THE NESTS AND NESTING SITES OF FOUR SPECIES OF POLISTES WASPS.¹

By Phil Rau, Kirkwood, Missouri.

In a paper on the nests of *Polistes*² I have stated that, broadly speaking, *P. pallipes* make nests in old buildings; *P. variatus* choose sites in obscure places close to the ground or in pockets beneath the surface of the ground; *P. rubigenosis* in inaccessible places in complete darkness between walls of old buildings or in hollow trees; and *P. annularis* nest in the tree-tops. Since the publication of that paper, I have added the following details.

Polistes pallipes.

The statement that pallipes wasps nest in the shelter of buildings of some sort still stands for this region. The only digression noted during the past few years is that sometimes a nest occurs under an overhanging rock. Not one nest of pallipes has been found attached to vegetation in exposed places. I want to emphasize the fact that thorough searches in the leafless vegetation in autumn have given negative data, because occasionally one sees references to pallipes building among the vegetation in other localities. Neither have I yet seen a pallipes nest in a ground situation which is the characteristic site for variatus, although as I shall later show, P. variatus occasionally adopts the sheltered locations of pallipes. Nor have I seen about this region pallipes choosing dark, secluded sites as does rubigenosis. When pallipes nests in buildings, she always chooses well lighted places.

When ample room for expansion is at hand, *pallipes* always makes a round nest with the peduncle in the center. When a wall limits the expansion, the nest assumes a semicircular form, and sometimes in narrow places, it takes on a skyscraper effect.³

Another aspect of nest-making sometimes appears in the work of certain individuals. With hundreds of square feet of horizontal ceiling space in a barn on which to make nests, occasionally a *pallipes* attaches her nest to a vertical wall. Since the cells must eventually open downward, the peduncle must be either elbowshaped or slope diagonally downward. One can readily see that,

¹ The specific names were recently verified from specimens submitted to Dr. Joseph Bequaert.

² Ecology **10**: 191–200. 1929 ³ Psyche **35**: 147–150. 1928.

since the petiole is always short, very little space for cells is available between it and the wall; hence the nest cannot grow round. Only a small proportion of the builders commit this blunder of attaching their nests to vertical surfaces. In ten years I have seen only about twenty such nests; in all but two of these, they had been abandoned as impossible before they had attained half a dozen cells. The two exceptions, however, are interesting, especially when one realizes that exceptions are often the forerunners of new habits.

One nest built on a vertical wall had, on June 17, sixteen cells, three of them sealed, and was being continued when the owner of the building destroyed the nest. Another built under this handicap was a very pretentious structure which maintained its brood during the season and in the winter following was still attached to the wall. This nest is shown in fig. 1, plate V.

As already stated, it is customary for pallipes to build circular nests, but this wasp, when she found that she could not build thus on account of the wall, extended the nest outward as far as she dared go on account of the weight in relation to the strength of the petiole, and then extended the sides, making the nest longer than wide. The figure shows how the nest curled upward on both sides and ended in a sort of second story on the roof at one end. There was no barrier preventing the nest from being built straight out from the wall, and the only reason that I can see for this upward curl and the two-story arrangement was that the mother or workers somehow sensed the fact that the weight must be kept balanced near the base. This surmise is justified by the fact that they had from time to time reinforced the petiole, until it was perhaps six times as thick as the peduncle of ordinary nests of that size. In this weird position, the colony had been exceptionally successful in maintaining a 168-celled nest.

Here is a combination of two mental traits, the stupidity of the queen, and the ingenuity of the workers offsetting it. In the great majority of cases, this stupid habit eliminates itself, but in this instance it has a chance of survival in the next generation. It appears probable that the blunder in beginning the nest will be repeated in this case. This habit of building abortive nests on vertical walls actually seems to occur more frequently in certain years and in certain regions than in others, as we may logically expect from the above incident. The summer of 1930 was such a year in the region south of St. Louis. More beginnings of nests

on vertical walls were found than ever before. Out of 20 observed in early June, 8 were so made. It is at once apparent that these builders are either hesitating or blundering in beginning their task, for such nests usually show where the wasp has deposited a single load of paper pulp in several places near by before continuing one of them into a stem for the proposed nest. In several cases there were a dozen or more such blobs of paper stuck on the wall, and in one case I counted 48 such beginnings. This uncertainty suggested to me that either the queen must be very stupid, to be so wasteful of labor and material, or else she must feel a degree of doubt or uncertainty regarding the situation which she had chosen for her nest. These wasted lumps of paper were never seen around nests normally built on ceilings.

An unusual type of nest sometimes built by *P. pallipes* is the two-story kind. There is a corn-crib at Rankin, Mo., so built that at regular intervals two uprights are placed with spaces of about six inches between them, completely open on the outside, but boards are nailed on the back edges of these uprights. There are in this building thirty such spaces, and they must have been peculiarly attractive to *Polistes*, for twelve of them contained nests, attached just under the roof. The most interesting feature was that three such nests from last year had beneath them and attached to them the new nest for this year, with one queen in charge of each (fig. 2, plate V).

Another nest of that type was found on a September day behind a sign-board on the station at Sunnyside, 25 miles distant from Rankin. This wasp could just as easily have built her nest alongside the old one, for there was much available space. This leads one to suspect that sometimes this form is adopted from choice and not merely from necessity.

These instances also illustrate the possible beginning of the habit of making nests of several combs, one beneath the other, as *Vespa* builds them, instead of the single open comb of *Polistes*. This economy of building has not yet been adopted by *Polistes*, but these occasional occurrences point to the possibility that somewhere in the future this type of nest may become customary among them.

Polistes variatus.

Further observations again find, as previously, that *P. variatus* nest close to the ground, in pockets in dirt banks and, more often

than previously recorded, in sheltered places frequented by *P. pallipes*. It seems that in certain localities *variatus* is coming more and more to adopt the ways of *pallipes*, for recently I have found their nests in old buildings more frequently than I formerly did. In fact, in one small group of buildings, I found eight nests of *variatus* and only one of *pallipes*.

A handsome nest of *P. variatus* (fig. 3, plate V) was found at the country home of Dr. Julius H. Gross, near Columbia, Illinois. This was in a pocket in a stone retaining wall, about thirty inches high. The nest was deep enough in the wall to be well hidden from view. The pocket was irregular in shape, but since it was surrounded by rocks and mortar, there was no chance for the wasps to enlarge it, as they sometimes do in soft earth, so they made the best of its possibilities. The result was the irregular shape as illustrated.⁴

The nest was large, and the adults were abundant and alert, bringing in meat for the larvae and caring for the eggs. This was in sharp contrast to those observed in other regions during the drought in 1930. The reason for this contrast is that the Illinois colony was in the Mississippi bottoms and near a spring-fed stream, where the green vegetation had supported an ample ration of caterpillars. Several cells contained large drops of clear, sweet honey. The nest contained 136 capped cells, 66 with larvae, 40 with eggs, and 12 empty, making a total of 254 cells. About 15 workers and 3 males were busy on the nest. As in other species of *Polistes*, some of the cells had been used two times. The adults, when placed in a cage, ate ravenously of honey.⁵

Another *variatus* nest was found in a spherical depression in a bank at Allenton, Mo. This nest (fig. 4, plate V) was attached by two peduncles to some fine roots, and was reasonably secure. The depression was so round and apple-like that I suspected that the wasps had assisted in making it so. Only two males and two females guarded over this nest of 109 cells, containing eggs, larvae, pupae and many drops of clear honey. Several cells gave evidence of having been parasitized. This nest offered a good example of the marked difference between *P. variatus* and *P. annularis* in the use of silk in the making of caps over the cells. *P.*

⁴ In roomy pockets and when the nest is in buildings, its shape is round with the peduncle in the center.

⁵ About 30 parasites identified as *Polistiphaga fulva* Cress. by Mr. R. A. Cushman emerged from his nest between Sept. 28 and 30.

variatus produces, apparently, only a small amount of silk and makes so shallow a cap that, after the emergence of the wasp, hardly a trace of it is left. In the nests of P. annularis, on the other hand, often nearly one fourth of the length of the cell is built up with silk spun by the larva. This variatus nest must have given forth a large number of adults which had deserted or died during the drought before we came upon the scene. The larvae were shrunken and half starved when the nest was discovered.

The apple-shaped pocket which contained the nest had undoubtedly been excavated, at least in part, by the wasps. Polistes have the same ability to carry out lumps of dirt as do Vespa germanica⁶ may be seen from quotations from letters from

Dr. H. B. Hungerford and Dr. Carl Hartman.

"There was a nest of Polistes on the under surface of a rock, the rock almost touching the ground. On turning the rock over a little further and throwing in a mass of dirt as an experiment, I noticed the next day that the wasps were still at work digging out and carrying away the dirt precisely like solitary wasps, showing that the insects can in an emergency dig in the ground, an emergency which must be very rare indeed among these wasps; but this is quite a different thing from a habit which is firmly established within all of the members of a particular race."—(Hartman.)

"I was walking across a pasture on one of our farms in northern Kansas when I came upon a Polistes nest that had been attached to a plant stem (goldenrod, as I recall). The weight of the nest had bent the slender stem to the ground, and the wasps, in order to have access to the comb, had excavated a large, saucerlike depression in the hard earth beneath it."—(Hungerford.)

Polistes rubigenosis.

These red wasps are not so abundant hereabout as are the others, but I have found no digressions from the nesting habits previously recorded. This species likes to build in dark, inaccessible places within walls or in hollow trees. Since one is rarely able to get their nests, I describe another one here.

On September 21, at Centaur, Missouri, I found a large colony of about 30 wasps (two thirds of them males) clustered around a small hole in a shed roof about six feet from the ground. nest was in the dark gallery between the inner and outer layers

⁶ Entom. News **41**: 185–190, 1930.

of the roof. They were lazily sunning themselves outside their door in the afternoon. In this case also the wasps had built the new nest on the edge of the old one, and had actually used the center of the old one for pulp for the new cells. In a portion of the nest the entire cells were removed, but the roof was left intact. The new cells were built on the edge of this roof, as the material was mined from the center. The nest showed evidence of having been used by at least three successive generations in as many summers. The petiole on the nest was unusually thick and one and one-half inches wide. In addition there was a second stem one-half inch wide. These showed evidence of having been varnished with the black rubbery substance so often used by other species of *Polistes*. Both males and females were active, and crawled into the crack or flew away when I tried to take them.

Polistes annularis.

The nests of *P. annularis* are built in the open tree-tops, where, exposed to wind and rain, the wasps carry on life's activities. The digressions from this standard are few and slight. As I get further into the Missouri hills back of St. Louis, I find more occasions where they have taken up their abode in dilapidated buildings, which offer no better protection from the elements than do the tree-tops. On only rare occasions is an *annularis* nest attached to the eaves of a building. These digressions from custom are always worth careful scrutiny.

In the wreck of an old pioneer's cabin which figured in the days of Daniel Boone, three nests of annularis were found, along with several of pallipes. At first I was surprised to find them in this unusual situation, but closer examination revealed that the sites they had chosen were not so different from their accustomed tree-tops after all. All of these nests were on the window sashes where light and weather were about equal to that of the outside; none of the wasps had ventured far into the room. One of them had even chosen the end of a wire which protruded horizontally from a nail on the window sash (fig. 5, plate V); apparently the wasp had found in it a close resemblance to the conventional

⁷ Nearby in this hollow space in among the material of an old rodent's nest was found the recently abandoned nest of the bumble-bee, *Bombus pennsylvanicus*. Both bees and wasps used the one entrance way.

twig. It seems that when *annularis* do build elsewhere than the trees, the old instincts still hold sway and prevent them from making a too radical change.

Here we see that on a basis of instinct, intelligence throws a pseudopod slowly and carefully and superimposes upon instinct a new habit, which in turn will probably be engulfed by instinct. Thus we can imagine a transition eventually to a line of annularis wasps that will follow pallipes in the selection of indoor, sheltered sites. One can easily see how this can come about when one remembers how persistent annularis queens are about coming back to the home site after hibernating, and founding their own colonies near by.8 It was by this method that annularis populated Chesley Island, and it will be by this means that young queens, returning in the spring to their old home in the cabin ruins, will found their own nests there and thus develop a shelter-using Thus the story of pioneering is repeated on this romantic spot; the first generation is imbued with those intangible qualities which impel it to strike out on new lines; the progeny continue life where they are born, making slight adaptations to the environment where they find themselves, merely to enhance their own comfort. Of course one wasp had to break away from habit and establish a new type of dwelling; she showed real intelligence and a true pioneering spirit. But her progeny coming after her, without inheriting these peculiar qualities but retaining a memory of the old home, build there generation after generation, until the chain is broken by some other type of queen pioneering.

In fact, I have actually seen this to occur. Under the narrow eaves of an old club-house at Allenton, Missouri, I noticed four years ago one nest of *P. annularis*. The woods extended for miles all around this place, and houses were few, but one wasp had dared to venture on something new. Two years later, there were seven nests of this species under the eaves of this little cabin. Apparently the pioneering spirit stirs in very few, but the conservative impulse to linger near the old home dominates the great majority of the population. Only in the light of these remarks can we appreciate McCook's observations. In his popular book entitled "Tenants of the Old Farm," he illustrates (p. 430) a nest of *P. annularis* showing conspicuously the peduncle at one side of the nest; this shows that at that time (1884) and place

⁸ Cf. Ann. Ent. Soc. Am. 23: 461–466, 1930; and Ecology 10: 191–200, 1929.

(New England), the form of nest differed in no wise from that of the annularis in Missouri in 1930. He also found them nesting in trees, and then recites the following significant narrative. On the premises of the old Springfield school stands a grove of more than a score of tall oak trees, the branches of which were thickly colonized by ringed wasps. On one tree he counted thirteen nests, and every tree was thus occupied, and several nests were hung on the blackberry vines that skirted the fence. Some nests were near the ground, and others were fifty or sixty feet above the ground. He further states that the colony had occupied the schoolhouse grounds for a half century, for men who were boys that long ago remembered it well. One can see only in retrospect the establishing of such colonies as those of Springfield and Chesley Island.

I have said that *annularis* would probably have to revert to ancestral habit if they were to go back to tree-dwelling after a number of generations had nested in the shelter of a building. This probably occurs in the various species of *Polistes*, and the following note indicates that in this case it probably did occur, even to a greater extent than that suggested above. In this case we see an *annularis* nest resembling very much the nest of the tropical *P. canadensis*. This is significant because Bequaert thinks that *annularis* is but a color form of *canadensis*. Here are the details.

At Old Mines, Missouri, on September 12, 1930, I was agreeably surprised to find a nest of *P. annularis* attached to a fencepost, near a small stream. About twenty adults were on it. If it had not been for the wasps occupying it, and the fact that *P. canadensis* is not found in this region, I should have declared it was a nest of *canadensis*, so much did it resemble it. Instead of being round or oval with the peduncle on the roof, and hanging aslant from a branch, it was pear-shaped with the stem at the top where it was attached to the post, and it hung vertically, parallel with the post, just as do many of the nests of *canadensis*. This in one case seems to be a return to the *canadensis* type of nest in a remote region.



Rau, Philip. 1931. "The nests and nesting sites of four species of Polistes wasps." *Bulletin of the Brooklyn Entomological Society* 26, 111–118.

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