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RESEARCH ARTICLE

Group hunting by workers of two Neotropical swarm-founding paper wasps, *Parachartergus apicalis* and *Agelaia* sp.

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Abstract Here we report field observations of group hunting by two Neotropical species of paper wasps, *Parachartergus apicalis* in Costa Rica and *Agelaia* cf. *angulata* in Peru. In both cases, multiple workers simultaneously attacked live caterpillar prey. We describe the wasps' behavior and their interactions with the relatively large-bodied (>80 mm length) caterpillars, and we discuss the implications of these observations for paper wasp behavior and ecology.

Keywords Epiponini · Lepidoptera larva · Polistinae · Wasp predation · Sphingidae · Vespidae

Introduction

Eusocial paper wasps (Hymenoptera: Vespidae, Polistinae) are predators of other arthropods. Wasp foragers fly from their nests to search for prey. Prey are subdued by biting or occasionally stinging (Olson, 2000; J. Kingsolver, pers. comm.). Often prey are masticated, and they are brought to the nest where they are divided among adult nestmates and fed to larvae (Raveret Richter, 2000). The few observations of prey selection by paper wasps suggest caterpillars comprise a large part of paper wasp diets, but other soft-bodied immature and adult arthropods are also taken (Rabb, 1960; Raveret Richter and Jeanne, 1991; JHH and SO'D, pers. obs.). Some paper wasp species are partly necrophagous, collecting flesh from large vertebrate and invertebrate carcasses (Greene, 1991; O'Donnell, 1995). Some species of yellowjackets (*Vespula*) and the Neotropical paper wasp genera *Agelaia* and *Angiopolybia* are noted for frequent necrophagy.

Unlike many species of ants and eusocial bees (Sanchez et al., 2011; Collignon et al., 2012; Couvillon, 2012), there is no evidence for social recruitment to food sources by wasps (Jeanne et al., 1995). In some wasps, incoming food resources and arriving foragers can stimulate nestmates to forage, but this social enhancement is not directed to specific locations or food resources (Taylor et al., 2012a, b). Wasp foragers sometimes encounter conspecific and heterospecific foragers, and forager responses to resources can be affected by the presence of other wasps at the food source (D'adamo et al., 2003). However, wasp workers are generally thought to forage independently. We present observations of attacks on prey by groups of foragers from two Neotropical swarm-founding wasp species (Epiponini).

Observations

The *P. apicalis* predation event took place on 8 July 2009 in Monteverde, Costa Rica, N10° 18.20′, W84° 48.82′, at an elevation of 1,375 m a.s.l. Beginning at approximately 1300 h, several *P. apicalis* workers hovered near an epiphytic mistletoe growing on a tree trunk 2.5 m above the ground. The wasps were within 0.5 m of a large hawk moth caterpillar (Sphingidae), later estimated to be approximately 90 mm in length. Wasps repeatedly landed on the caterpillar and walked over its body. In some instances, the wasps bit at

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the caterpillar's body. The caterpillar responded by thrashing and in some cases grasping wasp foragers in its mouthparts and removing them from its body. No wasps were evidently injured, but wasps departed after being grasped or contacted by the caterpillar when thrashing. Several wounds on the caterpillar's flanks issued green hemolymph. The caterpillar was moribund but mobile: it writhed and occasionally turned partly on its back, releasing its grip on the substrate at the posterior end (prolegs). Over the course of observation, the caterpillar fell in several steps from its original height to the soil surface, when it crawled at least 0.5 m along the ground. Throughout these observations, *P. apicalis* foragers hovered within 0.5 m of the caterpillar or walked on surfaces within 15 cm of the caterpillar. Wasp arrivals and departures made a count of the number of foragers impossible, but the number of *P. apicalis* foragers visible within 0.5 m varied from one to six. From one to three wasps were seen simultaneously walking on and biting the caterpillar. A single *Agelaia* sp. wasp forager also hovered within 0.5 m of the caterpillar and oriented toward it, but this wasp did not contact the caterpillar during observations. At 1320 h we lost the sight of caterpillar and collected three of the *P. apicalis* workers into 95 % EtOH as identification vouchers. Over the course of observations, we took six video recordings of the wasp/caterpillar interactions lasting 17–40 s, 640 × 480 pixel resolution, 30 frames/sec. We collected behavioral data from the video files. The collected *P. apicalis* workers were 15-mm long (measured with dial calipers). Based on measurements from digital photographs (still captures of the videos; Fig. 1), we estimated the caterpillar to have been 90-mm long. Fifth instar sphingid caterpillars in the field range widely in wet weight, from 0.6 g to 10 g (J. Kingsolver, pers. comm.). An 80-mm long 5th instar *Manduca sexta* caterpillar from a lab culture weighed 9.83 g (M. Clifford, pers. comm.). Based on the formula in Sage (1982), we estimated the wet weight of the *P. apicalis* foragers as 0.13 g, suggesting the caterpillar was nearly two orders of magnitude heavier than the wasps. We did not observe a *Parachartergus* nest at the site, and S. O'D. has not seen these paper wasp species nesting in Monteverde in over 15 field seasons of intensive searching for paper wasp nests. The observations were made at the edge of a steep hillside that drops toward the San Luis Valley to the west, where *P. apicalis* nests are common at 1,050 m a.s.l., approximately 3 km distance from the observation site (S. O'D., pers. obs.).

The *Agelaia* sp. predation event took place in disturbed lowland rainforest along the Rio Napo, Loreto Province, Peru, in June 1997. The site is at approximately S03° 28′, W72° 90′, 40 km by river from the confluence of the Rio Napo with the Amazon and roughly 60 km by air NE of Iquitos. A caterpillar approximately 7–8 cm in length and

Fig. 1 Still-capture frame from video of a group of paper wasp workers (*Parachartergus apicalis*) attacking a sphingid larva in Monteverde, Costa Rica. Four wasp workers can be seen arrayed around the caterpillar; one wasp is perched on the caterpillar while biting at its integument. A wound issuing *green* hemolymph (indicated by *arrow*) is visible on the caterpillar's flank

2 cm in diameter was seen writhing slowly on the ground in a path through the forest. At least five *Agelaia* cf. *angulata* foragers were standing on the ground, each working individually and using its mandibles to carve a circular piece of flesh from the flanks of the caterpillar. During 2–3 min of observation, at least two wasps departed with a piece of caterpillar flesh. The flesh loads appeared similar in volume to pieces of flesh these wasps remove from carcasses: spheroids approximately 2.5 mm in diameter. During the same period at least three additional wasps flew in, stood on the ground, and began to bite flesh from the caterpillar. The wounds made by the wasps were independent circular pits ca. 3 mm in diameter with no pit contiguous with another. The number of pits (not counted) along the caterpillar's flanks indicated that additional flesh loads had been collected previously by wasp foragers.

Discussion

These observations are significant for two reasons. First, they suggest the potential for paper wasp worker social cooperation and coordination in a context that to our knowledge has not been documented previously in paper wasps. Second, group hunting by paper wasps may remove upper limits on the range of caterpillar body sizes exploited by paper wasps.

With departures/arrivals of 2–4 wasps per minute it is possible that wasps had been recruited to the caterpillars, but we did not test for recruitment. We did not observe gastral rubbing or other wasp behaviors that would suggest the release of pheromones (Howard et al., 2002; Smith et al.,

2002). Potential for recruitment to food has not been tested in the genus *Parachartergus*, but Jeanne et al. (1995) found no evidence of recruitment to food in either *Agelaia multipicta* in Venezuela or *A. hamiltoni* Peru. The *A. hamiltoni* experiments took place ca. 40 km south of the Peru observations reported here. Those experiments used chunks of beef as baits. *Agelaia* species are known to forage at carrion, but failure to recruit to fresh carrion does not preclude possible recruitment to a food source of living tissue such as large caterpillars. It is also possible that wasp foragers were attracted to each other or to cues given off by the injured prey (Takagi et al., 1980; Raveret Richter and Jeanne, 1985; Raveret Richter, 1990). Individual wasp foragers may respond to local cues away from the nest when forming groups that attack large-bodied prey, without relying on recruitment.

We cannot assess whether wasp workers coordinated their attacks in any way. We observed workers biting the caterpillars, but we did not observe venomous stings being used (Olson, 2000). The fact that, in both cases, the wasp foraging groups comprised conspecifics suggests the possibility that the wasps were nestmate workers. We did not observe obvious aggression between wasps or displacements from the prey item, which were seen when *A. hamiltoni* and *A. multipicta* foragers from multiple colonies foraged at the same meat baits (Jeanne et al., 1995). Aggressive interactions at baits are not always directed at non-nestmates: *Polybia* wasp foragers tolerated conspecific nestmates and non-nestmates at prey baits (Raveret Richter, 1990). Our observations did not suggest that wasp forager groups function as task-performance teams, with individuals playing distinct integrated roles in a complex task (Jeanne, 1986; Anderson and Franks, 2001). However, by simultaneously attacking large prey as a group, wasps may increase their chances of exploiting these high-value but high-cost items.

Little is known about the prey size selectivity by paper wasps (Jeanne, 1986; Bichara et al., 2009). Variation in insect prey body size may place limits on prey species choice by wasps and on the developmental stages of prey attacked by paper wasp foragers. Like other flying social insects (Machado et al., 1988; Fewell and Winston, 1996), wasps are limited by the weight of prey items they can transport. Wasp foragers carry prey externally in their mouthparts, adding to costs of transport by increasing drag and moving the wasps' center of gravity. Furthermore, large-bodied prey may require greater handling times to subdue, and large prey may be more likely to retaliate as did the Costa Rica caterpillar in our observations. Single *Polybia* species wasp foragers often attacked and dismembered prey items too large to carry in one trip, cached pieces of prey not carried on the first trip, and returned to retrieve them (Raveret Richter and Jeanne, 1985, 1991). However, Rabb and Lawson (1957) noted that *Polistes* spp. wasp foragers often approached, but did not attack, relatively large 5th instar caterpillars of species they readily took as prey in earlier instars.

Group hunting behaviors may be favored in species with necrophagous (carrion-feeding) foraging. Necrophagous species regularly exploit food resources that are too large to be harvested by a single forager making multiple trips. Necrophagy is widespread and well-documented in the genus *Agelaia* (O'Donnell, 1995), and *Parachartergus apicalis* foragers collected flesh from carcasses in Paraguay (Bertoni, 1912). Group attacks on large caterpillars by *P. apicalis* foragers, similar to our observations, have been noted in Columbia, South America, suggesting this behavior is widespread for this species (C.E. Sarmiento, pers. comm). Species of *Agelaia* and *Angiopolybia* were the only epiponine wasps caught in carrion traps in 'terra firme' rainforest in Brazil (Silveira et al., 2005).

Group hunting differs from necrophagy in two important respects. First, living food items are mobile. If foraging wasp workers away from the nest can respond to each other they may enhance their ability to re-locate moving prey items. In both cases, we did not know the location of the wasps' nest relative to the prey items nor whether and how local wasp forager density affects the likelihood of group hunting. Second, live prey can retaliate. We did not observe wasp workers being killed or injured, but *P. apicalis* workers were grasped by the caterpillar's mouthparts several times. Wasp foragers departed after being grasped and took flight when the caterpillar thrashed, suggesting they perceived some risk.

In both North Carolina and Washington State, yellowjackets (*Vespula*, Vespinae) in groups attack larger 5th instar *Manduca* hawk moth larvae. These wasp foraging groups sting the larvae and remove flesh (J. Kingsolver, pers. comm.). Several yellowjacket species are necrophagous. If necrophagous species have adaptations for exploiting large food sources, such as local enhancement or reduced aggression when feeding, these behaviors may be employed in the context of group hunting. We predict more examples of group hunting by paper wasps will be found among necrophagous genera such as *Agelaia* and *Angiopolybia*.

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