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Geographic Variation in Host Location Cues for a Dipteran Parasitoid of *Paraponera clavata*[1]

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ABSTRACT

Parasitoid insects face considerable trade-offs in locating suitable hosts within complex environments. *Apocephalus paraponerae* (Diptera: Phoridae) locates its host ant *Paraponera clavata* (Formicidae: Ponerinae) using olfactory cues. Here, comparing two populations of *A. paraponerae,* I describe differences in host location cues between two sites, Barro Colorado Island (BCI) in Panama and La Selva Biological Research Station in Costa Rica. At La Selva, *A. paraponerae* uses the ant mandibular gland products 4-methyl-3-heptanone and 4- methyl-3-heptanol in host location, but does not do so on BCI. I propose that higher colony density of *P. clavata* causes *A. paraponerae* to use more species-specific cues on BCI. I also discuss how geographic variation in host location cues could lead to allopatric speciation.

RESUMÈN

Los insectos parasitoides enfrentan muchas dificultades cuando buscan hospederos en ambientes complejos. *Apocephalus paraponerae* (Diptera: Phoridae) localiza a su hormiga hospedera, *Paraponera clavata* (Formicinae: Ponerinae), a travéz de pistas olfativas. En este estudio describo las diferencias en los mecanismos de localización de hospederos en dos sitios, la Isla Barro Colorado en Panamá y La Estación de Investigación Biológica La Selva en Costa Rica. En La Selva, *A. paraponerae* usa productos de la glándula mandibular (4-metil-3-heptanona y 4-metil-3-heptanol) para localizar a su hospedero, pero no hace lo mismo en IBC. Considero que un mayor densidad poblacional de *P. clavata* hace que *A. paraponerae* tenga que usar pistas más específicas en IBC. Además, propongo la existencia de otros factores ecológicos y de comportamiento que pueden afectar los mecanismos de localización y discuto como la variación geográfica de las pistas olfativas afecta la evolución y especiación de los linajes de parasitoides.

Key words: Apocephalus paraponerae; *Costa Rica; 4-methyl-3-heptanol; 4-methyl-3-heptanone; host location; Panama;* Paraponera clavata; *parasitoids; Phoridae; reliability–detectability trade-off.*

The greatest challenge to ovipositing parasitoids is finding hosts in a complex environment (Vinson 1984, Godfray 1994). These small animals must locate rare, often ephemeral hosts that are behaviorally well-defended or hidden, in a large and diverse habitat. Parasitoids have developed a wide variety of methods and mechanisms to locate their hosts, including the use of olfactory, auditory, and vibrational cues (Cade 1975, Walker 1993, Feener *et al.* 1996, Feener & Brown 1997). Olfactory cues, the most common mechanism for host location, originate in the hosts' habitat or directly from a potential host (Vinson 1981, 1984; Godfray 1994; Wiskerke & Vet 1994). Parasitoids also may take advantage of their hosts' intraspecific communication systems to locate potential hosts (Brown & Feener 1991, Feener *et al.* 1996). Frequently, an arms race between the host and parasitoid results, with the parasitoid evolving to overcome its hosts' ability to hide from its natural enemies (Vet *et al.* 1991, Wiskerke *et al.* 1993, Wiskerke & Vet 1994). This evolutionary arms race may lead to differentiation among allopatric populations due to divergent selection pressures for host chemistry and host locating mechanisms.

Foraging parasitoids may experience a trade-off between use of cues that reliably indicate host presence and those cues that are easily detectable, called the "reliability–detectability problem" (Vet *et al.* 1991). Often, easily detectable, highly volatile cues are not reliable indicators of host presence since they may be compounds that are found throughout the environment; however, more host-specific and reliable cues are generally compounds of higher molecular weights, which are not as volatile and therefore more difficult to detect at a distance. Parasitoids must balance these competing factors to minimize the time spent in locating hosts.

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Parasitoids may encounter different hosts across their geographic range, and different parasitoid populations may modify the cues used to detect hosts. Associative learning, for example, is one mechanism by which parasitoids learn new cues associated with varying habitat use by hosts (Vet *et al.* 1991); however, the vast majority of studies describing host location cues and parasitoid foraging behavior are performed in the laboratory with organisms from one site, and do not identify geographic variation in host location (McCall *et al.* 1993, van Baaron & Nénon 1996). Geographic variation in host location cues within species may promote allopatric speciation through time by making host switching more likely (Thompson 1994).

In this study, field experiments showed that the long-range host location cues used by *Apocephalus paraponerae* (Diptera: Phoridae) to locate *Paraponera clavata* (Formicidae: Ponerinae), their primary host, differ between two tropical sites. I investigated variation in host location cues between the two populations and suggest that variation in host colony density may be an important factor in generating the geographic variation I describe. I also discuss how trade-offs within species between the use of reliable versus detectable cues may vary with changing resources or host abundances. Finally, I discuss the evolutionary implications of geographic variation in host location cues, including allopatric speciation.

METHODS

Study system.—*Apocephalus paraponerae* are attracted to injured workers of the ponerine ant *P. clavata.* Both male and female flies are attracted to injured workers of *P. clavata.* Mating, feeding, and oviposition occur at the host. Many females lay several eggs in one ant worker, and up to 40 eggs can be found in any given ant. Fly larvae develop rapidly within the ant hosts and emerge after about three days. In a population of *A. paraponerae* at La Selva, Costa Rica, flies located their hosts via two chemicals, 4-methyl-3-heptanone and 4-methyl-3-heptanol, found in the mandibular glands of *P. clavata* (Feener *et al.* 1996). These chemicals are believed to be part of the alarm communication system in ants (Hermann *et al.* 1984).

Study sites.—Experiments were performed on Barro Colorado Island in Panama (BCI) from June through August 1996 and August and September 1997, and at La Selva Biological Research Station in Costa Rica during June and July 1995, June and July 1997, and January through April 1998. BCI, which is located in Lake Gatun of the Panama Canal, receives *ca* 2500 mm of rainfall per year (Windsor 1990). La Selva is a well studied lowland tropical wet forest on the Atlantic slope of Costa Rica and receives *ca* 4000 mm of rain per year (McDade *et al.* 1994). *Paraponera clavata* and *A. paraponerae* are abundant at both sites. Voucher specimens were deposited with the Arthropods of La Selva (ALAS) project at La Selva, and with the insect reference collection at the Smithsonian Tropical Research Institute (STRI) in Balboa, Panama.

Chemicals used in experiments.—All experiments involving chemical attraction used a cotton ball containing a 10 μl mixture of 4-methyl-3-heptanone and 4-methyl-3-heptanol in a 9:1 ratio. This amount (300 μg) and mixture was equivalent to that contained in a single worker of *P. clavata* (Hermann *et al.* 1984) and sufficient to attract flies at La Selva (Feener *et al.* 1996). These chemicals were mixed with olive oil in a 1:10 ratio of chemicals to olive oil. Olive oil helps to slow the oxidation and release rate of the chemicals but has no apparent effect on fly behavior (Feener *et al.* 1996). Controls were 100 μl of olive oil on a cotton ball. I used two different batches of chemicals. One batch was the chemicals used for the experiments in Feener *et al.* (1996). I used these chemicals during 1996 at BCI and in the 1997 field season at La Selva. The other was a new batch from 1996 used in field seasons 1996 and 1997 on BCI, and in 1997 and 1998 at La Selva.

Chemical location experiment.—To locate (within the ant) the source of the long-range host location cues used by *A. paraponerae* on BCI, I asked which part of *P. clavata* workers (*i.e.,* the head, thorax, or abdomen) was most attractive, similar to the experiments of Feener *et al.* (1996) at La Selva. In these experiments performed during field season 1996 on BCI, *P. clavata* workers were cut into three parts (head, thorax, and abdomen) and placed in petri dishes 0.5 m apart in an equilateral triangle. For 15 minutes, the flies attracted to each part were collected with an aspirator and placed in plastic vials. The flies were counted and their sex determined under a dissecting microscope in the laboratory. I performed between one and four trials at each of nine *P. clavata* colonies.

Chemical attraction experiments.—To test if chemicals known to attract flies at La Selva would

function similarly at BCI, I carried out experiments on BCI during the 1996 and 1997 field seasons. I placed a pair of cotton balls, one with chemicals and one control, 1.0 m from a *P. clavata* nest entrance and 0.5 m from each other. I collected all flies attracted in 20 minutes using an aspirator. This experiment was performed between one and ten times at five different *P. clavata* colonies for a total of 25 trials. I compared the number of flies collected at the chemicals versus the olive oil control. The number of flies attracted at BCI was then compared to published results from La Selva.

ANTS WITH CHEMICALS EXPERIMENT.—On BCI and at La Selva, I determined if the addition of the mandibular gland chemicals would reestablish the attractiveness of headless ants to the flies. I performed a series of comparisons involving intact workers, headless workers, and headless workers with attractant chemicals added (hereafter called "test" workers). In all of the experiments, pairs of ants were immobilized by crushing the thorax. Headless workers were prepared by cutting off the head and removing it from the area at the time of the experiment. Workers were then placed on filter paper in small petri dishes, *ca* 1.0 m apart near a colony entrance. Three types of experiments were run: intact versus headless, intact versus test, and headless versus test. For each comparison, I performed one trial at each of six colonies at La Selva during 1995 and one trial at each of ten colonies on BCI during field season 1996. During each 15-minute trial, all flies attracted to the immobilized workers were collected with an aspirator. The flies were counted and their sex determined under a dissecting microscope in the laboratory.

MARK-RECAPTURE EXPERIMENTS.—At both BCI and La Selva, I estimated travel distance of the parasitoid by performing mark–recapture experiments. The assumption was that if the flies were traveling farther to locate odor sources, they would be less likely to be recaptured in the same location where they were marked. *Apocephalus paraponerae* were attracted to crushed *P. clavata* workers near colony entrances. The flies were aspirated into a plastic vial. Fluorescent marking powder was added to the vial, and as the flies moved around in the vial they coated themselves with the marking powder. If all the flies were not well marked, more fluorescent marking powder was tapped into the vial using a small paintbrush. When 15 to 20 individuals were collected and coated with fluorescent powder, the flies were released at the point of capture. I did not determine the sex of the flies as they were marked.

To recapture the flies, one hour later I set out crushed *P. clavata* ants at the location where the flies were marked and released. For 20 minutes, I collected all the flies attracted to the ants. The flies were immediately placed on ice to prevent them from grooming and removing the marking powder. In the laboratory, I recorded the number of flies attracted to each ant. Using a black light, I identified the flies that were recaptured. This procedure was followed at ten colonies of *P. clavata* at both BCI and La Selva. A total of 236 flies was marked on BCI, and 162 were marked at La Selva.

COLONY DENSITY.—Recent estimates of *P. clavata* colony density are available for primary forest on BCI but not at La Selva (Belk *et al.* 1989; Thurber *et al.* 1993; R. Perez, pers. comm.). Previous studies at La Selva have estimated colony density in the arboretum or in secondary forest at La Selva; however, these may not reflect colony density in primary forest (Bennett & Breed 1985, Breed & Harrison 1989). To obtain data for colony density within primary forest at La Selva, I surveyed five 0.5 ha plots for *P. clavata* colonies. These plots, associated with the Carbono project, were subdivided into 10 × 10 m subplots, each corner of which was marked by poles. I checked every tree within each subplot for *Paraponera* colonies. In general, the colonies were very obvious and formed a large mound of dirt at the base of trees; however, one colony was found nesting *ca* 30 cm above ground level within a tree buttress (Breed & Harrison 1989).

STATISTICAL ANALYSIS.—Results from the chemical location experiment on BCI were compared to published data from La Selva by pooling within body part across trials (because few flies were attracted in each trial) and then using log likelihood ratios (*G*-tests) between sites. The results of the chemical attraction experiments at both sites were analyzed by chi-square and sequential Bonferroni adjustment with an experiment-wide value of $\alpha = 0.05$ (Rice 1989). Results from BCI and La Selva in the ants with chemicals experiments were compared by pooling the number of flies attracted to each type of ant (*i.e.,* intact, headless, and test) within site and then testing between sites using log likelihood ratios (*G*-tests).

RESULTS

CHEMICAL LOCATION EXPERIMENT.—The head was the most attractive part of *P. clavata* at both La

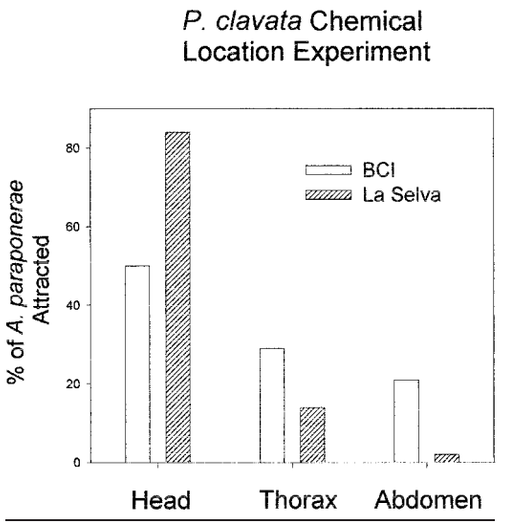

FIGURE 1. Ant body part experiment comparing BCI and La Selva. Percent of *Apocephalus paraponerae* attracted to the head, thorax, and abdomen of *Paraponera clavata* workers at BCI (open bars) and La Selva (crosshatched bars; from Feener *et al.* 1996).

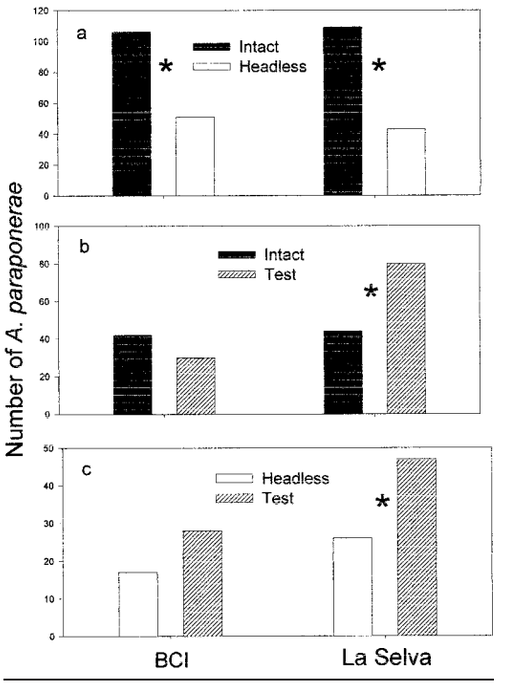

FIGURE 2. Chemical attraction experiment comparing *Apocephalus paraponerae* attracted to *Paraponera clavata* workers at BCI and La Selva. (a) Number of *A. paraponerae* attracted to intact (solid bars) versus headless (open bars) *P. clavata* workers. (b) Number of *A. paraponerae* attracted to intact (solid bars) versus test (crosshatched bars) workers. Test workers were headless *P. clavata* with attraction compounds (300 μg mixture of 4-methyl-3-heptanone and 4-methyl-3-heptanol in a 9:1 ratio) added. (c) Number of *A. paraponerae* attracted to headless versus test *P. clavata*. * indicates difference at $P < 0.001$.

Selva and BCI (Fig. 1). At La Selva, the thorax was less attractive than the head and only two flies in seven trials were attracted to the abdomen (Feener *et al.* 1996). On BCI, the thorax and abdomen of *P. clavata* workers attracted almost equal numbers of flies, about half as many as the head, and the number of flies attracted to each body part at BCI differed significantly from La Selva ($G = 42.36$, df $= 2$, $P < 0.00001$). The differences between sites suggest that even though *A. paraponerae* from both sites were attracted to volatiles found in the head of *P. clavata, A. paraponerae* on BCI were using those cues differently than *A. paraponerae* at La Selva.

Chemical attraction experiments.—The chemical cues used by *A. paraponerae* to find their host *P. clavata* were sufficient in attracting the flies to experimental sites at La Selva (Feener *et al.* 1996), but the chemical attractants 4-methyl-3-heptanone and 4-methyl-3-heptanol were not sufficient on BCI. At La Selva, large numbers of flies were drawn to the chemicals offered separately or in combination, whereas on BCI, no flies were attracted to the chemicals alone. On BCI, the chemicals 4-methyl-3-heptanone and 4-methyl-3-heptanol were not attractants to *A. paraponerae* in 1996. In twenty-five 20-minute trials on BCI, no *A. paraponerae* flies were drawn to either the chemicals or to the olive oil control, while subsequent experiments performed at La Selva in 1997 (see below) did attract flies.

Ants with chemicals experiment.—At both La Selva and BCI, more flies were drawn to intact workers than to headless workers (Fig. 2a). Intact versus test workers were similarly attractive on BCI, but test workers were highly preferred at La Selva (Fig. 2b). Headless versus test workers were similarly attractive on BCI, but test workers were highly preferred at La Selva (Fig. 2c). There were slight increases in the number of flies attracted to test workers, indicating a possible weak attraction of the chemicals; however, these were not significant.

Comparing La Selva and BCI (Fig. 2a) showed no difference in the number of flies attracted to the test and headless workers ($G = 0.64$, df $= 1$, $P =$

0.2); however, the number of flies attracted to test workers, when compared to intact workers, at La Selva was greater than on BCI ($G = 9.67$, df = 1, $P = 0.0015$; Fig. 2b). The attractiveness of headless versus test workers did not differ between locations (G = 0.05, df = 1, $P = 0.8$; Fig. 2c).

Mark-recapture experiments.—At La Selva, 1.8 percent of the marked *A. paraponerae* were recaptured, whereas 15 percent of the marked flies on BCI were recaptured. The number of flies recaptured on BCI was significantly greater than at La Selva ($\chi^2 = 22.5$, df = 1, $P < 0.0001$).

Colony density.—Previous estimates of colony density in the arboretum at La Selva have yielded estimates of 6 colonies/ha, which was similar to BCI densities (Breed & Harrison 1989). In primary forest at La Selva, I found 6 *P. clavata* colonies in 2.5 ha. *Paraponera clavata* colonies in primary forest were possibly less dense at La Selva (2.4/ha) than on BCI (6/ha; Thurber *et al.* 1993).

DISCUSSION

I describe the first reported example of geographic variation in host location cues for a phorid parasitoid. *Apocephalus paraponerae* on BCI uses a different set of long-range host location cues than at La Selva. Because greater numbers of flies were attracted to the thorax and abdomen on BCI, the chemical location experiments suggest that additional cues located in these body parts of *P. clavata* workers may be used by *A. paraponerae* in host location. At La Selva, 4-methyl-3-heptanone and 4-methyl-3-heptanol were sufficient to attract *A. paraponerae* (Feener *et al.* 1996); however, on BCI, the compounds were not sufficient to attract flies to *P. clavata.* Also, although the mandibular gland products did not increase the attractiveness of intact or headless workers on BCI, they significantly increased the number of *A. paraponerae* attracted to intact and headless workers at La Selva.

One result was contradictory: on BCI, intact workers attracted more flies than headless workers but not more than test workers, which were also headless. This could have been due to a weak attraction to the mandibular gland chemicals, counteracting the effect of headlessness. This was also supported by a weak but nonsignificant preference for test over headless workers. Alternatively, it may have been a type 2 error, and additional trials would reveal a preference for intact versus test workers. Weak attraction to the mandibular gland chemicals is more likely, however, because more trials were performed on BCI during these experiments.

Mark–recapture experiments also revealed differences between La Selva and BCI. *Apocephalus paraponerae* on BCI were recaptured more frequently than at La Selva. These results suggest that the flies on BCI may move relatively shorter distances immediately after locating a suitable host, possibly do not travel great distances to locate hosts, and therefore were recaptured close to their original collection site.

Because higher colony density is predicted to produce higher rates of intraspecific aggression (Jorgensen & Black 1984) and intraspecific colonial aggression provides injured hosts, I hypothesize that BCI may have a greater potential resource base for *A. paraponerae.* Therefore, *A. paraponerae* need not go as far to find suitable hosts, resulting in more flies recaptured at the colony where they were marked. If this is true and hosts are more abundant on BCI, then one testable prediction is that individual females may lay fewer eggs per host at BCI, and females at La Selva may be selected to lay their entire egg load on one injured worker.

Apocephalus paraponerae on BCI may use more species-specific, less volatile cues when traveling shorter distances to potential host ants. If hosts are more available, finding hosts would be easier, and using host-specific cues (rather than easily detectable cues) would be advantageous to host location in an environment with many possible sources of the volatile cues. A number of ants, including the ponerine genus *Pachycondyla,* have 4-methyl-3-heptanone and 4-methyl-3- heptanol as mandibular gland components, and these highly detectable cues may not reliably distinguish *P. clavata* hosts from other possible odor sources. *Apocephalus paraponerae* on BCI may use more reliable higher molecular weight cues, possibly compounds found in the Dufour's or poison gland of the abdomen, to distinguish among a variety of potential hosts. *Apocephalus paraponerae* at La Selva may rely solely on the highly detectable (yet less reliable) mandibular gland chemicals to locate acceptable hosts because resources are more dispersed. Previous studies of host location and acceptance of *P. clavata* by *A. paraponerae* at La Selva have shown that flies also use short-range visual signals (in addition to surface cuticle chemicals) to determine if a host is suitable (Morehead & Feener 2000). Perhaps these additional visual and chemical cues differ between the two sites as well, but this has not been tested.

The geographic differences in host location

cues I describe were not due to species differences at the two sites. *Apocephalus paraponerae* attacking *P. clavata* at the two sites did not differ in mitochondrial DNA sequence (Morehead *et al.* 2001). Analysis of major mandibular gland chemicals of *P. clavata* revealed that the ants at both sites have the chemicals 4-methyl-3-heptanone and 4-methyl-3-heptanol (A. Attygalle, pers. comm.). These results were therefore not due to the *P. clavata* on BCI lacking the major mandibular gland chemicals 4-methyl-3-heptanone and 4-methyl-3-heptanol or to *A. paraponerae* species differences; however, there may be other chemical differences in the ants at the two sites that the flies are utilizing in host location.

Because many of the previous studies describing olfactory cues used in host location were performed in the laboratory, variation due to population differences could not be detected in many olfactometer experiments (van Alphen & Vet 1986, Turlings *et al.* 1993, van Baaron & Nénon 1996). My study suggests that intraspecific geographic variation may be an important factor in the ecology of these parasitoids, and it may go undetected in laboratory studies.

Geographic variation in host location cues can be an important factor in allopatric speciation (Thompson 1994). Biotic interactions and selective environments may vary across the parasitoid's geographic range. In the *A. paraponerae–P. clavata* system, variation in host location cues correlated with changes in resource availability may lead to subsequent evolution of these populations. *Paraponera clavata* and *A. paraponerae* are common and widespread throughout Central and South America, and the populations described here represent the northern extent of their ranges. Therefore, further investigation into the extent of variation in host location cues across a wider geographic scale is necessary. Further study, in combination with examination of other possible ecological correlates, would enhance understanding the impact of host location cue variation on evolution in parasitoid systems and may support an olfactory mechanism for host switching.

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