Gaster-Flagging during Colony Defense in Neotropical Swarm-Founding Wasps (Hymenoptera: Vespidae, Epiponini)

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ABSTRACT: During colony defense, workers of several species of Neotropical swarm-founding wasps hold the distal tip of the abdomen erect in a behavior here termed gaster-flagging. Gaster-flagging can be accompanied by various combinations of wing fanning, waving of the gaster, and extrusion of the sting. Workers flag their gasters while perched either on or near the nest surface, or on the body of an intruder several meters from the nest. In many species that engage in this behavior, the gaster is brightly and contrastingly colored compared to the rest of the body. Gaster-flagging may play a role in communication among nest mates during defense, involving visual and/or chemical signals. Flagging may also serve to enhance visual warning signals of impending defensive stinging behavior to potential predators.

The Epiponini are Neotropical swarm-founding eusocial wasps, characterized by large colony sizes and complex nest architecture relative to independent-founding species (Jeanne, 1991). Epiponine defensive behavior often comprises large numbers of workers rapidly exiting the nest upon initial disturbance, followed by stinging attacks in response to further disturbance (Jeanne, 1981). We observed workers of seven species of epiponine wasps exhibiting a previously undescribed behavior, which we term gaster-flagging, in response to disturbance of their nests. Gaster-flagging is a posture where the entire gaster is held erect with the distal tip pointing upward from the surface on which the wasp is standing. The gaster is held perpendicular, or nearly so, to the longitudinal axis of the rest of the body. We describe additional body postures and movements that accompany gaster-flagging, and the behavioral contexts in which gaster-flagging occurs in eight epiponine species belonging to five genera. We hypothesize that gaster-flagging serves one or both of two communicative functions. First, gaster-flagging may function as a visual warning signal of impending defensive (stinging) behavior to vertebrate enemies, thereby decreasing the likelihood of attempted predation. Second, gaster-flagging may be a social display that coordinates defensive behavior among colony mates, possibly involving visual and chemical signals. We present behavioral evidence in support of these hypothesized functions.

Materials and Methods

We recorded observations of gaster-flagging while collecting wasp colonies (six species; Table 1) and during experimental trials of defensive behavior (*Polybia dimidiata,* below). Epiponine wasps respond to mechanical disturbance (jarring) of their nests with defensive responses as described by Jeanne (1981; see also Jeanne

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Table 1. Behavioral contexts, postures, and coloration of body parts associated with gaster-flagging in swarm-founding eusocial wasps.

Species	Substrate from which workers flag[a]	Position of wings during gaster-flagging[b]	Gaster color contrasting?[c]
Agelaia panamensis	I	F	N
A. yepocapa	I, N	R	U
Apoica albomacula[d]	N	R	E
Brachygastra augusti[e]	N	V	U
Epipona nigra	I	F (initially), R	E
P. dimorpha	N	V	N
Synoeca septentrionalis	I, N	R	N

[a] I: Workers flag while perched on the body of an intruder; N: Workers flag from the outer surface of the nest envelope or near the nest entrance.

[b] F: Workers fan their wings while flagging; R: Wings are held folded rigidly alongside the body during flagging; V: Wings are raised and spread in a "V"-pattern but held rigid.

[c] E: Entire gaster colored differently from remainder of body; U: Underside of gaster colored differently from remainder of body (underside exposed when flagging); N: Gaster color not different from remainder of body.

[d] Richards and Richards (1951).

[e] Also figured in Richards (1978).

et al., 1992). One or two observers simulated vertebrate attack to elicit colony defense. Defense was elicited either by sharply striking the subject colony's nest envelope or nest entrance one to five times with a gloved hand, an insect net, or a machete, or by climbing the tree in which the nest was located and thereby vibrating the nest. We estimated the numbers of workers engaging in gaster-flagging during the initial defensive response (within 30 sec of disturbing the nest), and recorded the body postures of flagging workers, the substrate on which flagging was performed, and whether discernible odors were emitted by the wasps. We also noted changes in the numbers of gaster-flagging workers during collection of the colonies. Observations were made in Costa Rica (*Agelaia panamensis, N* = 1 colony; *A. yepocapa, N* = 2 colonies; *Epipona nigra, N* = 1 colony; *Synoeca septentrionalis, N* = 1 colony), Panama (*E. nigra, N* = 1 colony), southeastern Peru (*Brachygastra augusti, N* = 3 colonies), northeastern Peru (*Polybia dimorpha, N* = 1 colony), and Amazonian Brazil (*Brachygastra* sp. (probably *B. augusti*), *N* = 1 colony; *P. dimidiata, N* = 1 colony).

During studies of defensive behavior in *P. dimidiata*, a colony was presented with a small plastic bottle covered with black paper, onto which the venom sac and sting apparatus of one worker was crushed. Worker responses to the target were recorded as above.

Results

As noted in studies of defensive behavior in *Polybia occidentalis* (Jeanne, 1981; Jeanne et al., 1992), the initial phase of defensive response in five of the six species we studied consisted of several dozen to several hundred workers rapidly exiting the nest. In four of the subject species, gaster-flagging was performed during this phase of nest defense by workers perched on the nest envelope, or near the nest entrance in the case of cavity-nesting species (Table 1). Gaster-flagging on the nest surface was performed simultaneously by all or nearly all workers that were visible outside the nest in *Brachygastra* sp. (Fig. 1; the same response was observed in three colonies of *B. augusti*) and *Polybia dimorpha*. In *P. dimorpha*, approximately 50

Fig. 1 (left).   Several dozen *Brachygastra* sp. (probably *B. augusti*) workers gaster-flagging on the surface of their nest. Note that the undersides of the workers' gasters are pale (yellow in life) in comparison to the rest of the body. The extruded sting is visible on several workers along the right-hand edge of the nest, indicated by the black arrow. The nest was jarred immediately prior to taking the photograph. A similar response was seen when nests of *B. augusti* were jarred during collection in Madre de Dios Province, Peru. Photograph taken near Santarem, Para, Brazil, 16 February 1969.

Fig. 2 (right).   Workers of *Polybia dimidiata* gaster flagging from an experimental target (plastic bottle covered with black paper; a venom sac and sting apparatus from one worker was crushed onto the target). Gaster-flagging workers initially moved their gasters from side to side while fanning their wings. Note that the gasters are pale (red-orange in life) in contrast to the rest of the body. The sting of the worker near the center of the target, indicated by the black arrow, is extruded. Photograph taken near Santarem, Para, Brazil, 28 October 1981.

workers already present on the nest envelope assumed the gaster-flagging posture when the nest was struck; additional workers did not exit the nest. A photograph of this group response was presented for *Apoica albomacula* (Richards and Richards, 1951, plate II, fig. 25), but the behavior was not described. In *Synoeca septentrionalis* and *Agelaia yepocapa*, a smaller proportion of the workers present performed gaster-flagging on the nest (one out of several dozen workers in *S. septentrionalis*; one to five out of several thousand workers in *A. yepocapa*). Individual workers flagging on their nests held the posture for approximately 45 sec following a single disturbance (*B. augusti* and *P. dimorpha*; durations of gaster-flagging were not recorded for individuals of the other species).

Following continued disturbance, either repeated jarring of the nest or movement by the observers, some workers of all species excepting *B. augusti* and *P. dimorpha*

flew from their nests. During this second phase of colony defense (Jeanne, 1981), workers landed on the observers' bodies (or a presented target) and grasped hair, skin, or clothing firmly in their mandibles (see also O'Donnell and Jeanne, 1990). In five of the species we studied, gaster-flagging was performed by workers clinging to the observer. Workers flagging from the bodies of observers apparently did not attempt to sting, as their gasters were held erect for periods of greater than 1 min. As was the case for gaster-flagging from the nest, the proportion of workers flagging when perched on the intruder varied among species. In *Epipona nigra* and *P. dimidiata,* several dozen and ten individuals, respectively, flew to the observer or target and began gaster-flagging immediately and simultaneously upon nest disturbance. In contrast, we estimated a total of fewer than ten out of thousands of workers that flew from the nest performed gaster-flagging on two observers within 30 sec of nest disturbance in *Agelaia panamensis* and *A. yepocapa*. In the *Agelaia* species, the number of flagging wasps increased gradually with the severity and duration of nest disturbance until a maximum total of approximately twenty workers were flagging on two observers; the proportion of defenders engaged in gaster-flagging could not be determined, but may not have increased as workers continued to exit the nests over periods of 15 min (*A. yepocapa*) to 1.5 hr (*A. panamensis*). Gaster-flagging was performed by workers clinging to observers at distances ranging from one meter (all species) to approximately twenty meters (*Agelaia* species and *E. nigra*) from the nest.

The sting was extruded and the gaster was pumped during gaster-flagging on the bodies of intruders in *P. dimidiata* (Fig. 2), *A. yepocapa,* and *E. nigra*. Gaster-flagging in *E. nigra* was accompanied by the release of a strong, irritating odor reminiscent of rotting celery (S.O'D., pers. obs.). A leather-like odor was discerned during disturbance of *A. yepocapa* colonies (see also O'Donnell and Jeanne, 1990).

Workers of three species fanned their wings while gaster-flagging from the bodies of intruders (Table 1). In *P. dimidiata,* wing fanning was accompanied by waving of the gaster; both fanning and waving lasted approximately 1 min, after which the wasps retained their grip on the target and held their gasters erect but stationary (Fig. 2). In the other subject species, workers' wings were either held rigidly alongside the body in their usual folded resting position, such that the gaster protruded between and above the wings (Table 1; see also Richards and Richards, 1951, Plate III, Fig. 25), or the wings were spread but not fanned (Fig. 1; Table 1).

During the defensive response of an *S. septentrionalis* colony, several of the wasps on the nest made the characteristic alarm sound of *Synoeca* spp. by scraping their mandibles across the nest carton (Overal, 1982). One of the wasps on the nest envelope engaged in gaster flagging while also scraping its mandibles.

Discussion

We hypothesize that gaster-flagging on the nest functions primarily as a visual signal to reduce the likelihood of predatory attack by vertebrates (Hermann and Blum, 1981; Starr, 1990), particularly in those species where gaster-flagging is performed simultaneously by dozens of workers. Gaster-flagging on the nest may also function to keep the colony in a state of alarm if workers waft venom into the air. Unidentified components of venom function as alarm pheromones in all eusocial Vespidae so far investigated, including the epiponine wasp *Polybia occidentalis* (Jeanne, 1981; Jeanne, 1996; Landolt et al., in press).

Gaster-flagging while clinging to enemies is potentially costly, at least to the in-

dividual worker. Workers engaging in gaster-flagging while perched on enemies do not attempt to sting, yet they expose themselves to retaliatory destruction if the predator attempts to swat or groom them from its body. We hypothesize that gaster-flagging in this context serves a communicative function to nest mates: gaster-flagging workers signal alarm directly from the intruder, where further stinging attacks would be most effective. Whether the cues involved are chemical or visual is not known, but our observations suggest that both sensory modalities may be involved. The fact that the sting was extruded and strong odors were produced in some species suggests that venom (or pheromones from other glands) was released. The venom sac is surrounded by a wall of muscle in vespid wasps, which allows workers to forcefully expel venom from the sting (Maschwitz and Kloft, 1971). Wing fanning in conjunction with gaster-flagging may volatilize and disperse alarm pheromones from venom or from other exocrine sources.

In several gaster-flagging species, all or part of the gaster is conspicuously and contrastingly colored compared to the rest of the body, suggesting its possible use as a visual signal. In *A. yepocapa* and *B. augusti,* for example, the underside of the gaster is pale yellow, contrasting with the darker markings of the upper body surface. In *P. dimidiata* the gaster is red, in contrast to the black color of the rest of the body. The waving of the gaster in *P. dimidiata* may enhance the visibility of the signal. More information on the distribution of gaster colors and of gaster-flagging behavior in other epiponine species are needed to determine whether contrasting gaster color represents an adaptation to enhance signal effectiveness.

The suggested coupling of chemical and visual signaling modes in colony defense could be adaptive. Release of alarm and attack behavior by the odor of venom is sudden and massive (Jeanne, 1981). However, its effectiveness is partly dependent on air movement. When workers engage in gaster-flagging from the body of an intruder they have attacked, the chemical signal may fail to reach colony mates on the nest from a distance of several meters if there is no wind or if the intruder is downwind from the nest. A visual signal might provide effective backup communication under these conditions. However, we have not observed workers to direct stinging attacks to the immediate vicinity (i.e., within a few centimeters) of gaster-flagging nest mates. The evidence for two modes of signaling is circumstantial, and experimentation is needed to test for the existence of each.

Gaster-flagging appears in a number of genera scattered across the epiponine phylogenetic tree, both in relatively basal and derived taxa (Carpenter, 1991; Table 1). To our knowledge, this behavior has not been observed in Neotropical independent-founding social Polistinae (i.e., *Polistes* and *Mischocyttarus,* sister taxa of the Epiponini). In some *Polistes* spp., workers bend the tip of their gasters laterally toward intruders when their colonies are disturbed (See Starr, 1990, Fig. 15.4). Although gaster-flagging may have evolved as an elaboration of such a lateral bending display, the postures and in some cases the behavioral contexts of flagging are different. If it serves a communicative function during colony defense, gaster-flagging may have evolved along with greater colony size in swarm-founding wasps (Kukuk et al., 1989; Jeanne, 1991). The ability to recruit large numbers of stinging nest mates in response to vertebrate assault may have been favored by selection as colony size increased in the epiponines (Starr, 1985). Similarly, a coordinated threat display involving dozens or hundreds of individuals may effectively repel vertebrate enemies from the large colonies of epiponines.

Acknowledgments

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