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Determinants of predation on phytophagous insects: the importance of diet breadth

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Abstract. To evaluate the role of predation in the evolution of diet specialization and to determine the effectiveness of various larval defenses, we offered lepidopteran larvae to colonies of the tropical ant *Paraponera clavata.* We recorded behavioral and physical characteristics of prey items and used log-linear models to analyze their importance as deterrents to predation by *P. clavata.* The most important determinant of probability of prey rejection by *P. clavata* was a prey's diet breadth; specialists were rejected by the ants significantly more than generalists. Other less important, but significant, predictors of prey rejection included ontogeny, morphology and chemistry. Late instar caterpillars were rejected more frequently than early instars, hairy caterpillars were rejected more frequently than caterpillars with other morphologies, and one caterpillar species with an unpalatable extract was rejected more frequently than two species with palatable extracts.

Key words: Diet specialization – Host plant chemistry – Lepidoptera – *Paraponera clavata* – Predation

Host ranges of most phytophagous insects are limited to a small proportion of potentially available plant taxa (Futuyma 1976; Jaenike 1978; Holloway and Herbert 1979; Barbosa 1988; Futuyma and Moreno 1988; Moran 1988; Weiss and Berenbaum 1989; Berenbaum 1990). Such specialization is typically viewed as a consequence of either the top-down effect of natural enemies or the bottom-up effect of host plant chemistry (see Strong 1988).

Bottom-up models rely on the assumption that host plant availability and apparency are the most important determinants of host range (Ehrlich and Raven 1964; Levins and MacArthur 1969; Feeny 1976; Rhoades and Cates 1976; Cates 1980; Berenbaum 1990). The top-down view holds that specialists are better able than generalists to utilize plant chemical or physical characteristics as defenses against enemies (Brower 1958; Atsatt 1981; Bernays 1988; Bernays and Cornelius 1989; Bernays and Graham 1989; Jones et al. 1989). For example, physical characteristics such as trichomes or a cryptic background have been shown to be important in providing refugia from predation and parasitism (Brower 1984; Gross and Price 1988; Hay et al. 1989; Kareiva and Sahakian 1990). If host plants offer only these physical safeguards to specialist herbivores, then predators should show no preference between generalists and specialists offered to them in the absence of host-plants. Bernays (1988), however, has shown that certain hymenopteran predators prefer generalist caterpillars over specialists in the absence of host-plants. These results suggest that specialists have gained some physiological benefit from their host plants or that they have sequestered plant secondary compounds, which, in general, have been shown to be important in deterring predators (Eisner 1970; Duffey 1980; Price et al. 1980; Brower 1984; Bowers and Larin 1989; Bowers 1990).

To test the assumption that diet breadth constitutes a major determinant of predation, we studied predation on lepidopteran larvae by the ponerine ant *Paraponera clavata* Emery (Hymenoptera: Formicidae). For three of the caterpillar species in our experiments, we also tested the assumption that plant chemistry is the mechanism which makes diet breadth an important determinant of predation. For example, herbivores that are more specialized may have evolved specific physiological adaptations that enable them to recycle plant defensive chemicals and accumulate them over time (see Bowers 1992). Alternatively, reduction in diet breadth may lead to greater casual sequestration of chemicals, imparting an effective chemical defense (Jones et al. 1989; Blum et al. 1990). We did not design our experiments to differentiate between these alternatives, but by offering caterpillars to ants in the absence of host plants we were able to eliminate physical benefits (such as trichomes) derived from the host plant.

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P. clavata is a generalist predator (Wilson 1971), an opportunistic nectivore (Young 1977), and possibly an herbivore and scavenger (Janzen and Carroll 1983; Breed and Bennet 1985). Colonies of *P. clavata* are located at the bases of large trees in lowland tropical rain forests, and foraging individuals use these and adjacent trees to reach the canopy and surrounding areas where they forage (Young and Hermann 1980). We used 5 colonies of *P. clavata* and 36 species of lepidopteran prey to address the following questions. Are specialist herbivores better protected than generalists against predation by *P. clavata?* If specialists are better protected than generalists, which characteristics make them less attractive to predators?

Materials and methods

We conducted all work at the La Selva Biological Reserve in Costa Rica during the period 1–30 January 1992. This site is located at 10° 25′ N 84° 05′ W on the Caribbean Slope of the country. Mean annual precipitation is 4000 mm, and the site is approximately 100 m above sea level. La Selva is comprised of primary and secondary lowland evergreen rain forest and is noteworthy for its great biodiversity (see Janzen 1983). Our experiments consisted of obtaining larval lepidopterans (hereafter, "caterpillars") and their host plants and observing consumption of caterpillars and host plant extracts and caterpillar extracts by *P. clavata*. We completed our work during La Selva's "dry" season (see Janzen 1983), during which caterpillars are comparatively scarce. We analyzed correlates of predation with log-linear models.

Caterpillars ($n = 36$ species) and their plant substrates were obtained and identified to the lowest taxon possible (Table 1). Caterpillars were either collected in the wild at La Selva or purchased from the *Finca Mariposa*, a commercial butterfly farm near Alajuela. Voucher specimens of many of the caterpillars and of some of the adults were deposited at the Instituto Nacional de Biodiversidad de Costa Rica (INBio) in San Pedro. Caterpillars were held in captivity for several days to verify that they actually were using their presumed host plants as food resources. Each caterpillar was evaluated for the following traits: coloration, diet breadth, developmental stage, morphology, and size. All of these characteristics, along with prey behavior, may act as important anti-predatory traits (reviewed by Edmunds 1974; Devries 1987; Evans and Schmidt 1990).

We used a taxonomic definition of specialization similar to definitions used by Bernays (1988) and others (Futuyma 1976; Price 1983); caterpillars known to feed on less than two families of plants (according to DeVries 1987), or caterpillars of unknown diet breadth that were found feeding on only one plant species, were classified arbitrarily as "specialists" ($n = 183$ individuals), while caterpillars found feeding on plants in greater than five families were classified as "generalists" ($n = 82$ individuals). The total number of host plant species (rather than families) for caterpillar species as well as for individual caterpillars may be better indicators of those caterpillars' diet breadth, but those data are not available for a majority of lepidopteran larvae in Costa Rica (Price 1991).

While using caterpillars with unknown diet breadths is problematic, our characterization of diet breadth is conservative and takes into account known diet-breadth patterns at La Selva. Our null hypothesis assumes that specialists are not protected more than generalists, so erroneously characterizing caterpillars as specialists would only contribute to accepting the null hypothesis. Furthermore, the chance of making such a mistake is quite low, since most herbivores at La Selva have very narrow diet breadths (Marquis and Braker 1991). For example, 75% of the butterfly species at La Selva with known host plant ranges are monophagous (only one host

Table 1. a Generalist caterpillars offered to *P. clavata* and their associated host-plants

[a] CATERPILLAR	[b] HOST PLANT	n
Arctiidae sp. 1	(Annonaceae) *Costus sp.* (Costaceae) *Welfia georgii* (Palmae) (Pteridophyta) *Myriocarpa longipes* (Urticaceae)	5
Arctiidae sp. 2	*Protium panamense* (Burseraceae) (Compositae) *Hernandia sp.* (Hernandiaceae) *Colubrina espinosa* (Rhamnaceae) (Rubiaceae)	5
*Geometridae sp. 1	*Ardisia sp.* (Myrsinaceae) *Colubrina espinosa* (Rhamnaceae) *Citrus sp.* (Rutaceae) (Solanaceae) *Passiflora sp.* (Passifloraceae) (Violaceae)	18
Hesperidae sp. 1	(Convolvulaceae) *Neea sp.* (Nyctaginaceae) *Piper urostachyum* (Piperaceae) *Colubrina sp.* (Rhamnaceae) (Solanaceae) (Urticaceae)	6
Lymantriidae sp. 1	(Fabaceae) *Heliconia imbricata* (Heliconiaceae) (Marantaceae) *Musa* (Musaceae) *Bactris gassipaes* (Palmae) *Crysophila sp.* (Palmae)	6
*Noctuidae sp. 1	(Convolvulaceae) (Cucurbitaceae) *Manihot sp.* (Euphorbiaceae) (Fabaceae) *Heliconia sp.* (Heliconiaceae) *Calathea sp.* (Marantaceae) *Hamelia patens* (Rubiaceae) *Cestrum rugosum* (Solanaceae) *Myriocarpa longipes* (Uritcaceae)	18
Noctuidae sp. 2	(Brassicaceae) *Wissadula excelsior* (Compositae) (Malvacae) *Pithecellobium sp.* (Mimosaceae) *Ficus sp.* (Moraceae) *Solanum sp.* (Solanaceae)	6
*Saturniidae sp. 1	*Anthurium sp.* (Araceae) *Philodendron sp.* (Araceae) *Mikania sp.* (Compositae) *Inga sp.* (Fabaceae) *Heliconia imbricata* (Heliconiaceae) *Colubrina sp.* (Rhamnaceae) *Cestrum rugosum* (Solanaceae) *Myriocarpa sp.* (Urticaceae)	18

[a] Those species that are preceded by an asterisk (*) had balanced replicates for ontogeny and were used in logit models 4 and 5

[b] Caterpillars were reared on host plants on which they were found. For each species, no one host plant was used more frequently for rearing than other host plants (exact n for each host plant is unknown)

Table 1. b Specialist caterpillars offered to *P. clavata* and their associated host-plants

[a] CATERPILLAR	[b] HOST PLANT	n
Arctiidae sp. 3	*Paullinia sp.* (Sapindaceae)	1
Arctiidae sp. 4	*Neea psychotriodes* (Nyctagenaceae)	4
Arctiidae sp. 5	(Melastomataceae)	1
*Geometridae sp. 2	*Adelia sp.* (Euphorbiaceae)	18
Geometridae sp. 3	*Myriocarpa longipes* (Urticaceae)	3
Geometridae sp. 4	*Piper sanctus felicitus* (Piperaceae)	3
Hesperiidae sp. 2	(Urticaceae)	1
Hesperiidae sp. 3	*Hampea sp.* (Malvaceae)	2
Hesperiidae sp. 4	*Costus sp.* (Costaceae)	1
Lymantriidae sp. 2	*Welfia georgii* (Palmae)	1
Noctuidae sp. 3	*Calathea sp.* (Maranthaceae)	3
Noctuidae sp. 4	(Convolvulaceae)	1
Noctuidae sp. 5	*Pterocarpus rhorri* (Papilionaceae)	1
**Adelpha fessonia* (Nymphalidae)	*Randia* (Rubiaceae)	18
**Caligo memnon* (Nymphalidae)	*Heliconia imbricata* (Heliconiaceae)	18
**Chlosyne hyppodrome* (Nymphalidae)	*Melanthera aspera* (Asteraceae)	18
**Chlosyne janais* (Nymphalidae)	*Odontonema* (Acanthaceae)	18
Chlosyne narva (Nymphalidae)	*Odontonema sp.* (Acanthaceae)	2
Danaus plexippus (Nymphalidae)	*Asclepias sp.* (Asclepiadaceae)	1
**Dione juno* (Nymphalidae)	*Passiflora vitifolia*	18
Dynastor darius (Nymphalidae)	(Bromeliaceae)	1
Prepona omphale (Nymphalidae)	*Inga vera*	2
**Papilio anchisiades* (Papilionidae)	*Citrus limon* (Rutaceae)	18
Papilio androgeus (Papilionidae)	*Citrus limon* (Rutaceae)	4
*Saturniidae sp. 2	*Pentagonia macrophila* (Rubiaceae)	18
Saturniidae sp. 3	*Ocotea sp.* (Lauraceae)	3
Saturniidae sp. 4	*Carica papaya* (Caricaceae)	1
Sphingidae sp.	(Euphorbiaceae)	3

[a] Those species that are preceded by an asterisk (*) had balanced replicates for ontogeny and were used in logit models 4 and 5

[b] Caterpillars were reared on host plants on which they were found; these host plants are the only plants listed in the table

plant species), and over 95% feed on plants within one family (Marquis and Braker 1991).

The ontogeny category referred to the developmental stages of the caterpillars and included: "early" (first through third instar) or "late" (fourth instar and later). Most caterpillars were reared in the lab after being collected and were offered to the ants as later instars. We offered both early and late instars to the ants if we could collect or buy enough replicates, and we used that subset of the data for the models that included ontogeny (see Table 1).

Morphology categories were: "spiny," "hairy," or "glabrous". These categories were based on visual inspection of the caterpillars. "Spiny" caterpillars had spines harder than the cuticle and at least 2 mm long. Caterpillars that possessed hairs and spines were rated as "hairy" only if more than 50% of their cuticle was covered with hair that was at least 5 mm in length. "Glabrous" caterpillars had no hairs or spines.

Coloration was also based on visual inspection of the caterpillars and included these categories: "brightly colored," "visually cryptic" or "other". Since *P. clavata* foragers seem to rely more on chemical than visual cues for locating prey (see Breed and Bennet 1985; Janzen and Carroll 1983), the coloration category was included to see if purported correlations between coloration and palatability (see Cott 1940) were valid for this invertebrate predator.

The size statistic was based on the length (in mm) of a caterpillar stretched to the point that slight pressure was felt on the cuticle. Size categories were: size$\leq$15 mm ("small"), 15 mm$<$size$\leq$38 mm ("medium"), and size$>$38 mm ("large"). The size categories were pooled in the preceding manner (based on the mean and standard deviation of all the lengths) to ensure sufficiently large cell sizes for data analysis.

For all predation experiments, we used 5 *P. clavata* colonies at the bases of trees in the Holbridge Arboretum at the La Selva Biological Reserve. Most experiments were conducted during the period 1600–0100 because *P. clavata* is crepuscular and/or nocturnal. Artificial illumination of the foraging trails did not seem to affect foraging or attack behavior by *P. clavata*. Using forceps, we placed live caterpillars on the main foraging trails within 3 m of colony entrances. If a caterpillar walked away or dropped from the main foraging trail, we returned it to maximize the chance of encountering a predator. We observed all caterpillar-ant interactions until either the caterpillar was carried into the colony or at least ten ants had physically encountered and then rejected the

Table 2. Summary of caterpillar extract and plant extract palatability

	Caterpillar	Host Plant[a]
SPECIALISTS	*Dione juno* (Nymphalidae)	*Passiflora vitifolia* (Passifloraceae)
	Papilio anchisiades[b] (Papilionidae)	*Citrus limon*[b] (Rutaceae)
GENERALIST	Noctuidae sp. 1	*Myriocarpa longipes* (Urticaceae)

[a] The host plant used for extracts was the plant most commonly used by the caterpillar

[b] Extracts from these species were consumed by the ants significantly less than the control ($p < 0.05$); consumption of other extracts was not different from the control

caterpillar. In pilot studies, we found that caterpillars rejected by 10 ants were never taken by the ants. An interaction was considered a "rejection" if the ant clearly touched the caterpillar (either with antennae or mandibles) and then continued foraging, retreated, or initiated but did not continue an attack. Caterpillar species were presented evenly to the colonies; for species which we were unable to collect 5 or more specimens, assignment to a particular colony or colonies was randomized. Each colony was exposed to 53 individual caterpillars (at least 36 specialists per colony and at least 16 generalists per colony).

The response factors recorded were number of prey rejections and behavioral response of a caterpillar. Rejections were pooled as follows: no rejections, some rejections (1–6 rejections), or complete rejection (10 rejections). Caterpillar behavioral responses were ranked as follows: no behavioral defense; thrashing and attempting to attach to foraging substrate; thrashing and biting or vomiting. All experiments were recorded with a Canon H850 Camcorder to permit thorough analysis of the encounters.

Additionally, we made crude water and acetone extracts of 3 caterpillar species and their host plants (Table 2). Host plants were dried at 40° C overnight, and 0.3 g of dried plant material was added to 10 ml solvent (boiling water or acetone). In having dried the host plants at 40° C, our plant extracts may have lost volatile terpenes and phenolics originally present in the plant material. The mixture was agitated frequently by hand and evaporated to 5 ml. Next, 0.3 ml of this solution was added to a micro-centrifuge tube into which was added a 50% v/v sugar water solution. Live caterpillars were starved for 24 hours, ground with a scalpel, and 50 mg of ground, homogenized caterpillar was placed in 10 ml of solvent. Both water and acetone extracts were made for all caterpillars and plants. As with the plant extracts, 0.3 ml of this solution was added to a micro-centrifuge tube into which was added a 50% v/v sugar water solution.

Caterpillar and host plant extracts, as well as sugar water controls, were offered to *P. clavata* colonies in microcentrifuge tubes. (Acetone controls, which were offered with the acetone extracts, contained sugar water plus 0.3 ml of acetone.) The tubes were weighed to ± 1.0 mg before and after being attached for 1 hour to trees containing foraging trails. Paired choice tests were conducted 3 times each at all 5 colonies. We used paired t-tests to compare consumption (i.e., change in weight of the extract before and after a feeding trial) of extract and control, with a Bonferonni adjustment of critical α to reduce Type I error in multiple paired t-tests (SAS 1990). The results of this experiment were used to create another predictor variable called chemistry for our analysis of predation determinants, described below. Chemistry was a dichotomous variable having these levels: "deterrent extract" or "palatable extract".

We used logit analyses to study the relative importance of the predictor variables as determinants of ant response (rejections). Logit analysis is a type of log-linear model in which one of the variables is treated as a response factor, dependent on two or more predictor variables (Agresti 1990). We used the Newton-Raphson algorithm for parameter estimation and model testing to permit use of nonhierarchical models (SAS 1990). We used the maximum likelihood method for parameter estimation of linear models and Chi-square statistics for hypothesis testing (see SAS 1990). We used data from 265 feeding trials at all 5 colonies. Cells that contained "sampling zeroes" (*sensu* Bishop et al. 1975) were assigned values of 1×10^{-20}, and cells that contained "structural zeroes" (*sensu* Bishop et al. 1975) were deleted (see SAS 1990).

We used species means to determine the rejection statistic and the predictor variables in the first three models (see Table 3). "Means" of strictly categorical variables (coloration, diet breadth, morphology) were simply the values specific to the species. The models for which we did not use species means dealt with subsets of the data that had balanced species replicates.

Results

We ran 6 logit models to test the relative importance of predictor variables of ant response (Table 3). We chose the models after looking at frequency tables for all combinations of variables (see Tabachnick and Fidel 1989); we ran six models because running one model with all the variables of interest would be uninterpretable (often containing biologically irrelevant interactions) and would require a prohibitively large sample size. The six models revealed that diet breadth, morphology, ontogeny, and chemistry were consistently important predictors of number of prey rejections.

Model 1 revealed significant associations between number of prey rejections and the following: diet breadth ($X^2 = 7.11$, v = 2, $P = 0.029$) and morphology ($X^2 = 9.58$, v = 4, $P = 0.048$). Specialists were rejected more often than were generalists (Fig. 1), and, in particular, the probability of complete rejection of a specialist was con-

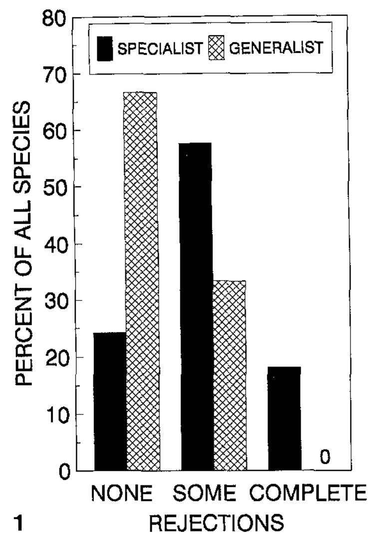
Table 3. Summary of log-linear models

Model[a]	Likelihood ratio probability[b]	Important predictors[c]
1. REJ, DBR, MOR	0.8926	DBR (2.64**) MOR (2.03*)
2. REJ, DBR, CLR	0.5349	DBR (3.21***)
3. REJ, DBR, SIZ	0.0791	DBR (2.58**)
4. REJ, CAT, INS	0.0911	INS (2.59**)
5. REJ, COL, INS	0.2579	COL (3.18**) INS (2.52**)
6. REJ, CHM, INS	0.1123	CHM (5.61***) INS (− 5.15***)

[a] The variables shown are those from the original saturated model. Variables are coded as follows: CAT = caterpillar response; CHM = chemistry; CLR = coloration; COL = ant colony; DBR = diet breadth; INS = ontogeny; MOR = morphology; REJ = number or prey rejections; SIZ = size

[b] The likelihood ratio probability is a goodness-of-fit test for the overall model, and p-values above 0.05 indicate a good fit (SAS 1990). P-values reported here are for the most parsimonious models

[c] Predictor variables were ranked by standardized parameter estimates, which are given in parentheses along with asterisks to indicate significance of the esimate (* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.005$)



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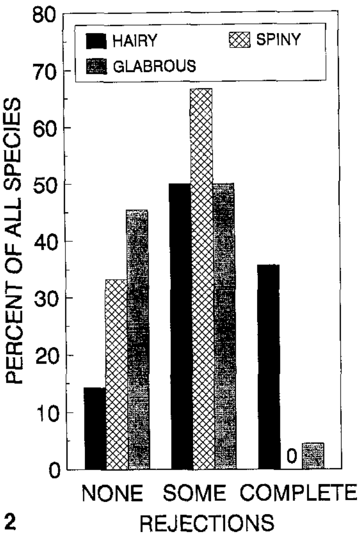

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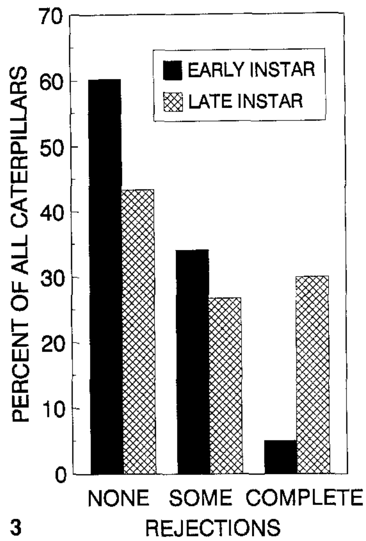

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Fig. 1. Diet breadth as a predictor of three rejection categories (no rejections, some rejections, and completely rejected). The vertical axis is the percent of all caterpillar species that were in the corresponding diet breadth and rejection categories. For example, about 67% of the generalist species were attacked by *P. clavata* without receiving any rejections, while about 58% of the specialist species received some rejections and 18% were completely rejected. The O indicates a sampling zero (see text for explanation)

Fig. 2. Morphology as a predictor of three rejection categories (no rejections, some rejections, and completely rejected). The vertical axis is the percent of all caterpillar species that were in the corresponding morphology and rejection categories. For example, less than 15% of the hairy caterpillar species were attacked without being rejected. The O indicates a sampling zero (see text for explanation)

Fig. 3. Ontogeny as a predictor of three rejection categories (no rejections, some rejections, and completely rejected). The vertical axis is the percent of all caterpillars that were in the corresponding ontogeny and rejection categories. For example, about 61% of the early instar caterpillars were attacked by *P. clavata* without receiving any rejections, while about 30% of the late instars were completely rejected

siderably higher than the probability of complete rejection of a generalist (from the logits, 65% probability of complete rejection of a specialist vs. 0.42% for a generalist). Hairy caterpillars were completely rejected more often than spiny or glabrous caterpillars, but all morphologies received at least some rejections (Fig. 2). It is interesting to note that for "glabrous" caterpillars, which seem to have no morphological defenses, there were more completely rejected species than spiny caterpillars and there were the same number of species receiving some rejections as hairy caterpillars.

Model 2 revealed significant associations between number of prey rejections and diet breadth ($X^2=9.88$, $v=2$, $P=0.0072$). Again, specialists were more frequently rejected than were generalists (Fig. 1). Coloration categories were not significant predictors of rejection ($X^2=6.47$, $v=4$, $P=0.1665$).

Diet breadth again predicted rejections in Model 3 ($X^2=7.46$, $v=2$, $P=0.0240$), while size did not ($X^2=1.53$, $v=4$, $P=0.8209$).

Models 4 and 5 included caterpillar species for which there were balanced replicates of different instars and balanced replicates at different colonies (Table 1). Model 4 examined the relationship between number of prey rejections, ontogeny, and caterpillar behavioral response. Here, we found that ontogeny was a significant predictor of prey rejections ($X^2=11.71$, $v=2$, $P=0.0029$) while caterpillar behavior was not ($X^2=7.29$, $v=4$, $P=0.12$). Late instar caterpillars were completely rejected more frequently than early instars (Fig. 3).

For Model 5 there were significant associations between ant response and the following: ontogeny ($X^2=7.24$, $v=2$, $P=0.0268$) and colony ($X^2=17.9$, $v=8$, $P=0.022$). Some colonies rejected caterpillars more readily than others. Again, later instars were rejected more frequently than early instars.

Model 6 dealt with the 3 species for which we did extract experiments and examined the relationship between extract palatability and number of prey rejections. *Papilio anchisiades* (Papilionidae) and its host plant *Citrus limon* (Rutaceae) were the only species that had deterrent extracts ($t=8.20$, $v=1$, corrected $P=0.042$; see Table 2). The model indicated that number of prey rejections was significantly associated with both chemistry ($X^2=20.49$, $v=2$, $P<0.0001$) and ontogeny ($X^2=30.81$, $v=4$, $P<0.0001$). There was no significant interaction between chemistry and instar, but analysis of the standardized parameter estimates indicates that chemistry was the more important predictor variable of number of prey rejections (Table 3). For example, late instars of *Papilio anchisiades* (which had a deterrent extract) were always completely rejected, whereas late instars of the two caterpillar species whose extracts were palatable were never completely rejected.

Predictor variables were ranked in importance by using standardized parameter estimates (Tabachnick and Fidel 1988). Whenever diet breadth was in a model, it was the most important predictor. Morphology, coloration, size, and behavior were all less important predictor variables than were diet breadth, chemistry, ontogeny and colony. Important predictor variables are summarized in Table 3.

Discussion

The tropical ant *Paraponera clavata* is a broad generalist predator on many invertebrates (Wilson 1971), including a wide variety of caterpillars. Even so, we demonstrate that prey choice by *P. clavata* is by no means random or unpredictable. An ant's "decision" to attack a caterpillar depends on many characteristics of the caterpillar. Our study indicated that diet breadth, extract palatability, ontogeny, morphology, and colony are highly correlated with probability of predation by *P. clavata.*

Diet breadth consistently represented the most important determinant of predation in our study. Specifically, specialists were victims of successful predation much less frequently than were generalists, a pattern which suggests the importance of top-down forces. Generalists and specialists were offered to colonies of *P. clavata* on foraging trails, thus diminishing any physical protection derived from the host plant (see Brower 1984; Gross and Price 1988; Hay et al. 1989; Kareiva and Sahakian 1990). For example, cryptic specialists were rejected frequently, despite the absence of the host plant's correct background, which points to some other (presumably chemical) benefit derived from the host plant. Alternatively, chemical defense in this situation could have arisen from de novo synthesis, rather than from direct acquisition of host plant chemistry. We did not test this alternative hypothesis of de novo synthesis.

Other predictor variables also point to the potentially important role of chemistry as a deterrent to predation. For example, the dramatic effect of extract palatability on probability of predation provides anecdotal support. In particular, the caterpillar *Papilio anchisiades,* from which unpalatable extracts were obtained and from whose host plant *(Citrus limon)* unpalatable extracts were likewise obtained, was often completely rejected by *P. clavata* and was never attacked without at least some rejections. The two species that had palatable extracts (both from the caterpillar and host plant), one of which was a specialist *(Dione juno),* were seldom rejected by *P. clavata.*

In addition, caterpillar ontogeny, another consistently important predictor of predation, suggests the importance of chemistry. Colonies of *P. clavata* routinely preferred earlier instars to later instars, and we suggest that increased accumulation of plant toxins in later instars of caterpillars may contribute to the negative relationship between caterpillar development and probability of ant predation. While it could be argued that ontogeny-related rejections may have reflected difficulty in subduing and transporting large caterpillars (independent of their chemistry), in the context of foraging theory (see Pyke 1984), we point out that species size was not a significant predictor of rejections, despite the wide variation in sizes between species (7 to 135 mm).

Lastly, the significant inverse relationship between caterpillar hairiness and probability of predation may also have chemical origins. Caterpillar hairs are frequently urticating and may contain plant secondary compounds (Kawamoto and Kumada 1984), and for this reason vertebrate and invertebrate predators and specialist parasitoids may avoid hairy prey or attempt to remove hairs from caterpillars before eating them (Edmunds 1974; Heinrich 1979; Heinrich and Collins 1983; Bernays 1988; Sheehan 1991). Alternatively, the deterrent value of caterpillar hairs may be due to their allergenic proteins, abrasive surfaces, or difficulty in handling, all of which are independent of host plant derived allelochemistry (Kawamoto and Kumada 1984).

Evidence against the importance of chemistry arises from an analysis of coloration characteristics. Visual crypsis and bright coloration, for example, are typically a consequence of chemistry, and one would expect that brightly colored caterpillars would be unpalatable and frequently rejected by predators, while cryptic caterpillars (away from their host plants) would be palatable and not rejected by predators (Cott 1940; Edmunds 1974, 1990; Guilford 1986, 1990). However, we found that caterpillar coloration did not affect predation.

Evidence against the importance of predation by *P. clavata* as a selective force arises from analysis of intercolony variation. Some colonies were more likely to reject caterpillars than other colonies; such variation lessens the importance of this predator as a selective force. Since our work was conducted in the dry season, when caterpillars are relatively scarce, it is possible that some ant colonies were being less selective about which prey items to attack.

We were not able to use specific host plants as predictors of caterpillar rejection. Thus, while our data suggest that specialists derive some chemical benefit from their host plants that generalists do not, we are unable to distinguish whether this benefit results from the specialists eating more toxic plants or from generalists diluting toxins by eating multiple plant species. We are also unable to address the possibility that specialists are better physiologically equipped than generalists to sequester secondary compounds. We do, however, demonstrate that a broad suite of caterpillar characteristics, all centered around diet specialization, serves to deter predation by *P. clavata.*

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