doparasitoid of the tobacco budworm, *Heliothis virescens* (Lepidoptera: Noctuidae), was significantly prolonged when its host was treated with ENT-70221 (5 or 50 mg). He also noted that the sex ratio of parasitoid populations emerging from treated as compared to untreated hosts differed significantly. My results and those of Vinson (*8*) demonstrate that endoparasitoids may be seriously affected when they develop in hosts treated with juvenile hormone analogs.

If juvenile hormone analogs can significantly reduce the reproductive potential of certain insect pests (*2*), it is reasonable to assume that similar reductions might also occur in the reproductive potential of parasitoids developing in treated hosts. The possible changes in parasitoid biology caused by juvenile hormone analogs could seriously limit the role of parasitoids in the natural regulation of insect pests.

The usefulness of juvenile hormone analogs in integrated control programs utilizing biological control agents is questionable, particularly if, as shown in my study, parasitoid mortality far exceeds that of its host (the insect pest) even at very low rates of application. Comprehensive studies are essential to evaluate fully the off-target effects of these "third generation" insecticides prior to their use on a commercial scale in natural ecosystems. These considerations are particularly important in view of the undesirable side effects already observed (*9*) when host-parasitoid complexes are disrupted by the application of organochlorine hydrocarbon, organophosphorus, and carbamate insecticides.

JEREMY MCNEIL

Département de Biologie,
Université Laval,
Québec, Canada G1K 7P4

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Swarming Behavior: Evidence for Communication in Social Wasps

Abstract. *Behavior of wasps at sites around swarms and along emigration routes suggests the use of odor marks. Wasps perform breaking runs through swarms, resulting in dispersal of clustered wasps. Orientation in flight of swarm mates to specific trail sites facilitates swarm emigration to the new nest.*

Swarming among social insects serves to establish new colonies or move a colony to a new nest site. Of necessity, it requires communication among individuals so that they cluster together and emigrate more or less as a group. In highly social bees, swarming is well known and some of the behavioral and chemical mechanisms are known in the honey bee (*1*). However, in other groups such as neotropical social wasps (*2*), generally regarded as primitively social, the mechanisms of swarming in relation to emigration and nest-founding are not understood.

While studying social wasps as prey of army ants in the rain forests of Ecuador and Panama, I observed swarms of 15 species of wasps (*3*). The swarms consist of one or more queens accompanied by many workers. The evacuation of the nest, formation of the swarm cluster, emigration of the swarm to a new nest site, and construction of the new nest are distinctly separate processes rapidly executed. The orientation of the swarming wasps, the selection of the new nest site, and the emigration of the swarm to the site appear to be facilitated by both communication within the swarm and orientation to marked trail sites.

Although swarming is primarily thought of in association with colony reproduction, swarms are of two distinct types: founding swarms, consisting of queens and workers that leave the mother colony in response to cyclic intracolony factors; and absconding swarms, consisting of the entire adult population of a colony that leaves its nest upon the destruction of the nest or brood (*4*). The swarms discussed here are absconding swarms, formed after loss of the nest to army ants, particularly *Eciton hamatum* and *E. burchelli.*

After an attack on the nest by *Eciton*, the entire adult population flies for only a short time; small, scattered clusters of wasps form immediately on nearby ant-free vegetation, uniting within an hour into a single, large swarm cluster on a leaf or branch near the old nest. Large populations may form two or three separate swarm clusters, but small species or colonies may form a single swarm on the underside of one large leaf. There is usually no strong defense of the nest and no attempt to reoccupy it even after the ants have left.

In these early stages of swarm formation, some of the flying wasps hover or land at specific sites on leaves and stems about the nest area. Close observation at these sites showed that some wasps made straight, short runs while dragging the ventral surfaces of their gasters on the substrate (Fig. 1), but others merely landed and antennated the site (Fig. 2). All wasps landing at a site responded in either of these two ways, dragging or antennating, while still others hovered near the sites momentarily. These behavior patterns, seen in five species (*5*), suggest that the dragging of the gaster served to deposit a mark, even though no substance could be seen on the substrate.

The gastral sternites that are pressed against the substrate during the runs have already drawn the attention of investigators (*6*). Richards has noted a subcuticular gland of unknown function on the fifth gastral sternite of four genera of social wasps, and I have seen a similar gland in *Stelopolybia myrmecophila.* Jeanne (*7*) has associated a small tuft of hair on the terminal gastral sternite of *Mischocyttarus drewseni* with the rubbing application of ant repellant on the nest petiole. It is probable that dragging the gaster serves to lay down a glandular secretion which other wasps, that is, antennating wasps, use for orientation.

Dragging *Angiopolybia pallens* and *Leipomeles dorsata* make upward runs several centimeters long on nearly vertical surfaces. *Polybia catillifex* runs were short and performed slowly on the large horizontal leaves under which they nest. When running wasps drag or rub their gasters on a narrow substrate such as a stem, the gasters move back and forth in a conspicuous lateral wagging movement. During the run, the wings are either held up at an angle or are moved rapidly. The antennae may touch the substrate or be held above it.

Antennating wasps when visiting sites walk slowly forward; the abdomen is held high and still, antennae are in contact with the substrate, and the wings are held up but are never moved rapidly. Their visits are shorter, and they sometimes move only a few millimeters forward before flying on.

The dragging behavior is often seen during and immediately after swarm formation but as flight activity around the forming swarm decreases, it becomes less evident even though wasps continue to visit the sites.

Visited sites describe a circular area less than 2 m in diameter around and below the absconding swarm. There are more sites near the center of the area below the swarm than near the edge, although this depends somewhat on the availability of objects suitable for substrate. The heights of most visited sites around low swarms were between 0.5 and 1 m, but *Stelopolybia myrmecophila* was seen to stop repeatedly at a site about 6 m in the lower forest canopy. No particular type of substrate seemed characteristic; the wasps visited to the same degree small herbaceous stems, tree trunks, rotting twigs, woody vines, and large leaves.

Once the flying wasps have coalesced into a single swarm cluster, additional visited sites appear away from the nest area forming corridors or trails along which the wasps fly to and from the swarm area.

Angiopolybia pallens in Ecuador was using such a trail 3 hours after swarm formation. It led 10 m through ground vegetation to the underside of a *Cyclanthus* leaf, where from one to three wasps were chewing and removing detritus particles and licking the leaf surface as if preparing it for nest construction. Flight patterns of other wasps flying to and from the swarm indicated that additional trails were being used, and wasps leaving or arriving at the swarm area also stopped or hovered at sites near the swarm.

At the swarm itself, wasps arriving from flights along the trails may walk rapidly through the swarm in a manner distinct from that of returning foragers. Motion pictures of this behavior indicate a strong tendency for the arriving wasps to walk or run through or over clusters of inactive wasps, and to turn at the edge of the swarm and continue the walk. This behavior is most conspicuous and best observed in the small flat swarms clustered on leaves, but it can be seen on the surface of large spheroid swarms as well. The rate of movement is variable. Before emigration of the swarm, highly excited wasps make buzzing runs through the swarm and cause considerable agitation. There is no discernible repetitive pattern in any one running wasp. This running disruptive behavior appears to be associated with nest site searching and may stimulate emigration to a new nest site. It is similar to the buzzing run seen in *Protopolybia pumila* (*8*) and to the *Schwirrlauf* or "breaking" behavior seen in honey bees (*9*), which alerts the colonies to swarming.

The first indication of an impending emigration is an increase in both the frequency and intensity of dragging behavior. Dragging wasps make as many as three vigorous runs at a given site and initiate dragging at new sites. So many wasps suddenly become active that a specific site may receive multiple dragging runs from each of several wasps in rapid succession. Wasps are active at sites along a single corridor, that is, the emigration route, which leads away from the swarm area. Breaking behavior in the swarm increases and highly excited wasps make fast headlong runs through or over clusters of other wasps, causing the entire swarm to become more active. Clusters of wasps begin falling from the swarm and flying.

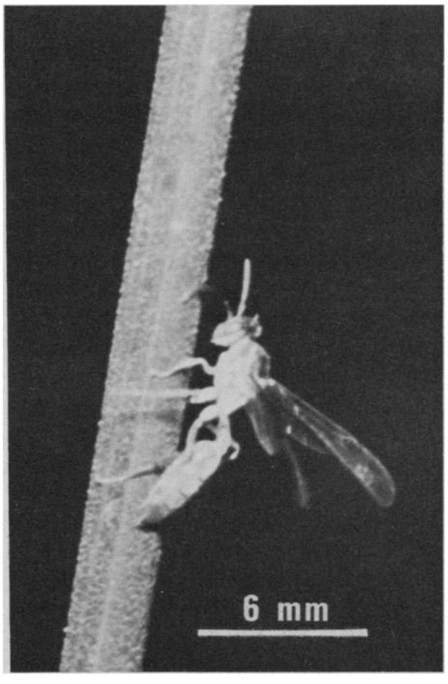
With the dissolution of the swarm, wasps exhibiting only antennating behavior begin flying singly from site to site along the emigration trail to the new nest area, making approximately one stop every meter. Once the emigration of the swarm is well under way, flight becomes so rapid and directional that the entire process is over in less than an hour, even in large colonies.

The new nest site at the far end of the trail is surrounded by visited sites arranged within a circular area 2 to 3 m in diameter, similar to that established around the absconding swarm after nest evacuation. Wasps following the sites along the emigration trail fly in wide meandering circles in this terminal area, eventually settling at the new nest site. Length of emigration routes varied from 3 to 33 meters.

The sudden increase in dragging behavior and the subsequent emigration from the old site may be stimulated by the deposition of nest material at the new site. All swarms seen at the new site shortly after the arrival of the wasps or while emigrations were in progress had deposited some nest material. In *A. pallens* contruction of both the envelope and the first cells had been initiated by the time emigration began.

If the first nest site becomes untenable after occupation, the swarm will emigrate to another site, presumably repeating the emigration process described above. In this way the total emigration distance or dispersal of the colony is effectively lengthened and an unfavorable site is rejected early in the nest cycle.

Investigation of army ant predation on wasp colonies has shown that few species of wasps are free of predation and that some are attacked repeatedly. In response to this random disruption of the nesting cycle and total loss of brood and nest, there has been strong selection favoring escape of the adult population, immediate relocation of the colony, and rapid replacement of the nest. The apparent suppression of a concerted defense of the nest by the colony, thereby conserving workers, is an understandable adaptive response to mass-foraging ants. The emigration mechanisms described above likely result in a decrease in the time the colony is exposed and a reduction of loss of individuals during the emigration. It is noteworthy that the orientation of colony members, including recently emerged naive wasps, to a predetermined route has been seen only in as-



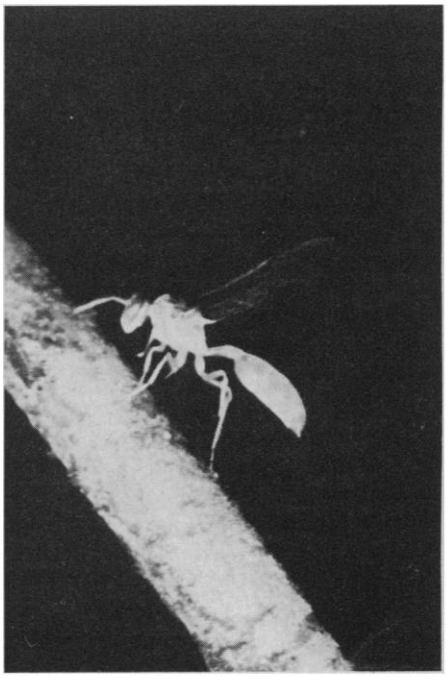


Fig. 1 (left). *Angiopolybia pallens* performing a dragging run on a herbaceous stem. The gaster is held down against the stem and moved from side to side while the wasp runs upward. Fig. 2 (right). *Angiopolybia pallens* worker antennating a site previously visited by a dragging wasp. The wasp walks slowly forward a few millimeters before flying onward.

sociation with swarming in wasps, even though it resembles the orientation-recruitment seen in foraging behavior of some stingless bees (*10*). The swarm formation and emigration processes that occur after nest loss may not be fundamentally different from those of colony founding, but the retention of the colony's ability to initiate the process at any time in its nesting cycle, regardless of the nature of the colony population, is probably also a response to predatory pressure on the nest.

MARTIN G. NAUMANN*
Biological Sciences Group,
University of Connecticut, Storrs 06268

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4. Even though both types of swarms result in the construction of a new nest, a founding swarm may be considered as founding a new colony with population characteristics different from those of the mother colony. The absconding swarm, in retaining the same adult population, is constructing a replacement nest.
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* Present address: Simon's Rock, Great Barrington, Mass. 01230.

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Persistence of Foreign Innervation on Reinnervated Goldfish Extraocular Muscles

Abstract. *Behavioral observations have suggested that the function of foreign synapses on goldfish extraocular muscles can be repressed after reinnervation by the original nerve without any ultrastructural alterations. The present experiments demonstrate that even after behavioral repression foreign synapses are physiologically functional and that the original and foreign nerves can simultaneously innervate goldfish extraocular muscles.*

A number of investigators have suggested that although a foreign nerve can temporarily innervate an experimentally denervated target, these foreign synapses cease to function or are displaced when the original, appropriate nerve regenerates (*1–3*). These conclusions are largely inferential, since most of the experiments involve the demonstration of foreign innervation in one group of animals soon after removal of the nerve and the demonstration of less foreign innervation in another group of animals after the original nerve has regenerated. Behavioral observations and electron microscopic examination of seemingly functionless synapses led Mark and co-workers (*3*) to conclude that in fish extraocular muscles foreign synapses are rapidly shut off or "repressed" without ultrastructural alteration when the original nerve reinnervates the muscle.

The phenomenon of repression has further been implicated in the reestablishment of coordinated movement following the regeneration of severed nerves to muscles that receive polyneuronal innervation (*4*) but not to those innervated by a single nerve fiber (*5*). The appropriate motoneurons may regain control of multiply innervated fibers through a process of competition for various synaptic sites followed by repression of inappropriate synapses. Such competition apparently cannot happen on singly innervated fibers (*6*). A similar process may occur during embryonic development (*6, 7*). It has even been suggested that synaptic repression plays a role in learning and memory (*8*).

If repression occurs during normal embryonic and postnatal development, during nerve regeneration, and during memory storage, then morphologically normal but functionless synapses should be common, and many neuroanatomical studies would need to be reevaluated. The phenomenon of repression is thus of great importance, yet it has never been properly tested physiologically. The following experiments were designed to test the physiological function of foreign synapses on extraocular muscle fibers in goldfish using the same preparation that Mark used to demonstrate behavioral repression (*3*).

The inferior (IOM) and superior (SOM) oblique extraocular muscles, innervated by the oculomotor (NIII) and trochlear (NIV) nerves, respectively, mediate a reflexive ocular counterrotation that tends to keep the eye horizontal when the body is tilted. This reflex can be employed to assess innervation behaviorally (*2, 3*). When a fish is tilted to a head-up position NIV fires, the SOM contracts, and the eye rotates downward. When a fish is tilted head-down NIII fires and the IOM contracts, rotating the eye upward. The separate sources of innervation allow selective stimulation of either an entirely appropriate or entirely foreign population of motoneurons. In order to demonstrate repression physiologically Marotte and Mark's behavioral experiments (*2*), which involve observations of behavioral manifestations of cross innervation, reinnervation, and repression, were repeated. In addition, animals in which behavioral repression occurred were killed, and muscle tension in response to stimulation of the appropriate and foreign nerves was measured in vitro in order to determine whether foreign synapses were actually functionless.

Goldfish, 7 to 10 cm long, were anesthetized with MS-222 (Eastman). The IOM was removed, NIII was tied to NIV near the SOM, and NIV was cut just as it entered the orbit. As a result, NIII had a shorter distance to grow to reach the SOM than did NIV, which enhanced initial foreign innervation. Behavioral reflexes were tested about every 3 days. Thirty-four animals were killed 3 to 14 weeks after surgery. The intracranial portions of NIII and NIV were exposed and stimulated with suction electrodes. In some animals contraction of the SOM was only observed visually, while in others isometric tetanic tension (expressed as kilograms per square centimeter) in response to indirect stimulation (500-msec train of 0.01- to 0.05-msec pulses, 200 to 300 per second) was measured with a Harvard Apparatus model 363 force transducer. Animals that had not undergone surgery served as controls.

The surgery described above does not completely abolish reflex eye rotation. The residual ocular rotation is presumably mediated by the four remaining rectus extraocular muscles. The behavioral manifestation of cross innervation of the SOM by NIII is therefore usually a lessening of the residual upward rotation when the fish is tipped head-down, for NIII fires and the SOM contracts, rotating the eye down. In some cross-innervated animals downward eye rotation actually predominates. Reinnervation of the SOM by NIV is signaled by an increase in downward eye rotation in the head-up position. Behavioral repression following reinnervation is marked by resumption of the residual upward eye rotation in the head-down position.