Novel method of swarm emigration by the epiponine wasp, *Apoica pallens* (Hymenoptera Vespidae)

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Wasps in the Neotropical genus *Apoica* engage in swarm emigration behavior unlike any other swarm-founding wasp. We observed three emigrations by a colony of *A. pallens* in Costa Rica. Following absconding, the colony clustered on leaves as individuals flexed the terminal segments of the gaster dorsally. This posture exposed the bases of the 5th and 6th metasomal sternites, suggesting that the wasps were releasing a pheromone from the sternal glands on these segments. At sunset, wasps left in an explosion of departures and formed a diffuse swarm as they flew to a new site. No wasps marked trails by gaster dragging nor did scouts leave prior to departure of the whole swarm. Individuals at the new site ran along the substrate with the gaster held in the position of the calling display. We conclude that emigrating *Apoica* wasps use the calling display to guide the swarm to new nest sites.

KEY WORDS: social wasps, swarms, Hymenoptera, Vespidae, *Apoica pallens*, calling display.

INTRODUCTION

Social vespids initiate new nests either by independent founding, in which reproductive females initiate new colonies alone or in small groups, or by swarm founding, in which a group comprising queens and a larger number of workers initiate nests (JEANNE 1980, 1991). Swarm founding has evolved from independent founding at least 4 times in vespid wasps (CARPENTER 1991). The ability of swarms to emigrate and found new nests has enabled the 20 genera of the polistine tribe Epiponini to become the ecologically dominant eusocial wasps of the New World tropics (JEANNE 1991). In all epiponine species in which swarm emigration has been observed, scouting individuals investigate potential nest sites prior to emigration and recruit colony members to them via a scent trail. The trail is applied by dragging the gaster on leaves and twigs along a path to the new site (SMITH et al. 2002). Experiments on *Polybia sericea* demonstrated that the trail pheromone is produced by an exocrine gland opening on the 5th gastral sternite (JEANNE 1981) and observations on a number of other epiponine genera suggest that they also lay down chemical emigration trails (SMITH et al. 2002).

There is reason to suspect that *Apoica*, a genus of nocturnal wasps that is the sister group to all other epiponine genera (CARPENTER 1991), may have a different mode of swarm emigration. HUNT et al. (1995) noted that, unlike *Polybia*, *Apoica pallens* does not mark the substrate on which the swarm temporarily clusters prior to emigration. Instead, clustering wasps performed a distinctive calling behavior, in which, wasps remained motionless while holding their gasters rigid above their wings and flexing the terminal segments of the gaster dorsally, exposing gland openings (JEANNE et al. 1983) at the bases of the 5th and 6th metasomal sternites.

HUNT et al. (1995) were unable to observe whether similar behavior is used during the actual emigration. Although SCHREMMER (1972) described an emigration of *A. pallens*, he did not describe the behavior of wasps leaving the old nest and travelling to the new nest site. Here we describe for the first time the behavior of *Apoica* during swarm emigration and show that they communicate via aerial calling behavior, rather than substrate marking.

METHODS

We observed three emigrations by one colony of *Apoica pallens* on private property (adjacent to the La Pacifica field site), 5 km west of Canas, Guanacaste, Costa Rica (10°25'N, 85°7'W). For a description of this site see JEANNE (1996).

We induced the colony to emigrate on August 4 at 10:00 hr by enclosing the nest in a plastic bag and clipping the branch to which the nest was attached. We transported it to a convenient study site at 12:00 hr, then counted wasps as they flew out of a constricted opening in the bag (emigration #1). The colony moved again on August 7 without any disturbance by us (emigration #2). This same colony was forced to abscond again on December 1 at 14:30 hr, this time by clipping the branch to which the nest was attached and removing the nest (emigration #3). On the first and third occasions the absconding wasps formed a cluster on a patch of leaves nearby, which we observed until the swarm emigrated. On December 1 and 2, we videotaped the swarm cluster prior to and during swarm departure and as it arrived at the new site. A count of the adults in the swarm was made from the videotape.

Sunset at our site occurred at 18:03 hr on August 4, at 18:02 hr on August 7, and at 17:16 hr on December 1 (from the U.S. Naval Observatory, Astronomical Applications Department). Ambient light levels decreased until total darkness (skyline disappeared), approximately 30 min after sunset.

RESULTS

During emigration #1, we were unable to observe wasps arriving at the new nest site. During emigration #2, all the wasps had already entered the air prior to our arrival at the site. For emigration #3 we observed both departure from the clus-

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ter site and arrival at the new nest site. Therefore, we describe emigration #3 in detail, then give additional information from emigrations #1 and #2.

At 14:30 hr, we bent the branch so as to lower the nest from its location 4.5 m high in a tree to 2 m high. The wasps performed looping flights downwind, returning to the nest over a 20-min period. Looping flights consisted of wasps flying between a few centimeters and up to 2.5 m off the nest, and immediately returning close to or landing on the nest. For the next 20 min, up to 40 wasps at a time on the nest performed the calling display as described by HUNT et al. (1995) (Fig 1). At 14:50 hr, we removed the nest and the wasps again absconded and performed looping flights downwind at a height of approximately 2 m. Within 10 min the wasps clustered on a leafy twig 2 m high and 0.5 m to the south of the original nest site. The wasps repeated this behavior when we removed the leafy twig. By 15:20 hr, arrivals to the cluster ceased. The number of wasps calling gradually decreased until 15:30 hr and occurred sporadically for another hour and 40 min.

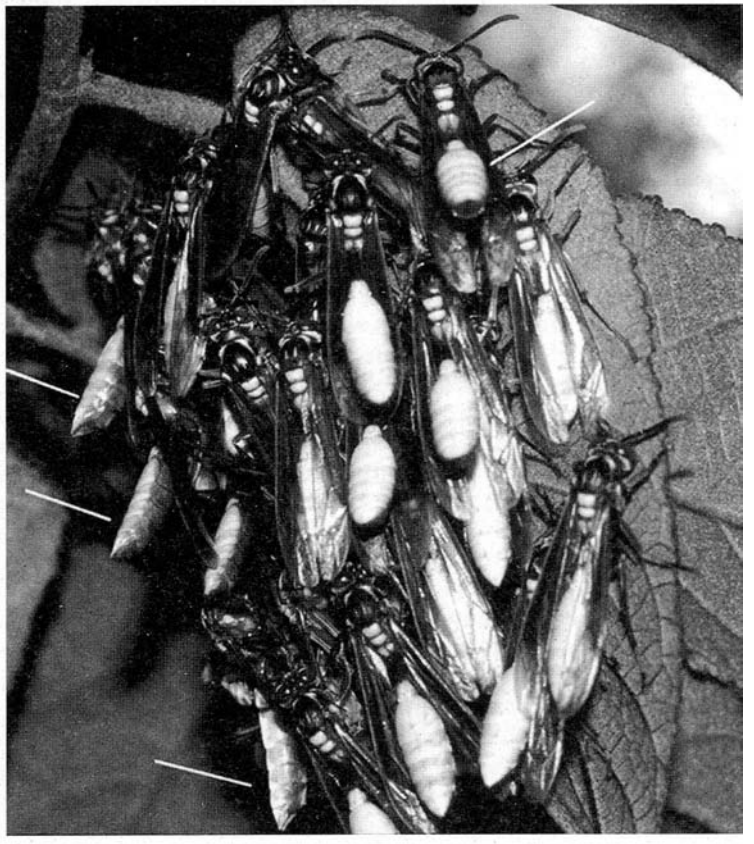

Fig. 1. — The largest swarm cluster during initial cluster formation at approximately 12:30 hr on 4 August 2000, five and a half hours prior to emigration #1. A majority of wasps in the colony were still flying when the photograph was taken. Three individuals along the left edge of the picture can be seen performing the calling display in profile. The wasp at the top right is performing the calling display directly at the camera, so that the opening between sternite 5 and 6 is visible.

The cluster remained motionless and no wasps arrived or departed the cluster until 17:20 hr. At 17:10 hr, activity in the cluster increased and the cluster expanded into an open network of wasps connected to one another by linked legs. At 17:19 hr (3 min after sunset), large numbers of individuals repeatedly groomed their gasters by rubbing their metathoracic legs against the four posterior sternites of the gaster, then rubbing the legs together, against the wings, and over the top of the gaster. At 17:21 hr, a single individual performed a short looping flight. Upon its return to the nest, movement within the cluster increased dramatically. At 17:25 hr, the wasps began to separate from the cluster, run up and down the cluster substrate branch, and then take flight. By 17:26 hr, all wasps had left the site. This explosion of departures preceding emigration strongly resembled the explosion of departures that initiated foraging, as described by HUNT et al. (1995). From analysis of the video we counted 150 wasps departing the site.

An observer (K.J. Howard) standing at a distance of 3 m estimated the swarm to be centered at a height of 2 m during the entire emigration. After leaving the cluster site. most wasps flew in wide arcs in a diffuse cloud within 10-20 m of the previous cluster site, but some wasps rangcd up to 50 m away in all directions before arcing back towards the central region of the swarm. Individuals within the swarm landed on branches and ran around and along the branches rapidly while holding their gasters in the air. Several times the density of hovering wasps noticeably increased within a meter of these individuals. We were unable to observe the postures of the gasters of these wasps due to their rapid movement. At three sites north of the cluster site, at least two wasps landed and about 20 wasps were seen to fly closer to the branch. The increased density persisted for 4 to 5 min while up to two wasps at a time landed and ran along the branch. The density decreased after no more wasps landed, although wasps were still observed flying through the area.

At 17:45 hr, more than 30 wasps were hovering within 1 m of a 1-cm diameter branch in the center of a tree crown 10 m south of the cluster site. Wasps landed at the new site, ran along the branch with their gasters held in the air, and then quickly took flight. By 17:47hr, wasps accumulated at the new site by landing and climbing on top of one another on the branch. At 17:48 hr, wasps began departing, until only five individuals were left at the site. By 17:49 hr most of the wasps had returned, and by 17:51 hr over 100 individuals were clustering on the branch. Analysis of the video from 17:46 hr to 17:47 hr revealed that several wasps landing at the site ran along the branch rapidly with their gasters held over their motionless wings and flexed upward in the manner of the calling display. Individuals performed the calling display in a stationary stance starting at 17:50 hr. No individuals were observed to drag their gasters on the substrate at any point.

The next day looping flights began at 17:20 hr. At 17:22 hr the entire swarm left the site in a large explosion. We observed no nest at the site. The swarm appeared to increase in density at a site about 0.5 m higher in the tree, where two or more wasps were landing on a small branch and quickly taking off. By 17:25 hr wasps were landing at the original site, running along the branch with their gasters in the position of the calling display. By 17:30 hr most of the wasps had returned there.

During emigration #1 (August 4), cluster formation and emigration proceeded as in emigration #3, but with minor differences. We counted 263 wasps flying out of the plastic bag. From 12:00 hr to 14:00 hr, the swarm formed three clusters of 70, 45, and 10 wasps on leaves, and probably more that we were unable to locate. At 17:50 hr, wasps from the two smaller clusters took off 3-5 min prior to initiation of departures from the largest cluster. More than 20 individuals arrived at the

largest cluster approximately 5 min prior to the explosive departure of individuals from the site at 18:15 hr. We did not observe arrival at the new site following emigration #1. The next morning we located the colony 3 m high in a tree 4 m to the north. The colony stayed at this new site for 3 days without building a nest, then emigrated again on August 7 (emigration #2).

On August 7, we arrived at the site at 18:15 hr to discover a diffuse swarm flying around the cluster site at a height of approximately 4 m. The swarm emigrated to a tree branch 15 m to the south and 4.5 m high, arriving in the manner described for emigration #3. On August 8, the day after emigration #2, wasps departed at 18:04hr in the same manner as emigration #1 and #3, and by 18:05hr the entire swarm had left the site. By 18:09hr, the wasps accumulated back at the cluster site in the same manner as emigration #2 and #3. The swarm repeated this sequence at 18:15 hr and at 18:22 hr.

During emigration #1, we observed two males resting on leaves following release of the colony from the plastic bag. One male arrived at the main cluster approximately 15 rnin after release. Two males were seen on the swarm cluster on August 5, following emigration #1, and on the pre-emergence nest 23 days after emigration #2.

DISCUSSION

We conclude that chemical marking of substrates at cluster and emigration sites does not occur in *A. pallens.* Unlike all other swarm-founding wasps in which swarm emigration has been observed (SMITH et al. 2002), gaster-dragging was not observed at any of the initial cluster sites or at any point during the emigration process. Instead, the wasps appear to release pheromone directly into the air via the calling behavior. The grooming behavior prior to swarm lift-off may spread a pheromone over the body surface, enhancing signal dispersal and thereby facilitating swarm cohesion during flight. The presence of curved bristles associated with the sternal glands in *A. pallida* and *A. flavissima,* just as in *A. pallens,* suggests that this form of swarm emigration behavior characterizes the genus.

The swarms selected the new sites without sending out scouts prior to departure. During emigration #3, wasps visited at least three sites well after the entire swarm had departed the initial cluster site. Other wasps were attracted to these sites and many inspected the branch, even though those sites were eventually rejected. The positions of these sites north of the cluster site indicate that they were not marked sites directing the way to the eventual emigration site to the south. Scouting could have occurred prior to emigration #2, but likely could not have occurred prior to emigrations #1 and #3, since the colony was moved prior to emigration 1 and in both cases wasps had no warning of impending disturbance. Arrivals at the main cluster 5 rnin prior to emigration #1 were likely not scouts, but wasps joining the main cluster from the other clusters.

Our observations on males are consistent with previous reports of males found in swarms of *Apoica pallida* (DUCKE 1905) and on pre-emergence nests of *A. flavissima* (RICHARDS 1978). Taken together, they suggest that, in contrast to *Polybia occidentalis* (BOUWMA et al. 2000), males in this genus follow swarm emigrations and may remain with the colony for at least 3 weeks after construction of the new nest.

The fact that each of the three emigrations began at about sunset and was completed before skylight completely disappeared suggests that *A. pallens* consistently emigrates at sunset, using falling light levels as the stimulus to move. In addition, the day after emigration #2 and the day after emigration #3, the entire colony departed from the cluster site at about sunset, and returned prior to total darkness. This diurnal activity is of interest because *Apoica* performs all other activity only at night and has evolved morphological specializations for nocturnal behavior such as enlarged ocelli and lightly-pigmented cuticle. The only other nocturnal eusocial wasps are the three species in the swarm-founding vespine genus *Provespa,* which has been observed emigrating only at night (MATSUURA 1999).

Because *Apoica* is the basal genus among the Epiponini, its behavior may shed light on the evolution of swarm founding from independent-founding ancestors. WEST-EBERHARD (1982) postulated that independent-founding species evolved the use of assembly pheromones (e.g. *Mischocyttarus immarginatus;* O'DONNELL 1992), followed by the evolution of short, directional recruitment trails using scent marks, (e.g. *M. labiatus,* LITTE 1981), eventually leading to the trail communication found in other epiponine genera in which workers scout for nest sites and mark trails to guide the rest of the colony (JEANNE 1981). The method of swarm emigration described here for *A. pallens* does not fit well into this sequence.

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