Spatial Scale and Density Dependence in a Host Parasitoid System: An Arboreal Ant, *Azteca instabilis*, and Its *Pseudacteon* Phorid Parasitoid

STACY M. PHILPOTT,[1] IVETTE PERFECTO,[2] JOHN VANDERMEER,[2,3] AND SHINSUKE UNO[2]

ABSTRACT   Much literature is dedicated to the study of density dependence in host-parasitoid systems. The theoretical literature identifies two potential stabilization mechanisms relating the response of the parasitoid to host density. One is a behavioral response that occurs at a local level, and the other is a demographic response that occurs at a larger spatial scale with heterogeneous patches of host concentrations. In a series of field trials at the small spatial scale (tens of meters) and a 10-mo census at the large spatial scale (hundreds of meters), we examined the attack rates of *Pseudacteon* sp. phorid flies on *Azteca instabilis* F. Smith ant hosts. At the local scale, we examined phorid attack rates on ants placed at increasing distances from ant nests (0–12 m) and on different densities of ants (1–50 workers) placed near the nests. At the large scale, we placed whole body extracts of *A. instabilis* in areas with several *A. instabilis* nests and in areas >100 m from the nearest nest. For all observations, we recorded the time of the first phorid attack and the number of phorid attacks in a defined time period. We found clear density-dependent responses at both scales. Phorid attack rates were highest within 2 m of *A. instabilis* nests and at ant densities >25. At the larger scale, phorid attack rate was greater in areas with *A. instabilis* nests, although this result was obscured during the dry season when the population of parasitoids is dramatically reduced. We propose several behavioral and population-level responses that may contribute to the observed results and propose several testable hypotheses. We conclude that, in this system, density dependence does happen through a behavioral mechanism of the phorid actively seeking concentrations of ants, but also, a population level response is likely caused by the significant difference in phorid attack rates in areas far from ant nests compared with areas nearby to nests.

KEY WORDS   coffee agroecosystem, olfactory cue, host-parasitoid, density dependence, scale-dependent effects

Theoretical formulations of predator prey or host parasite systems suggest that these systems will be unstable in time, leading to the local extinction of either predator or prey (parasite or host). The formulation in discrete time (Nicholson and Bailey 1935) is inherently unstable, yielding expanding oscillations until one of the components becomes extinct. The formulation in continuous time (Lotka 1926, Volterra 1926), if reasonable biological terms, such as satiation of the predator, are included, also leads to locally unstable results, sometimes resulting in permanent oscillations that are sufficiently large to ensure the extinction of one or the other elements. As a consequence of these seemingly inherent unstable situations, much literature has evolved exploring the possible mechanisms that could stabilize such systems (Beddington et al. 1976, Hassell 1978). One way to stabilize such a sys-

tem, repeatedly noted by many authors, is if the parasite concentrates on locally dense populations of the host (inverse density dependence), wherein seemingly any model formulation results in a stabilizing effect. Seeking data that suggest density dependence of the parasite has thus been common in both practical and field research.

Among the proposed specific mechanisms of inverse density dependence, we suggest that it is possible to recognize two general categories—behavioral and populational. Behavioral responses of the parasitoid easily stabilize the elementary system if the parasitoid actively searches out local concentrations of the host (Hassell 1978, Rohani and Miramontes 1995). Qualitatively, because the parasitoid is focusing on finding locally concentrated hosts, the host is relatively safe if it is somewhat isolated from other members of its species. In contrast, it has also been shown that environmental heterogeneity (Maynard Smith 1974, Murdoch 1977, Brockhurst et al. 2006) or simply spatial dynamics (Pascual and Caswell 1997) can produce the same sort of stabilization if the host population rapidly builds up in areas of concentrated hosts. In this case, the problem becomes one of determining

[1] Corresponding author: Department of Environmental Sciences, University of Toledo, 2801 W. Bancroft St., Toledo, OH 43606 (e-mail: stacy.philpott@utoledo.edu).
[2] School of Natural Resources and the Environment, University of Michigan, Ann Arbor, MI 48109.
[3] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109.

the relative scale at which such a variable population surge occurs either because of population or behavioral changes on the part of the parasitoid can stabilize the system (Pascual and Levin 1999). Thus, populational control results from relative changes in population densities mediated by births and deaths.

We approached this question in a system of an arboreal nesting ant, *Azteca instabilis* F. Smith (Hymenoptera: Formicidae), and its main parasitoid, *Pseudacteon* sp. (Diptera: Phoridae), in an organic coffee agroforest in southern Mexico. A species of phorid fly (*Pseudacteon* sp.) impairs *A. instabilis* recruitment and also limits the ability of this ant to attack larvae of *Spodoptera frugiperda* J. E. Smith (Noctuidae) in coffee plantations (Philpott et al. 2004). In a 45-ha permanent plot in which we located ≈300 ant nests (of ≈11,000 trees in which they might be located), we asked whether there would be a difference in detectable density dependence at two spatial scales. On the one hand, we asked whether an effect could be detected at a scale of tens of meters; on the other, whether an effect could be detected at a scale of hundreds of meters. Our reasoning is that the effect detectable at a scale of tens of meters is probably mainly caused by a local behavioral response of the parasitoid to the host, whereas the effect detectable at hundreds of meters is likely caused mainly by a population dynamic response of the parasitoid. Naturally, both mechanisms could be operative, and casting the problem in this dichotomous light is for experimental convenience alone.

Materials and Methods

Sites and Study System. We conducted our study in a 45-ha plot set up in an organic coffee farm, Finca Irlanda, in the Soconusco Region of Southwest Chiapas, Mexico (15°11′ N, 92°20′ W). The farm covers >300 ha, is located between 950 and 1,100 m elevation, and receives ≈4,500 mm of rain/yr. The management system is classified as a commercial polyculture (Moguel and Toledo 1999) with ≈90 species of shade trees, ≈70% of which are in the genus *Inga* (Vandermeer et al. 2008). Canopy cover within the farm varies between 40 and 70%. Within the 45-ha plot, we mapped the location of all shade trees >10 cm circumference and assessed each tree for presence of nests of *A. instabilis*, an aggressive ant species that nests within shade trees in coffee farms and forests of southern Mexico and Central America (Philpott et al. 2004). We have conducted surveys of the *A. instabilis* nests throughout the plot in June and December 2004, 2005, and 2006. Of 10,576 trees potentially capable of housing an ant nest, 282, 348, 378, 321, 291, and 349 trees (between 2.7 and 3.6%) were occupied in the six censuses (Vandermeer et al. 2008). *A. instabilis* forms clusters of nests ranging from a single occupied tree to 10 or more occupied trees located near to one another (Fig. 1). The clusters occupy areas of a few square meters to hundreds of square meters, depending on the definition of cluster. We here define a cluster as a group of trees with *A. instabilis* in a 10-m-radius area
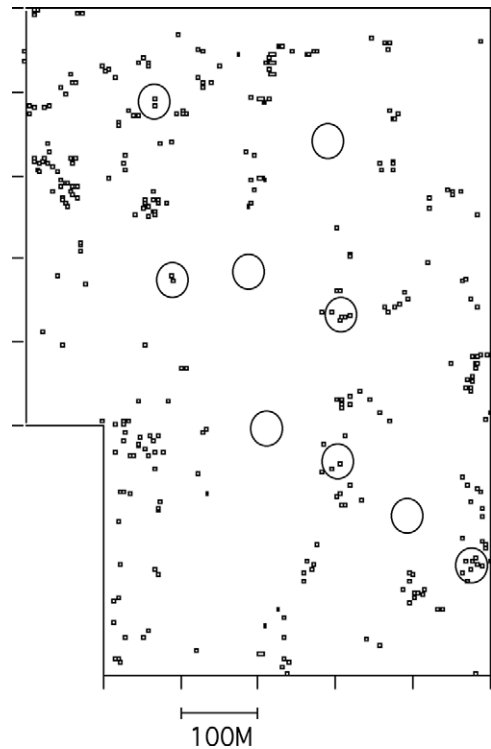

Fig. 1. Distribution of nests of *A. instabilis* (small back squares) over the 45-ha plot for the census conducted in December 2006. Circles indicate the areas that were sampled near and far from *A. instabilis* clusters.

(see Vandermeer et al. 2008 for details). The dynamics of the *A. instabilis* colonies between sample dates is discussed elsewhere (Vandermeer et al. 2008).

Local Distance and Density Effects on Phorid Attacks. We examined density dependence in phorid attack rates on ants at the local scale using two separate types of observations. Specifically, we examined the effects of both distance from *A. instabilis* nests and ant density on phorid attacks at the local scale by conducting phorid attack trials. First, we collected ants into plastic sandwich tubs painted with fluon, a slippery substance over which ants cannot walk. For each distance trial, we collected 300 ants from *A. instabilis* nests, placed 50 individuals in each of six tubs, placed lids on the tubs, and carried the tubs to other *A. instabilis* nests located at least 30 m away from where ants were collected. We placed tubs at 0, 2, 4, 6, 8, and 10 m from trees with *A. instabilis* nests to observe phorid attacks. We either placed tubs directly on the ground or hung tubs from coffee branches ≈1.5 m off the ground to examine whether observation strata affected phorid attack rates. At the time of the start of the observation, we removed lids and recorded (1) time elapsed to the first phorid attack in each tub and (2) the number of phorid attacks observed in each tub during 15 min. Because other species of phorids and small flies are common in the area, we only registered observations of a phorid diving toward an ant

to oviposit as attacks. Each nest was used for two observations: one where tubs were placed on the ground, and another where tubs were placed 1.5 m off the ground. Three additional nests were used for trials where tubs were placed above ground. There were two species of tree with *A. instabilis* nests we used for trials: *Alchornea latifolia* Swartz (Euphorbiaceae) (*n* = 8 for trials on the ground and 8 for trials at 1.5 m above ground) and *Inga micheliana* Harms (Fabaceae) (*n* = 2 for ground and 4 for trials above ground).

For trials to examine the influence of ant density on phorid attack rates, we collected *A. instabilis* ants in tubs following the same protocol described above, placed tubs near *A. instabilis* nests, and observed attacks following a similar protocol. Instead of placing 50 ants per tub, however, we placed 1, 5, 10, 15, 20, or 25 individuals in tubs, and for observations, all tubs were placed 0 m from *A. instabilis* nests. In the analyses, we also included data from 50 ant tubs at 0 m from the distance trials as a high-density treatment. There were several species of trees used for trials with 1–25 ant individuals: *A. latifolia* (*n* = 4), *I. micheliana* (*n* = 8), *Inga rodrigueziana* Pittier (Fabaceae) (*n* = 1), *Trema micrantha* Blume (Ulmaceae) (*n* = 1), *Trichospermum mexicanum* Baillon (Tiliaceae) (*n* = 1), *Yucca elepahntipes* Regel (Agavaceae) (*n* = 1), and one unknown species of Malvaceae (*n* = 1). All observations for both distance and density dependence took place during June–July 2007.

We examined differences in phorid attack rates, and time to first phorid attack using a two-way analysis of variance (ANOVA). For distance trials, we examined the influences of distance (0, 2, 4, 6, 8, and 10 m) and tub location (ground versus above ground) on (1) no. of attacks during 15 min and (2) time to first attack. For density trials, we examined the influences of ant density (1, 5, 10, 15, 20, 25, and 50 ants) on (1) no. of attacks during 15 min and (2) time to first attack. We determined statistical differences between density and distance treatments using Tukey's post hoc tests. The number of phorid attack rates was log-transformed to meet conditions of normality. All statistical tests were carried out using SPSS v. 10.

Density Effects at Large Scales. We selected nine sites from the 45-ha plot to observe potential density dependence of phorids on ant densities at a larger scale. We chose four areas that have no nearby colonies of *A. instabilis* and five in areas with *A. instabilis* colonies (Fig. 1). Within these nine sites, we estimated the number of phorid attacks using a method similar to that described above but with the following modifications. We only placed tubs 1.5 m from the ground, each with 50 *A. instabilis* workers. Because we also wanted to make sure to capture any phorids in the area (even in areas >200 m from the nearest *A. instabilis* nests), we added two types of attractants for the phorids to each tub. One attractant was artificial nests, consisting of small bits of carton from a natural nest, and the other was whole body extract of *A. instabilis* prepared by smashing ant bodies. We prepared the extract by smashing 200 workers in 5 ml of hexanes. For each trial, we added 200 μl of extract to a cotton

swab placed inside the tub at the exact time observations began. Thus, extract for each observation was roughly equivalent to the chemicals extracted from eight ants. We observed tubs for attacks during a period of 5 min.

Three trials were performed at 0 (next to the tree), 1, 3, and 5 m from the tree containing the *A. instabilis* colony, with the exact orientation chosen randomly from the four cardinal directions. Trials lasted 5 min from the time that the container was open and the extract was added to the end of the trial (when the container was closed again). We observed tubs for phorid attacks during each trial and the time of first phorid attack. The same procedure was repeated in the areas with no *A. instabilis* colonies, but an arbitrary shade tree was used as a reference point, and all trials were located with reference to that tree. The sampling protocol was repeated approximately once a month from August 2005 to May 2006. The same nine trees were used for three observations during each month: five trees in areas with *A. instabilis* (*A. latifolia*, *n* = 4; *I. micheliana*, *n* = 1) and four trees at least 100 m from the nearest *A. instabilis* nests (*I. micheliana*, *n* = 2; *I. rodrigueziana*, *n* = 1; and *A. latifolia*, *n* = 1).

Results

Local Distance and Density Effects on Phorid Attacks. Both the number of phorid attacks and the time to the initial phorid attacks significantly differed with distance to *A. instabilis* nest and with the density of *A. instabilis* individuals used in the trial. There were between 4 and 16 times more phorid attacks at *A. instabilis* nests (0 m) than at any distance away from the nests (2, 4, 6, 8, and 10 m; F = 15.551; df = 5,120; P < 0.001; Tukey's test between 0 m and all other distances, P < 0.001; Fig. 2a). There were no additional differences in attacks between other distances. Numbers of phorid attacks in 15 min did not depend on the location of tubs on the ground or above ground (F = 1.998; df = 1,120; P = 0.16), nor was there a significant interaction between distance from nest and location (F = 0.93; df = 5,120; P = 0.464). Similarly, initial phorid attacks took place more quickly at *A. instabilis* nests (0 m) than further from nests (2, 4, 6, 8, and 10 m; F = 14.92; df = 5,120; P < 0.001, Tukey's test between 0 m and all other distances; P < 0.001; Fig. 2b). There were no additional differences between other distances. On average, initial phorid attacks on ants occurred 1.8 times sooner when tubs were on the ground than when they were located 1.5 m above ground (F = 10.746; df = 1,120; P = 0.001). However, this pattern was inconsistent with phorid attacks happening more quickly on the ground only at closer, but not at larger, distances from *A. instabilis* nests, leading to a significant interaction term between distance and tub location (F = 3.381; df = 5,120; P = 0.007; Fig. 2b).

Ant density also influenced the phorid attacks. There were virtually no attacks during 15 min for the lowest ant densities (1, 5, 10, or 15 ants), but there were ~18 times more phorid attacks at the highest ant densities (25 and 50 ants; F = 4.601; df = 6,100; P <
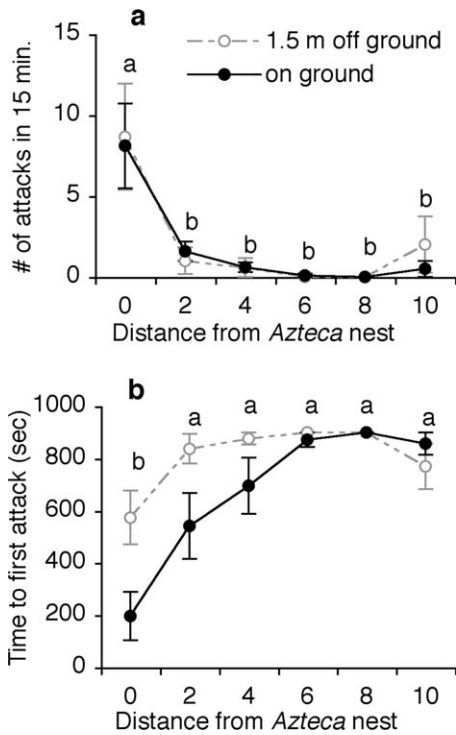
Fig. 2. Phorid attack rates (a) and time to initial attack (b) of *Pseudacteon* sp. phorid attacks on *A. instabilis* ants as a factor of distance from ant nest sites. Error bars show SE, and lowercase letters above points show significant differences between distances for attacks or time to first attack across both treatments (ground and above ground).

0.001; Fig. 3a). Phorid attacks on tubs with 20 ants were intermediate not differing from lower ant densities (Tukey's tests, $P > 0.05$) or from the higher ant densities ($P > 0.05$). The time to the first phorid attack was significantly faster at the highest ant density (50 individuals) than at all lower densities ($F = 9.437$; df = 6,100; $P < 0.001$; Fig. 3b). There were no significant differences in time to initial attack for any other density combinations ($P > 0.05$).

Density Effects at Large Scales. Attack rates were significantly higher in areas with *A. instabilis* clumps than in areas without *A. instabilis* nests (Fig. 4). Over the 10-mo period, a total of 143, 154, 142, 140, and 100 attacks were observed within the five clusters of ant nests, whereas 44, 89, 74, and 81 attacks were observed outside of those clusters. At seven of the eight sampling dates, the attack rate was higher within compared with outside of the ant clusters (Fig. 4), and an analysis of variance (ANOVA; repeated measures) showed a highly significant difference ($F = 22.0$; df = 7,26; $P = 0.002$). At the height of the dry season, in February and March, attack rates were very low and not different inside and outside *A. instabilis* clusters. All other times of the year, there was an obvious higher rate of attack within *A. instabilis* clusters (Fig. 4). There was, however, no difference in the time at which phorids first attacked in areas with and without *A. instabilis* ($F = 0.051$; df = 1,32; $P = 0.823$).
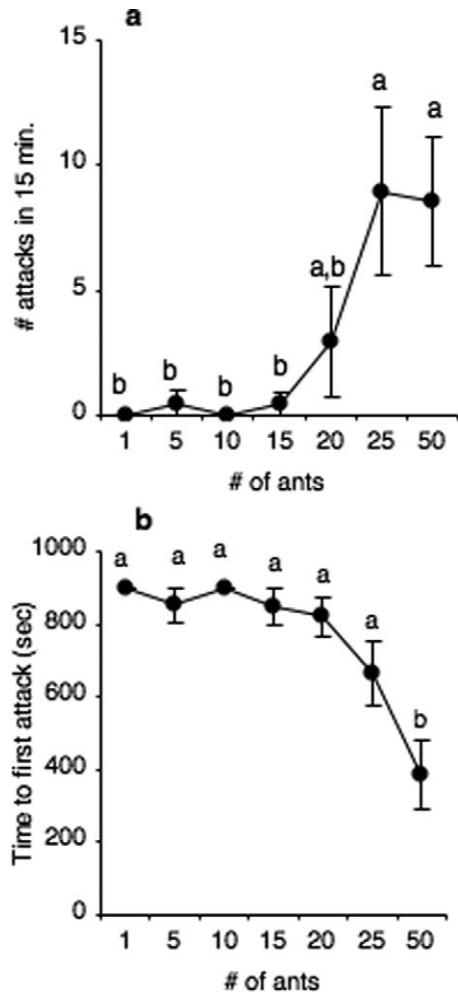

Fig. 3. Phorid attack rates (a) and time to initial attack (b) of *Pseudacteon* sp. phorid attacks on *A. instabilis* ants as a factor of ant density. Error bars show SE, and lowercase letters above points show significant differences between densities for attacks or time to first attack.

Discussion

Our results bring up two interesting points deserving of further discussion. First, our results show support for density-dependent attacks of *Pseudacteon* sp. phorid flies on *A. instabilis* ants at two distinct spatial scales. Second, although overall, phorids seem to be density dependent with regards to ant density at the larger scale, during two study dates, this was not the case; thus, there is temporal variation in the degree of density dependence. The correlation between host density and parasite attack is likely a result of local population densities of both species, the parasite population density building up in areas where the host populations are high, and within those patches behaviorally responding to high densities of ants at the local level. We argue that at the local level, behavioral differences caused by detection of ants are likely responsible for density dependence, whereas at the
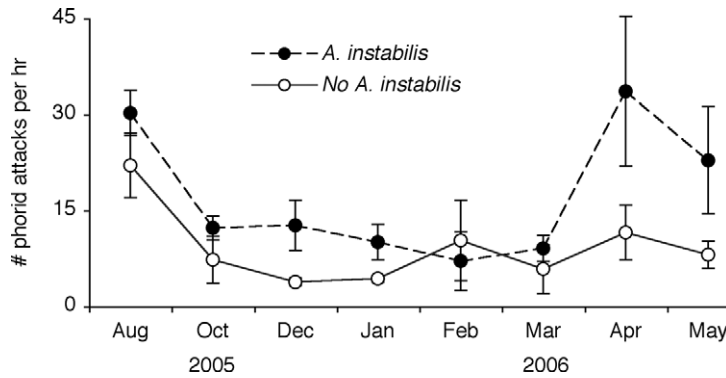
Fig. 4. Phorid attack rates during 10 sample mo for areas with *A. instabilis* nests (●) and areas without *A. instabilis* nests (○). Error bars show SE.

larger scale, that population level responses of the phorid are likely leading to density dependence. However, it is difficult to actually assess what the size of a phorid population density in an area is—we do not claim to do this. Some *Pseudacteon* sp. live only for ~1 wk in laboratory conditions, and thus quick population turnover is possible (Morrison et al. 2000). We partially base our behavior/population dichotomy on the assumption that phorids will generally use chemical cues to find ants at the local scale and that changes in relative phorid abundance will produce density-dependent patterns at the larger scale.

Phorid flies reportedly use chemical cues to find ant hosts (Brown and Feener 1991, Feener et al. 1996, Morehead and Feener 2000, Chen and Fadamiro 2007), although the types of pheromones and the body parts from which phorid-attracting pheromones are found differs for distinct phorid–ant relationships. Furthermore, it has often been suggested that species of *Pseudacteon* first use some sort of olfactory cue to locate hosts and then switch to visual cues once near to hosts (Orr et al. 1997, Morrison and King 2004). It is still unknown what precise pheromones attract the *Pseudacteon* sp. to *A. instabilis*, but preliminary studies indicate that pheromones excreted from the dorsal side of the abdomen (likely alarm or defense pheromones) are the main olfactory cue (K.A. Mathis, unpublished data). These pheromones, although relatively volatile, probably act to attract phorids to tubs from a short distance. Thus, the local density dependence is likely a result of changes in behavior because of phorids detecting chemical cues from ants in tubs and finding those ants (1) closer to the place from which chemicals usually come (the nest) or (2) exerting stronger visual cues because of the larger number of ants in the tubs. Further evidence of this can be seen from other observations. At the end of our 15-min local-scale observations, we smashed a few ants in each tub, and the numbers of phorids attacking increased dramatically (S.M.P. et al., unpublished data). At the larger scale, despite that extracts were used, fewer phorids were attracted to areas without *A. instabilis*. If a behavioral response was driving the density dependence of phorid attack rates on ants, we

might expect that initial phorid attacks would be delayed far from *A. instabilis* nests because of longer travel distance. However, the time at which phorids first attacked ants did not differ in areas with and without *A. instabilis*, indicating that phorids are present in both areas, just at a lower population density in areas without *A. instabilis*. Although to our knowledge it is unknown exactly at what spatial scale phorids are able to detect olfactory cues, it is unlikely that phorids can be attracted by chemical cues from a great distance (Morrison and King 2004). Specific tests in laboratory conditions may help to elucidate at exactly what spatial scale that chemical cues and visual cues operate, helping to detect specific mechanisms determining relative phorid abundance and the effect of ant density on phorid abundance. Thus, at the larger scale, density dependence is likely caused by changes in phorid populations rather than changes in their behavior.

Attack rates were relatively constant in areas with *A. instabilis* at both spatial scales examined, but attack rates varied greatly across different seasons. The number of phorid attacks was relatively similar for tubs placed nearest to *A. instabilis* nests (0 m), for high ant densities at the local scale (50 ants), and for attack rates in areas with *A. instabilis* at the larger scale. On average, all three ranged from ~7.5 to 10 attacks per 15 min during the time of the year at which local scale observations were conducted. Attacks for areas without *A. instabilis* were lower and significantly lower than those areas with *A. instabilis*. However, there was some seasonal variation in phorid attack rates, especially for the dry season (February and March), where attack rates did not differ between areas with and without *A. instabilis*. Changes in phorid attack rates and ant detection in areas with and without *A. instabilis* most likely result from differences in behavior or phorid survival and pupation during the dry season. Behavior of phorid flies is known to change with ambient conditions and some species of phorid parasites may be more active and or more abundant during cooler wet temperatures such as observed during the wet season in Mexico (Folgariat et al. 2007). Soil moisture and relative humidity are also important correlates of phorid relative abundance in the southern

United States, with generally higher phorid relative abundance during the spring (when conditions are more moist) than in July and August (when conditions are more dry) (Morrison et al. 2000). If individuals of the *Pseudacteon* species examined here are primarily found in the leaf litter (as suggested by their slightly faster responses to ants in tubs on the ground) and if they experience greater pupation success under moister conditions as found for other species (Vogt et al. 2003), lower relative abundance of phorids in the dry season could be a result of less favorable resource conditions. If these phorids have similar environmental responses as do hymenopterous parasitoids, poor resource conditions may have various negative effects on adult phorids perhaps including decreases in longevity, fecundity, and even search efficiency (Bezemer et al. 2005). This conforms well to our observed data showing overall phorid attack rates were generally lower in the dryer months and higher in the wetter months, being highest during the wet season and lowest during the driest months. Relative phorid abundance of the *Pseudacteon* sp. attacking *A. instabilis* may be lower in the driest months, thus explaining the greater difference in attack rates during the rest of the year.

What implications do these results have for stability of the *Pseudacteon--Azteca* relationship described? *Pseudacteon* phorid flies that attack *A. instabilis* in coffee agroecosystems seem to be density dependent at two distinct spatial scales, and this density dependence may in fact create spatial heterogeneity in the ant population densities across the landscape. Recent evidence finding substantial similarity in distributions of *A. instabilis* in the field to a distribution created with a cellular automata model shows that density-dependent predation or parasitism could be responsible for creating the patchy distributions of *A. instabilis* ants (Vandermeer et al. 2008) and could create stability in the host–parasitoid system. Although our system includes a long-lived host (the ant) and therefore the classic Nicholson/Bailey model will not likely be appropriate, it is almost certain that the phorid will exhibit a saturating functional response, thus setting up the possibility of unstable oscillations and a problem similar to the problem well known in the discrete system. One way of stabilizing such an unstable situation is with a positive density-dependent response of the predator/parasite (Vandermeer and Goldberg 2003), effectively the same biological mechanism that stabilizes the discrete system. Given that the response of the parasite is qualitatively similar at two spatial scales suggests that either a local behavioral response or a regional population-level response could act as a stabilizing force. Thus, whereas dynamical extension in space could be stabilizing, it seems that the local dynamics are likely to be stable as well, regardless of the larger scale dynamics. We here propose several ideas about the behavioral and population level responses of phorid flies to ant density that might be causal mechanisms driving these relationships. Future research in the *Pseudacteon–Azteca* system certainly should further study phorid behavior, seasonal variation in phorid attack rates and relative abundance, environmental correlates of phorid attacks, and details of the chemical cues attracting phorids to further elucidate some of these questions.

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