which enter the



Paralyzed horsefly is carried into the nest as food for larval *Bembix*. When larva is young, three flies a day may suffice; later, twenty may be needed.

cell and lay their eggs through the wall of the cocoon. Others live upon the bodies of the flies in the cell, forcing the mother wasp to bring in a great many additional flies and often causing the wasp larva. in spite of this increment. to die of starvation. This type of parasitism is exhibited by quite a number of small flies that deposit small. live-born maggots in the cell or on the body of a fly as it is brought into the nest. These larvae grow rapidly into ravenous maggots. as many as a dozen or more of which may inhabit a single cell.

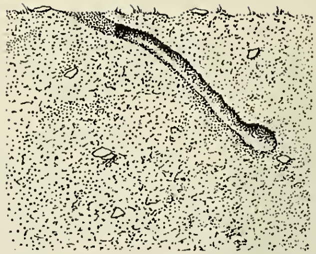
Bembix spinolae seems to have few means of avoiding these parasites. The wasps do remove the telltale pile of sand at the entrance to the burrow, and they do keep the burrow closed at the entrance nearly all the time—mechanisms doubtless functioning to make the nest as inconspicuous as possible to parasites—but apparently the species thrives mainly because it is ecologically so versatile. That is. if parasites become overly abundant. individuals radiate out into neighboring habitats and establish new colonies — something a species like *pruinosa* is unable to do.

The nesting behavior of *pruinosa* is very much more elaborate than that of *spinolae*. As might be guessed, the nests are very much deeper than *spinolae*'s. The top layers of sand, in a dune, are dry and exceedingly hot; but a foot or two down, the sand is much cooler and more moist. Also, in a shallow nest the cell might soon be exposed to the deadly heat of the

An associate professor of entomology at Cornell, Dr. Evans has studied solitary wasps from coast to coast. He is now spending a year in Mexico.

surface by the action of the wind. In small, sheltered dunes I have found the average depth of the cell to be only about eight inches. In larger dunes the depth of the cell varies from ten to twelve inches, and in one very large dune system along the banks of the Red River in Texas, I found the cells to be nearly two feet beneath the surface. Apparently, isolated colonies of the wasp become adapted to conditions in their area: the more blowing sand, the deeper the nests. It would be interesting to transplant wasps from a colony in a small, protected dune to a very large dune and study their survival.

Not only is *pruinosa*'s nest deeper than *spinolae*'s, it is considerably more complex. When the female is about to start a nest, she digs a bit in one spot, then backs up an inch or two, digs again, backs up again and so on. The result is a series of little pits connected by a straight line. If the texture of the sand is suitable, she then digs down an inch or two and prepares a broad, horizontal tunnel below the sand surface—and just beneath her line of little pits, which clearly function to insure that no serious cave-ins would occur here. This "preliminary burrow" may be as much as twenty inches long. After it is finished, the wasp returns to the entrance. levels off the pile of sand that has accumulated, then enters the

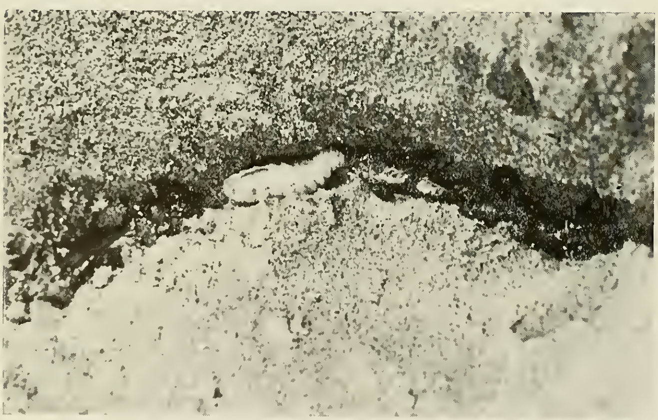


Burrows of *B. spinolae*, shown above, and *B. pruinosa*, seen in two stages at right, illustrate complexity and size of

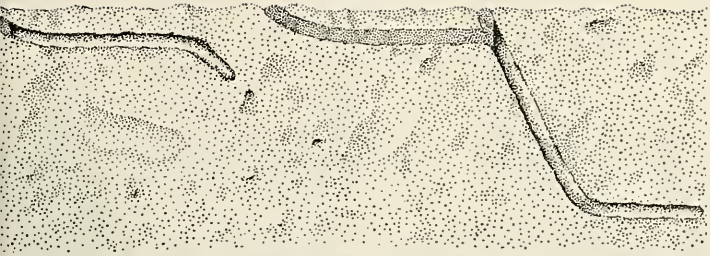
burrow and closes it from the inside. She then goes to the far end of the preliminary burrow and begins to dig obliquely down into the sand, pushing the soil from this "true burrow" into the preliminary burrow, which is soon completely filled up. At the bottom of the true burrow, which may also be twenty inches long, she then constructs a cell—not a simple, oval cell as in *spinolae*, but a slender chamber averaging eight inches in length. Thus, the total length of the nest excavated by the half-inch *pruinosa*, including preliminary burrow, true burrow and cell, may be as much as a yard and a half. Yet this nest is used for rearing only a single larva, and a new one is constructed for each successive offspring.

After finishing her nest, the female wasp lays her egg at the far end of the cell and proceeds to wait inside the nest until the egg is nearly ready to hatch, a matter of about two days. Then she leaves the nest, going out this time not by way of the preliminary burrow, which has been filled with sand and abandoned, but directly up the true burrow and out to the surface. This involves preparing a new nest entrance, which is first cleared out by digging and then filled in briefly to make a temporary closure while the wasp goes off to catch a fly for her larva. Each day, the larva receives a few freshly paralyzed flies. But these are not merely packed into the cell as in the case of *spinolae*; they are lined up in single file along the very long brood chamber. The larva moves down the chamber as it feeds, consuming the flies one after another and leaving their remains behind. It is a temptation to say that the *pruinosa* larva is fed cafeteria-style!

If you examine a nest after the



Cross section of cell shows *pruinosa* larva with flies arranged in a row to be eaten. Method contrasts with *spinolae*'s, where food is packed in cell at random.



pruinosa's burrow. *Spinolae*'s is only a shallow tube ending in an oval cell. *Pruinosa*'s is twice as deep, including preliminary burrow and long, thin cell for larva. Half-inch-long *pruinosa* may dig a yard and a half in building nest.

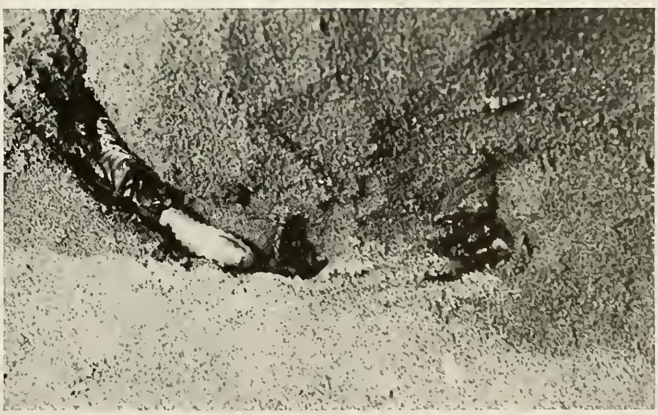
larva is three or four days old, you find that the larva has moved the greater part of the length of the cell. A short row of fresh flies, recently added by the mother, still confronts it. Behind it ought to lie the loose wings and hollowed-out carcasses of flies that have been devoured: but where are they? Does this larva eat the entire fly? A little further study shows that the cell is considerably shorter than it ought to be, and some further digging reveals the fly remnants in a compacted mass at the end of the original cell, walled off by a barrier of sand. Apparently, the mother wasp has raked all the debris into the end of the cell and then thrown up a barrier of sand to seal it off from the larva and the fresh flies. At about this time, the wasp closes up her burrow completely, leaving the larva to finish its growth on the remaining flies and to spin its cocoon. If, for some reason, the final closure of the nest is delayed a day, the wasp may prepare a second cache of fly remains and thereby shorten the cell still further.

For a long while, I was at a loss to explain this odd behavior. What possible difference could it make whether or not the larva lives in a clean cell or in a cell glutted with the remains of consumed flies (as in *spinolae* and most other species)? After digging out over eighty nests of *pruinosa*, I remarked upon one fact: this species is apparently never successfully attacked by the inquilinous, or commensal, maggots, which commonly infest the nests of other species. Such maggots live primarily in the fly debris, but when they are large they compete with the wasp larva for fresh flies, too. Perhaps *pruinosa* has found a way of overcoming them—for as a result of its practice, any small, developing maggots would soon find themselves segregated from the main part of the cell. It may be that *pruinosa* long ago, through mutation and natural selection, acquired the ability to sweep fly bodies into the tip of the cell. Once this was achieved, natural selection doubtless favored any elongation of the cell, so that this sweeping behavior could be performed more effectively. The remarkably long cell of the pruinose *Bembix* may have evolved in such a way.

At least, this seems the most plausible hypothesis for the strange nesting behavior of *pruinosa*. It seems probable, too, that the long, complex burrow has evolved as a means of deterring parasitism by flies and velvet ants. The closures of the nest, both temporary and permanent, are so thorough that the nest entrance is at all times quite invisible to a human observer, unless he sees the wasp entering or leaving. And perhaps it is as confusing to a parasite as it long was to me, to have the nest entrance shift as much as twenty inches between the start of the preliminary burrow and the completion of the nest!

Concealing the nest so thoroughly, and living as it does in broad areas of uninterrupted shifting sand, this wasp must have remarkable powers of orientation. I have often sat in the midst of a great colony of *pruinosa*, watching females return again and again to nest entrances that were completely invisible to me. All the while, the breeze blows lightly, and swirls of sand continually change the contours of the dune. The nearest tree is several rods away and the nearest tufts of grass lie well outside the wasp colony. And yet the wasps go back and forth without error, finding their own nest among the hundreds of seemingly identical nests scattered over the dune.

How do they do it? What landmarks can possibly be used? Much has been learned about animal orientation in recent years, but it would seem that *Bembix* is confronted with a far more difficult situation than, for example, the honeybee. Yet somehow it has solved this problem, too, just as it has solved the problem of rearing its offspring under seemingly impossible physical conditions and in the face of seemingly inescapable attacks by wide-ranging parasites. *Bembix pruinosa* is a remarkable animal—and probably even more so than we can yet appreciate.



Few-days-old larva has already moved greater part of cell's length. Remains of flies it has eaten have been swept behind it and walled off by the mother.