Argentine Ant Iridomyrmex humilis (Hymenoptera: Formicidae) Predation on Yellowjackets (Hymenoptera: Vespidae) in California

by

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ABSTRACT

Colonies of four yellowjacket species were monitored during a two year period to quantify interactions with ants. *Iridomyrmex humilis*, an introduced alien species, was the only ant detected; it was present at 25 (22.1%) of 113 wasp nests. *I. humilis* preys on yellowjackets and is able to recruit large numbers of workers to invade yellowjacket colonies. Ant attendance was greater at colonies manipulated to reduce the defending worker force than at unmanipulated colonies. At lightly attended colonies the number of ants increased in response to manipulations 77.8% of the time, whereas only 11.1% of colonies lacking ant attendance had ants after being manipulated. Defensive behavior of yellowjacket workers was observed in *Vespula pensylvanica* and *V. germanica*, and inferred in *Dolichovespula arenaria*. Components of wasp defensive behavior included aggregations of guard workers near the colony entrance, pecking at ants to sever their bodies or dislodge them from the substrate, and grasping them with the mandibles and flying away.

INTRODUCTION

The relative influence of vertebrate and invertebrate predators on the evolution of sociality is a subject of recent debate. Starr (1985; 1989) has argued that once social insect colonies pass a certain size threshhold, their attractiveness to vertebrate predators necessitates specific anti-vertebrate defenses, and that the

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preadaptation of the sting accounts for the success of Hymenoptera in exceeding this size threshhold. Kukuk *et al.* (1989) discount the importance of the sting as an anti-vertebrate defense in the origin of sociality, citing numerous accounts of invertebrate predation on social Hymenoptera colonies.

The Vespinae are advanced eusocial wasps that form large colonies (Akre & MacDonald, 1986); as such, a study of their defensive mechanisms would reveal little regarding the origin of sociality, but would provide evidence of the selective pressures that must be addressed for the advanced eusocial state to be maintained. Against vertebrates, the deterrent effects of the sting and the ability to recruit workers to colony defense are well known (Akre & Reed, 1984). In contrast, interactions with invertebrate predators have received little attention. There are several records of ants associated with vespine wasp colonies (Stone, 1865; Kleinhout, 1958; Kemper & Dohring, 1967; Grant *et al.*, 1968; Janet, cited in Edwards, 1980; Akre & Reed, 1984), but detailed investigations of these interactions are lacking.

This study examines associations between four vespine species and the Argentine ant *Iridomyrmex humilis* (Mayr), a south temperate species that has become widely distributed. *I. humilis* forms large polygynous colonies and uses efficient recruitment behavior to exploit concentrated food resources (Van Vorhis Key & Baker, 1986), occasionally attacking honey bee colonies (Woglum & Borden, 1921; DeJong, 1978). Interactions described here include ant attraction and predation, and wasp defensive behavior.

MATERIALS AND METHODS

During 1986-1987 naturally occurring colonies of four vespine yellowjacket species (*Dolichovespula arenaria* (Rohwer), n=63; *Vespula pensylvanica* (Saussure), n=21; *V. vulgaris* (L.), n=26; and *V. germanica* (L.), n=3) were located in San Francisco, Alameda, and Contra Costa counties, California. Nests were observed for fifteen minutes for the external presence of ants. At *D. arenaria* colonies initial observations were made at night, and only ants on the nest envelope were counted; most nests were also then removed, placed in a sealed bucket, frozen, and dissected to search for ants or ant fragments internally; external and internal ant counts were combined. At *Vespula* spp. colonies the entrance hole leading to the nest cavity was observed during the day; ants were counted only if they disappeared into the hole or emerged from it. Ant attendance during the 15 minute observation period at a nest was scored 0=no ants; 1=1-20 ants; 2=20-200 ants; 3=>200 ants.

Additional observations of interactions between *I. humilis* and yellowjackets were made under unusual circumstances at three colonies. At two aerial *D. arenaria* nests, combs heavily laden with brood had fallen to the ground; the combs contained larvae and capped cells, from which adults were emerging. At one aerial *V. pensylvanica* colony, adult workers, males, and queens had fallen to the ground. At all three colonies the main nest was at least 3m high and was not examined. Adults on the ground were sluggish. Ant activity scores for these colonies were not included in the statistical treatments described below, unless otherwise noted.

At all nests scored 3 (n=9, including 2 intact *D. arenaria* colonies studied during 1985 and the fallen combs of 2 *D. arenaria* colonies) *I. humilis* foragers were observed for an additional 15 minutes to search for differences between ants going toward and away from the wasp nest. Six of the nests scored 3 were immediately dissected to observe the behavior of ants within the nest.

To test the deterrent effect of a yellowjacket colony's worker force against ant invasion, manipulations that reduced the number of workers at a colony were carried out on a subset of 18 colonies. Colonies were scored before and after treatments: at six colonies, workers were collected with a vacuum cleaner-powered aspirator as they exited from the nest, and ant infestation was scored again after 10 days; at eight subterranean *Vespula* colonies, an inverted funnel trap was placed over the entrance at night and removed after several hours of daylight the next day, followed immediately by a 15 minute observation; at four subterranean *Vespula* colonies, a water suspension of the entomopathogenic nematode *Neoaplectana carpocapsae* Weiser was poured into a hole poked through the nest envelope, and ant attendance was scored two days later. The degrees of ant attendance (counting the final score for each colony) at unmanipulated and manipulated colonies were compared using the Mann-Whitney test, adjusted for tied ranks (Zar, 1974).

Table 1. Argentine ant attendance at California vespine colonies

	Unmanipulated Colonies			Manipulated Colonies			
	N	No. With Ants	Mean Score	N	No. With Ants	Mean Score	Manipulations*
<u>D. arenaria</u>							
1986	11	7	1.00	1	1	2.00	1RE
1987	50	6	0.16	1	1	3.00	1RE
<u>V. pensylvanica</u>							
1986	5	1	0.20	6	5	1.67	3TR, 3NE
1987	7	0	0.00	3	1	0.67	2RE, 1TR
<u>V. vulgaris</u>							
1986	15	0	0.00	2	1	1.50	1TR, 1NE
1987	4	0	0.00	5	1	0.20	2RE, 3TR
<u>V. germanica</u>							
1986	1	0	0.00	0	-	-	
1987	2	1	1.50	0	-	-	
	95	15	0.25	18	10	1.11	

*RE = Workers removed with vacuum aspirator
TR = Workers collected at entrance with funnel trap
NE = Subterranean nest treated with nematode suspension

Since manipulations might attract ants to colonies from which they were initially absent (thus obscuring the extent to which *I. humilis* was naturally associated), the effects of manipulations on colonies lacking ant attendance (pretreatment score=0) were compared with those lightly attended by ants (pretreatment score=1). Nine colonies in each category were artificially manipulated; in response, scores either remained the same or increased. Results were analyzed with the G test (Sokal & Rohlf, 1981).

To test for a yellowjacket species effect on ant association, the presence/absence of *I. humilis* at colonies of *D. arenaria*, *V. pensylvanica*, and *V. vulgaris* was analyzed with a chi-square test (there were too few *V. germanica* colonies for inclusion in the analysis). Because manipulations had only a small effect on attracting ants to previously unattended colonies, numbers of manipulated and unmanipulated colonies were pooled for this analysis.

At three nests scored 3 (one of *V. germanica*, two of *V. pensylvanica*) defensive behavior of yellowjacket workers in the vicinity of the nest entrance was observed and described.

RESULTS

A summary of the distribution of ants among vespine colonies is presented in Table 1. *I. humilis* was the only ant species detected. Twenty five (22.1%) of 113 nests had at least some ants. Ant attendance at manipulated colonies was greater than at unmanipulated ones (mean scores of 1.11 and 0.25, respectively; $U=4.01$; $df = 18, 95$; $P<0.01$). Treatments resulted in increased scores for 7 (77.8%) of 9 colonies originally scored 1, but only 1 (11.1%) of 9 colonies scored 0 ($G=8.90$; $df=1$; $p<0.01$). Ants showed no preference among the wasp species analyzed (chi-square=4.82; $df=2$; $p>0.05$).

I. humilis workers were attracted to and clustered around weakened or unprotected larval and adult yellowjackets on the soil surface, as in the cases of combs fallen from *D. arenaria* colonies, individuals fallen from the aerial *V. pensylvanica* colony, or adults caught in traps above subterranean *Vespula* colonies. Ants departing from yellowjackets on the ground, or from successfully-penetrated nests, had more-swollen gasters than arriving ants, indicating fuller crops from the ingestion of liquids (presumably wasp fluids). In nests dissected while heavy ant attacks were in progress, ants were distributed throughout the envelope and interior of the nest, but were clustered around adults and larvae, where attack and feeding were taking place. In one *D. arenaria* nest ants tugged small larvae about, possibly in preparation for transport to the ant colony. Wasp immatures in capped cells were apparently immune from ant attack, but teneral adults were attacked as soon as they chewed through the silken cap before emerging from the cell. Ants leaving attacked nests rarely carried solid insect parts in their mandibles; of the thousands of ants observed leaving wasp nests, only one carried a wasp egg, and one carried a small larva.

Yellowjacket colonies were able to defend themselves against ant attacks. Workers at three colonies exhibited defensive behavior; the most extensive behavioral repertoire was shown by workers at a *V. pensylvanica* colony during a heavy ant attack that lasted at least three days. The unmanipulated colony, approximately six meters above ground in a cavity between the inner and outer walls of a wooden house, had four nest cavity entrances. Worker ants ascended the outer building surface from the ground in two dense parallel trails about 1.5m apart. As they approached the wasp colony they dispersed over a wide area with smaller, less distinct trails leading to the various nest cavity entrances; many individuals wandered about singly, separate from any apparent linear trails.

A variable number (2-15) of yellowjacket workers patrolled the immediate vicinity of the main nest entrance (Fig. 1). The three secondary entrances were guarded by smaller contingents. Guard workers alternately walked about and paused, continuously antennating the substrate, and rarely strayed outside a radius of approximately 15 cm. Wasps showed several different reactions to encounters with ants; some elicited no visible response, especially if contact was made with the wasp's legs, thorax, or gaster.

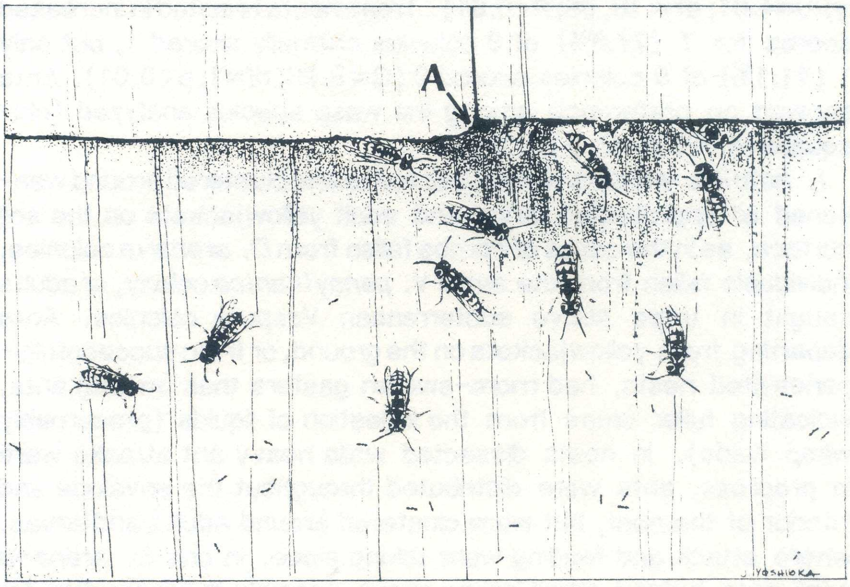

Fig. 1. Workers of *Vespula pensylvanica* guarding the colony against invading *Iridomyrmex humilis* foragers. A=location of main nest entrance

Wasps were apparently able to detect ants from a short distance (~2mm); upon locating an ant, the wasp oriented its body so that the ant was directly in front of it. Next, the wasp either lunged forward, grasping the ant with its mandibles and immediately flying away (presumably to drop the ant some distance from the nest), or it lunged forward while remaining on the vertical surface, rapidly closing its mandibles on the ant (in a few instances the clicking of the mandibles was audible one meter away). Some ants attacked this way were merely dislodged, but many had the body severed (Fig. 2), or were otherwise disabled. Individual wasps were able to switch between these two behaviors, as a single wasp dislodged two ants and then captured and flew away with a third, all within 15 seconds. The defensive behaviors of the wasps caused ant cadavers (and fragments) to accumulate on an awning directly beneath the entrance to the nest cavity. A total of 4847 ant cadavers were collected from the awning during three days of intermittent observation; this figure underestimates the total number of ant casualties, since ants that were carried away by wasps, removed by other ants, or did not

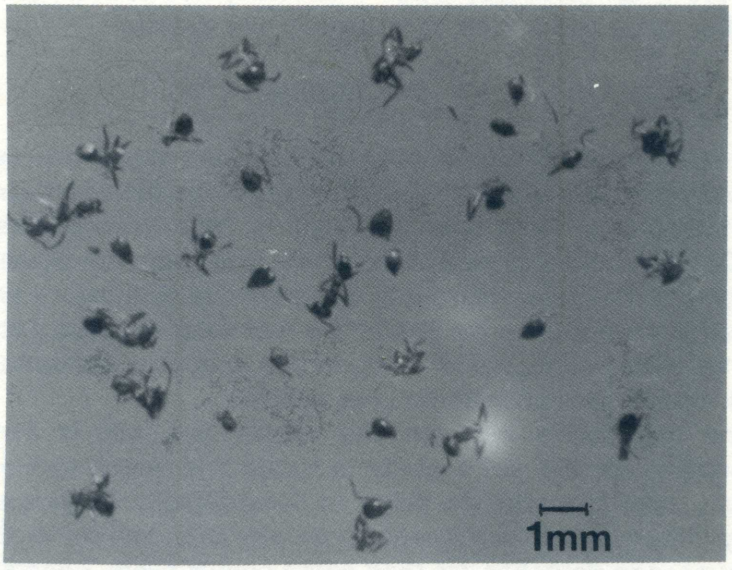

Fig. 2. Severed ant bodies generated by wasp defensive behavior

otherwise accumulate on the awning could not be counted.

The ant attack did not totally disrupt other colony activities. During daylight hours, foraging wasp workers carrying prey items returned to the nest throughout the course of the ant attack. By the third day of observations, ant attendance at the colony had dwindled to zero, and external signs of yellowjacket activity returned to normal. The colony was treated with insecticide after the sixth day, and the long term effect of the ant attack on the colony could not be evaluated.

Fragments of ants similar to those generated by *V. pensylvanica* defensive behavior were found inside three nests of *D. arenaria*, indicating that workers of this species also defend the colony, with some combat occurring within the nest. One *D. arenaria* colony had over 200 such fragments, yet had fewer than 10 intact (= live when collected) ants. This colony had both an abundant worker force and a crop of emerging new queens.

DISCUSSION

Iridomyrmex humilis is able to locate and exploit the concentrated resources accumulated at vespine colonies, feeding readily on wasps that have been subdued. *I. humilis* was observed at 22.1% of the colonies in the study area, with ant attendance ranging from fewer than 20 to thousands of workers. It showed no strong preference for any of the four vespine species studied, as would be expected of a generalist predator presented with four closely related potential prey species.

The relationship between the wasps and ants is dynamic, depending on the ant's ability to locate and recruit to the wasp colony, and the colony's ability to defend itself. Chance events may influence the discovery of a colony by ants, and some colonies may escape detection for their entire annual cycle. Experimental depletion of a colony's worker force did not render it substantially more prone to discovery, at least over short time intervals. However, once a colony is discovered the risk of predation increases. Light ant attendance poses little immediate threat, but *I. humilis*'s efficient recruitment behavior provides a mechanisms for rapid mobilization of an invading force. In contrast to the effects at unattended colonies, the experimental removal of wasp workers from colonies where a few ants were already present caused an increase in the number of ants at 77.8% of the colonies.

Wasp colonies resist ant invasions through the defensive behavior of workers. Although active colony defense was observed only during heavy ant attacks, it would also seem useful in preventing massive ant invasions by discouraging ant scouts before they can initiate large-scale recruitment. The outcome of even a massive ant invasion is not certain. At least one *V. pensylvanica* colony repulsed thousands of ants while maintaining typical prey foraging activities, and a vigorous *D. arenaria* colony apparently repulsed a major ant attack to proceed well into the reproductive phase of the colony cycle. However, most colonies under heavy attack were clearly overrun, with little chance of any recovery.

Some aspects of defensive behavior of yellowjacket workers resemble those of polistines; pecking at ants with the mandibles while remaining on the substrate has been described in *Polistes canadensis* (L.) (West-Eberhard, 1969) and *P. fuscatus* (F.) (Post & Jeanne, 1981), and the tactic of grasping an ant and flying away is also recorded for *Apoica pallens* (F.) and *Polybia velutina* Ducke (Chadab-Crepet & Rettenmeyer, 1982).

Estimates from this study of the rate of ant visitation and the impact of ant attendance at wasp colonies are conservative. The experimental observation periods were brief relative to the longevities of both the ant and wasp colonies, and ants are likely to attend or rediscover wasp colonies over extended intervals. Major recruitment may be deferred until the wasp worker force is insufficient to provide adequate colony defense. This condition occurs early in the colony cycle when biomass is small, and during the reproductive phase when biomass is large but the majority of colony resources are allocated to rearing reproductives.

Vespine colonies are susceptible to vertebrate as well as ant predators, but the relative importance of these two classes is hard to predict. Predation pressure on any one prey species is not likely to be uniform throughout its range, but will vary according to the distributions of potential predators. In coastal California, subterranean *V. pensylvanica* and *V. vulgaris* colonies are attacked by both the Argentine ant and the striped skunk *Mephitis mephitis* (Schreber) (unpublished data), an important predator of *Vespula* colonies elsewhere (Preiss, 1967). *D. arenaria* and the North American strain of *V. germanica* have for the most part escaped skunk predation, the former by nesting aerially (Greene *et al.*, 1976), the latter by nesting primarily in cavities in artificial structures (MacDonald & Akre, 1984). However, the recorded *I. humilis* attacks on aerial *D. arenaria* nests and *Vespula* colonies (including one of *V. germanica*) in wall voids indicate that these are not effective refugia from ants.

The importance of ants as predators of temperate Polistinae (Rau, 1930; Spieth, 1947; West-Eberhard, 1969; Reed & Vinson, 1979; Turillazzi & Ugolini, 1979; Strassmann, 1981; Post & Jeanne, 1981), and the antiformicid defense mechanisms shared by vespines and polistines suggest that ant predation ought to be a concern of the Vespinae as well, but there are few records to support this contention. Several factors may contribute to this discrepancy. This study focused on *I. humilis*, a species not native to North America, and fundamental behavioral differences between it and native ant species, many of which it actively displaces (Newell, 1908; Erickson, 1971; Ward, 1987), may account for an elevated frequency of association with wasp colonies. Alternatively, predation pressure from native ants may be similar to that of *I. humilis*, with the paucity of records reflecting the difficulty of observing ant/vespine interactions. Compared to skunk predation, or even ant predation on polistine colonies, ant predation on vespine colonies is fairly inconspicuous, especially at subterranean *Vespula* colonies. An episode of heavy ant attendance may last only several days, leaving no residual evidence. Results presented here demonstrate that large insect colonies, such as those constructed by the Vespinae, remain sensitive to predation pressure from ants.

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