A Solitary Wasp (*Aphilanthops Frigidus* F. Smith) that Provisions its Nest with Queen Ants

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Reprinted from THE JOURNAL OF ANIMAL BEHAVIOR
September-October, 1913, vol. 3, no. 5, pp. 374-387

A SOLITARY WASP (*APHILANTHOPS FRIGIDUS* F. SMITH) THAT PROVISIONS ITS NEST WITH QUEEN ANTS[1]

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Several years ago a correspondent sent me a few specimens of a beautiful black and yellow wasp, *Aphilanthops frigidus* F. Smith, each mounted on a pin with a winged queen of the typical *Formica fusca* L. These specimens were collected August 21, 1903, at Silver Creek, Baraga County, in northern Michigan, by Mr. Morgan Hebard. Although it seemed very probable that the ants had been taken as the prey of the wasps, I was not sure of this fact till the past summer, when I was able to study the habits of these insects in the neighborhood of Boston. During this season, in fact, they seem to have been so abundant as to have attracted the attention of other entomologists in New England and Canada.

The nearctic genus *Aphilanthops* was first separated from the closely related *Philanthus* by Patton in 1880 and based on *Ph. frigidus* F. Smith as the type. Since that time Cresson (1865), Fox (1894), Baker (1895), Cockerell (1895, 1896) and Dunning (1896, 1898) have described a number of additional species. Eleven of these altogether are enumerated by Dunning in his monograph of the genus (1898), all confined to the western states, except the type *A. frigidus*. This was originally described from Nova Scotia, but is now known to range over Ontario and New England, as far west as Illinois and Chicago and as far south as New Jersey. Two other species from Mexico have been referred to the genus *Aphilanthops* by Cameron, but Cockerell believes that they really belong to the genus *Eucerceris*.

Concerning the habits of *Aphilanthops* nothing has been published, except the following observations by Ainslee (1909) on *A. taurulus* Ckll.: "Early in August, 1908, while marooned at

[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 71.

Albuquerque, New Mexico, waiting for delayed mail, I noticed one day beside a concrete walk that bordered a vacant lot in that city a throng of large red ants which resembled *Pogonomyrmex occidentalis*. The bunch was seething with excitement, and stragglers were continually coming and going. As I watched I noticed a small quadrate-headed wasp drop from the upper air to the hard-trodden soil, alighting without previous reconnoitering. She stood perfectly motionless, not even dressing herself after the manner of her kind when idle. Presently an ant hurried by, busy about nothing, as usual, when instantly the wasp gave chase. The ant dodged and doubled as it fled, but the wasp overtook and seized it after a very brief and intensely active resistance, for a *Pogonomyrmex* is by no means a helpless infant in a skirmish. The wasp and its riotous victim rose heavily into the air and ascended at a sharp angle of flight, until they were lost in the blue of the sky. During the next few minutes I saw the same performance repeated again and again, with variations, until dozens of the ants had disappeared heavenward with the predatory wasps.

"So intent were the wasps on this work that they seemed not in the least disturbed by my presence, and I managed to secure a number of both wasps and ants by taking quick advantage of the struggle always incident to the moment of capture.

"Occasionally an ant, when pursued, would dodge around a blade of grass or rush beneath some welcome shelter and elude its hunter, but this happened in only a few cases. So swift and certain were the motions of the wasps that even with a vantage of six inches or more an ant once followed was almost certainly doomed. The wasps never, so far as I observed, assisted themselves with their wings to gain speed, but played fair with their victims and ran them down. The struggle generally lasted a second or two on the ground, and, as I have said, appeared to be continued fiercely in the air, judging from the frenzied actions of the two as they rose aloft." Ainslee mentions another, possibly undescribed species of *Aphilanthops* which he took at the same time preying on the same ants. Specimens of these, sent me for identification, proved to belong to the large, coarsely sculptured form of agricultural ant, *Pogonomyrmex barbatus* F. Smith subsp. *rugosus* Emery, which makes extensive clearings in the deserts of New Mexico and Arizona. Although not ex-

pressly stated, it is clear from Ainslee's vivid description, that *A. taurulus* preys on the workers of the *Pogonomyrmex*. As will be seen from the following account, our eastern *A. frigidus*, though it also provisions its nests with ants, selects only the fertile females, or queens.

My observations on *frigidus* were made in the Blue Hills, near Boston, during July and August. The wasps were found to be at the height of their activities from July 26 to August 16. By the end of the latter month all the wasps had disappeared and the nests had been effaced by recent heavy showers. Like the species of *Bembex*, *frigidus* nests in colonies. Several of these were located, but observations were confined to three, which happened to be within easy reach from Boston. They were situated in the ravine that separates Great Blue Hill from the adjacent portion of the range, two of them being in the stony and sandy trail passing through Wild Cat Notch, the other on Administration Road. Each colony covered several square yards of territory and comprised from about 30 to 60 nests, the entrances of which were often within an inch or two of one another. In two of the colonies the nests were interspersed with the burrows of large Crabronid wasps and of Cicindelid larvæ. The wasps prefer to make their burrows on slightly sloping surfaces. The opening, a little more than a quarter of an inch in diameter, is semi-circular and lies in front of a little pile of earth that has been thrown out by the burrowing insect. The wasp spends much time, especially during the morning hours or on cloudy days, sitting in her burrow and looking out with her conspicuous black face, marked with three vertical yellow bands like exclamation points. As the heat of the day increases, however, she becomes more active and either does more or less excavating in the nest, kicking the earth out backwards from the entrance to a distance of a few inches, or goes off foraging for her prey. In all of this behavior she exhibits a striking resemblance to *Bembex*.

The burrow descends obliquely and abruptly to a depth of only six to eight inches, where it terminates in a small cell. There are also two or three other cells, but it was found impossible to determine their precise relations to the other portions of the nest, owing to the very dry and crumbling condition of the soil and to the fact that each cell is closed off from the main

burrow. A slender twig or grass culm carefully introduced into the opening of the nest as a probe was invariably stopped a few inches below the surface by an earthen plug or partition which has to be removed by the wasp whenever she enters the deeper portions of the nest.

The prey of *A. frigidus* consists exclusively of winged queen ants belonging to the genus *Formica*. Specimens wrested from the wasps while being brought in and also dug from the nests, belonged to the following four forms:

Formica fusca L. var. *subsericea* Say.

F. fusca L. (typical).

F. (*Neoformica*) *pallidefulva* Latr. subsp. *nitidiventris* Emery.

F. (*Proformica*) *neogagates* Emery.

Most of the specimens belonged to *subsericea*, very few to *neogagates*, while the true *fusca* was more abundantly represented than *nitidiventris*. The nature of the prey, however, depends on the situation of the *Aphilanthops* colony. Thus the prey in the Administration Road colony, which was situated very near the northern side of Great Blue Hill, consisted almost exclusively of the typical *fusca*, which is the only form of the species on this more boreal slope, whereas the more xerothermic *subsericea* and *nitidiventris* were the only forms found in the colony situated on the southern slope. As these two colonies were less than a mile apart, it is clear that the wasps do not range very far in search of their prey. The same wasp may collect queens of two or even three of the four *Formicæ* enumerated above. The pronounced preference for the queens of *fusca* and its variety *subsericea* is shown also in other portions of the geographical range of *A. frigidus*. I have already stated that the specimens of this wasp taken by Hebard in northern Michigan had been preying on *fusca*. Recently while I was visiting my friend Dr. C. Gordon Hewitt at Ottawa, Ontario, the noted melittologist, Mr. Sladen, showed me a specimen of the wasp taken August 12, 1913, with a winged queen of the typical *fusca*. He pointed out to me the site of the colony where he had seen this and other specimens of the wasps carrying in their prey, in the midst of a cultivated plot on the Central Experimental Farm, but all traces of the nests had disappeared at the time of my visit (September 2). During August, Mr. C. W. Johnson brought me a specimen of *frigidus* mounted on

a pin with a winged female of *subsericea*, which he had taken July 31 at Westport Factory, Mass., where he had found a large colony of the wasps nesting in a pebbly wood-road. They were bringing in the *subsericea* queens in great numbers and, curiously enough, were themselves being captured and destroyed by large robber-flies (*Deromyia umbrina*).

The queens of the four *Formicæ* enumerated above, differ considerably from one another, those of *subsericea* being much larger than any of the others and those of *nitidiventris* differing greatly in color, as they have the head and thorax red instead of black. The queens of the true *fusca* and *neogagates* are much alike in size and in being very smooth and shining, but the latter species is readily distinguished by the red color of the legs and the erect hairs on the lower surface of the head. It is significant that all these queens belong to species noted for their cowardly disposition, and as the normal hosts of the slave-making ants (*Polyergus lucidus* Mayr and the various subspecies of *Formica sanguinea* Latr.) and of a long series of temporary social parasites (the various subspecies of *F. rufa* L., *truncicola* Nyl., *exsectoides* Forel, etc.). Although nearly all of these predatory and parasitic ants are abundant in the Blue Hills, none of their queens is captured by the *Aphilanthops*. We must assume, therefore, that this wasp has learned to discriminate between different species of *Formica* and to avoid the more vigorous and aggressive queens of the *sanguinea*, *rufa* and *exsecta* groups. The queens of the *microgyna* group, represented in the Blue Hills by *F. difficilis* Emery, are in all probability avoided on account of their diminutive stature.

That the wasps capture the *Formica* queens while they are celebrating their nuptial flight and do not take them from their nests, was clear from observations made July 26, for on that day flights of *subsericea* and *sanguinea* subsp. *rubicunda* Emery were observed in the Blue Hills and the wasps were seen bringing in numbers of the queens of the former variety. Still I did not see the wasps in the act of capturing their prey till August 15, when there was a great flight from all the colonies of *subsericea* in Forest Hills and Jamaica Plain, Boston. While walking along the street I saw an *Aphilanthops* suddenly swoop down onto a queen that had just settled on the ground. Before I could reach the spot the ant had been stung and the wasp

was dragging her along by the antennæ and trying to rise with her into the air.

The queen ants attract the attention of the wasps only during the few hours that intervene between the nuptial flight and the loss of their wings. On several occasions I saw dealated queens crossing the roads near the wasp colonies or even running near their nest entrances without being noticed by the wasps that were flying about. And on one occasion when I confined a dealated *subsericea* queen in a bottle with an *Aphilanthops*, the ant was still uninjured more than 24 hours later. It is probable, therefore, that the wasp responds only to the visual stimulus of the winged queen, which is, of course, very different from that of the same insect with her wings removed.

The ants are merely stung and paralyzed. The wasp does not mutilate or malaxate her victims, which still move their palpi, legs and antennæ either spontaneously or when touched, for several hours or even for a few days after they have been captured and placed in the nest. In the course of a few days and often sooner, however, all signs of movement have ceased, although the insects still have a fresh appearance, with flexible limbs and without any indications of the drying up of the tissues.

The wasp carries the ant under her body, supporting it by means of her middle and hind legs, while she holds its antennæ in her mandibles. Sometimes when she happens to settle for a moment on a slanting leaf-blade and is therefore obliged to stand on her legs, one may see the ant dangle for a moment from her jaws. On reaching the nest she may begin to enlarge the entrance by digging, still holding the ant by its antennæ and kicking the earth backward around it with her hind legs. Sometimes she may go directly into the nest without any preliminary digging and without dropping her prey. Occasionally, however, she may be seen to drop it just at the entrance, then go into the burrow, turn around and pull the ant in after her by one of its antennæ. This method of getting the ant into the nest is sometimes very awkwardly executed. Once I saw a wasp seize her ant by the petiole and with much effort pull it in doubled on itself. While the wasp is taking the ant into the burrow, she may be closely watched by two parasites, a beautiful metallic green *Chrysis*, or cuckoo-wasp, and a small gray Tachinid fly. I have not seen either of these insects oviposit-

on the wasp's prey, nor have I found their larvæ in the nests. The wasp usually introduces her prey into the burrow so expeditiously and then buries it so completely that these parasites must encounter great difficulties in gaining access to it.

After the ant has been dragged a few inches down the burrow, the wasp proceeds to cut off its wings. Usually she does this very neatly, although the stubs she leaves attached to the body are a little longer than they are in queen ants that have dealated themselves. More rarely the wasp simply gnaws off the tips or apical halves of the wings. That this dealation is accomplished before the ant is carried to the lower portion of the nest is shown by the fact that while excavating the nest one always finds the detached wings only a few inches below the surface and some distance from the bodies of the stored ants.

Although I excavated a considerable number of nests with the aid of Messrs. W. M. Mann and F. X. Williams, I have had some difficulty is ascertaining the precise method employed by the *Aphilanthops* in rearing its young. By piecing together the observations made on different nests I have reached the conviction that the wasp secures several queen ants, usually five to seven, often belonging to more than one species, and stores them in two or three cells. Sometimes only a single ant is deposited in a cell, more frequently two, rarely three. No eggs were to be found on such stored individuals, but in each of two nests, a young larva was found in a small cell devouring a single ant, which had been cut in two at the petiole. The mother *Aphilanthops* was sitting in the burrow in each of these nests and in one of them there was a paralyzed ant in a chamber separated from the one in which the larva was feeding. Several older nests were excavated in which there was a single adult larva spinning its cocoon and surrounded by fragments of three or four queen ants. These conditions seem to me to prove that the *Aphilanthops* feeds her single larva from a store of several ants deposited in several cells. The egg is evidently laid on an isolated ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the other ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate. As the wasps were found in the nests even after the larvæ had pupated and

in nests containing old and empty cocoons and freshly stored ants but no larvæ, we may infer that after one larva has been reared in the manner described above the mother sets about providing for another in the same nest but in a fresh chamber. Pupæ nearly ready to hatch were found August 5 and freshly pupated young August 16; young larvæ were found on the latter date and on August 8. The larva and cocoon closely resemble those of *Cerceris rybiensis* as figured by Marchal (1887).

If my interpretation of the feeding of the larva is correct, we have in *Aphilanthops* a very interesting condition intermediate between that of the great majority of solitary wasps, which first collect provisions and then lay an egg upon them, and that of *Bembex*, which lays its egg on a single fly and feeds the hatching larva from day to day with fresh flies. If Fabre is right in supposing that *Bembex* does not always give all the captured prey to its young but keeps a portion of it temporarily out of the larva's reach in the burrow, we should have an approach to *Aphilanthops*, which brings in its store before beginning to feed its larva. This temporary storing of ants and the fact that they are not killed outright as in *Bembex*, but merely paralyzed, calls for an explanation. This, I believe, must be sought in the peculiarity of the prey, which is quite unlike that of other solitary wasps in that it can be obtained only at considerable and irregular intervals of time, namely, during the marriage flights of the various species of *Formica*. These flights may, to be sure, occur any time between the middle of July and the first of September, but nearly all the colonies in a given locality celebrate their flight on the same date and often during only a few hours, so that many days may elapse before there is another flight. And although the wasps draw their supply of prey from several different species of *Formica*, this does not very greatly improve matters. In any event, the wasps have to make hay while the sun shines and carry in as many ants as they can secure before beginning to rear the larvæ. The need of thus temporarily storing the prey also explains why it is paralyzed and not killed outright as in the case of *Bembex*, nor mutilated before it is really fed to the young. Of course, it is not impossible that the Bembecine method may also be employed by *Aphilanthops* if nuptial flights of the ants occur in quick succession so that there is no need to store the prey before

feeding it to the young, but whether this is the case or not can be determined only by future observations.

The behavior of *Aphilanthops* stands out in an interesting light by comparison with that of the other genera of Philanthidæ, *Philanthus* and *Cerceris*, which, unlike *Aphilanthops* are represented by several species in Europe as well as in North America. Fabre (1891) has given us a fascinating account of *Philanthus apivorus* (=*triangulum*), which preys on the honey bee. He shows how this wasp kills the bee outright and then gorges itself with the honey which it presses out of the body of its victim. This extraordinary behavior he explains as a necessary adaptation to the diet of the larva, as he found by experiment that the insect in this stage thrives on nitrogenous food but is poisoned if it eats honey. The great depth of the nest of *Ph. apivorus* is given as one meter. The egg is laid on a dead bee and recently killed bees are fed to the growing larva from time to time after the manner of *Bembex*. Fabre also made some observations on *Ph. coronatus* Fabr. and *venustus* Rossi (=*raptor* Lep.) and found that the former provisions its nest with larger, the latter with smaller bees of the genus *Halictus*. He believes that in these cases also the honey is expressed from the bodies of the victims, but this opinion has not been confirmed. Ferton (1905) has also studied *Ph. venustus* and enumerates 14 different species of *Halictus* and one of *Andrena* which he found in the nests. He calls attention to the depth of the burrows but says nothing about the method of feeding the larvæ;

The only American *Philanthus* whose habits have been described is *Ph. punctatus* Say. According to the Peckhams (1898) this wasp nests in very small colonies and preys on bees of the genus *Halictus*, which it kills outright, but it does not malaxate them, nor express the honey from their bodies. The main burrow of the nest reaches a length of 22 inches. The following quotation shows that the method of rearing the young is very different from that described by Fabre for *Ph. apivorus:* "We did not find distinct pockets, as the soil was very crumbly and fell in as we worked, but we came upon clumps of bees an inch or so to one side of the gallery and about three inches apart, with larvæ in different stages of development. In one nest we found 26 bees in two clumps, some of them half-eaten

and some of them fresh, but all quite dead. We have no doubt that punctatus completely provisions one pocket and closes the opening from it into the gallery, before she starts another, making a series of six or eight independent cells. The provision for one larva is probably 12 or 14 bees, the capture of which, in good weather, would be a fair day's work." Melander and Brues (1903) have seen this same species of *Philanthus* nesting in the midst of colonies of *Halictus pruinosus* Roberts. and ruthlessly preying on the bees.

We are also in possession of a number of published observations on various species of *Cerceris*. Fabre (1894) describes the habits of several of these. One of them (*C. bupresticida* Duf.) provisions its nest with Buprestid beetles, five others (*C. arenaria, ferreri, truncatella* (=4-*cincta*), *labiata* and *julii*) prey on weevils and another (*C. rybiensis* =*ornata*) preys on bees of the genera *Halictus* and *Andrena*. Marchal (1887) shows, in a beautiful study of this last species, that the wasp not only stings the bee but also crushes, or malaxates the back of its neck and laps up the exuding juices and honey. As a result of this treatment the bee dies in the course of a few hours. Adlerz (1900, 1903) lists *C. 5-fasciata, arenaria* and *truncatella* as provisioning their nests with weevils, *C. hortivaga* as preying on bees of the genus *Hylæus* and *C. labiata* as collecting both Chrysomelid and Curculionid beetles. Ferton (1901, 1905) cites *C. specularis, truncatella* and *ferreri* as preying on weevils, *C. emarginata* on bees of the genera *Halictus, Prosopis* and *Andrena*, and *C. magnifica* on *Halictus* and *Andrena*. This last species laps the honey from the body of its victim through a hole made in the back of its neck, as described by Marchal in the case of *C. rybiensis*.

The Peckhams (1898, 1900) find that the American *C. clypeata* Dahlb., *deserta* Say and *nigrescens* F. Smith all prey on weevils, like the majority of European *Cerceris*, but that *C. fumipennis* Say preys on a Buprestid beetle, *Chrysobothris 4-impressa*, which it kills outright. In all the species of *Cerceris* observed up to the present time the cell is first provisioned with numerous specimens of the prey, the egg is then laid and the cell closed as in the great majority of solitary wasps.

It would seem, therefore, that the method of rearing the young in *Aphilanthops* is intermediate between that of *Cerceris* and *Philanthus punctatus* on the one hand and of *Ph. apivorus*

on the other. The question then presents itself: Do *Ph. apivorus* and *A. frigidus* represent an advance on *Cerceris* or are the conditions in this genus derived from those of *Ph. apivorus?* In other words, is the Bembecine a primitive or a secondary method of caring for the young among the solitary wasps? Undoubtedly most observers would be inclined to regard *Bembex* as representing a later phylogenetic stage and one leading to the conditions in the social wasps, but the Peckhams take a different view. "It may be possible, then," they say, "that all wasps originally fed their larvæ from day to day as *Bembex* now does, and that while the instinct of paralyzing the prey and of storing the whole supply of food once for all was working itself out among the solitary wasps, the instincts connected with life in a true society, and of joining together in the work of feeding the larvæ, have, on the other hand, developed into those of our wasp communities."

It is difficult to decide between the evolutionary alternatives here indicated, but analogy with the phylogenetic history of the bees, in which two precisely similar methods of rearing the young occur, certainly points to the Bembecine method as secondary. This view is also sustained by the sporadic and independent occurrence in several highly specialized groups of wasps of this method as the one best adapted to certain peculiar conditions. Such cases are *Aphilanthops frigidus* and *Philantus apivorus*. Two others are cited by the Peckhams, one in the genus *Sphex* (*Ammophila*), where they found "an instance which looks like a connecting link between the habits of *Bembex* and those of the solitary species. *A. urnaria* stores one caterpillar, lays an egg on it, catches another and stores it as soon as she can and then closes the nest. As a usual thing, no doubt, the nest is finally closed before the egg is hatched, so that she never sees her larva. In one of our instances, however, the capture of the second caterpillar was so much delayed that when it was brought in the mother wasp found a larva of a day old feasting on the one already provided." The other case is that of *Lyroda subita* Say, which these authors found to resemble *Bembex* in feeding its larva from day to day on small crickets. Most instructive in this connection, however, is the *Aphilanthops*, because its method of collecting a supply of queen ants before feeding them one by one to the growing larva, indi-

cates very clearly that this wasp originally had the storing habits of the allied genus *Cerceris* and of *Philanthus punctatus* and has secondarily acquired the Bembecine method of feeding its young. I am, therefore, inclined to regard the Bembecine method as derivative, or secondary, and find further confirmation of this view in the fact that in all cases, except *Lyroda*, the prey of those solitary wasps which feed their larvæ from day to day, belongs to highly specialized groups of insects of comparatively recent phylogenetic origin—ants in the case of *Aphilanthops*, honey bees in the case of *Philanthus apivorus* and higher Diptera in the case of *Bembex*.

The species of *Aphilanthops* are not the only solitary wasps that prey on ants, for some four small Mediterranean Crabronids, belonging to two genera, are known to provision their nests with these insects. Ferton (1890) describes the habits of *Fertonius luteicollis* Lep. in Algiers, where it digs its nest in sandy soil, making burrows only about 4 cm. deep, but also nests in the crevices of walls. It preys exclusively on workers of *Tapinoma erraticum* Latr., storing in each cell 40 to 50 of these strong-smelling ants, which are merely paralyzed and far from motionless at first. There are three generations of the wasps in the course of the year. Later (1895) Ferton described from Corsica a second species of the same genus (*F. formicarius* Fert.) which also preys on *Tapinoma erraticum* workers and closely resembles *F. luteicollis* in its other habits. In 1893 Emery described the habits of *Brachymerus curvitarsis* H. Sch., a Crabronid that preys on the workers of *Liometopum microcephalum* Panz. in Italy. He saw it pounce on the ants as they were moving along in files. The nest was found in a fig-tree, in the abandoned burrows of a longicorn beetle. The ants were stored in numbers (about 40) in each cell and were "imparfaitement paralysés, quelques uns capables même de se traîner sur leur pattes." More recently (1901) Ferton has figured a second species of the same genus (*B. 5-notatus* Jur.) which, like the species of *Fertonius*, preys on workers of *Tapinoma erraticum*.

It is interesting to note that all of these Crabronids prey on strong-smelling ants of the subfamily Dolichoderinæ and that they select only the workers. Ainslee's observations show that the latter statement is also true of *Aphilanthops taurulus* but

that in this case Myrmicine ants are selected. *A. frigidus*, as I have shown, confines its depredations to Camponotine ants of the genus *Formica* and selects only the queens, which are, of course, the largest and most nutritious caste. This specialization in diet, while highly advantageous to the wasps, is very destructive to the ants, since each fecundated queen is really a potential colony. Still the prey preferred by *frigidus*, namely *F. fusca* and its var. *subsericea*, notwithstanding the depredations of the wasps and of our numerous slave-making and temporarily parasitic species of *Formica*, maintain their status as far and away the most abundant ants of their genus in the northeastern states and Canada. They are able to support this greedy host of prædators and parasites because they are extremely prolific, hardy, or eurythermic, and of a very industrious and peaceable disposition.

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