

Effectiveness of caterpillar defenses against three species of invertebrate predators

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Abstract. The efficacies of larval defenses against invertebrate predators representing different (but overlapping) foraging guilds were compared by offering 34 species (287 individuals) of lepidopteran larvae to *Paraponera clavata* ants, *Apiomerus pictipes* bugs, and *Polistes instabilis* wasps. Overall, the ants were the most likely to eat caterpillar prey, and the wasps were the most cautious. Larval chemistry and diet breadth were significant predictors of rejection by the group of predators; chemically defended specialist herbivores were better protected than generalist herbivores without known chemical defenses. These results provide evidence for the potential importance of predators in maintaining diet breadth of phytophagous insects, and they suggest that plant chemistry is part of a mechanism for restricting diet breadth. Other important larval defenses included size, morphology, and coloration. Large prey (heavier than 1 g) were less acceptable than smaller prey (lighter than 200 mg) for the wasps and bugs but not for the ants; hairs deterred predation by the ants and bugs but not by the wasps; and brightly colored caterpillars were frequently rejected by the wasps but not by the ants and bugs.

Key Words. Caterpillars, defenses, diet breadth, predation, *Apiomerus pictipes*, *Polistes instabilis*, *Paraponera clavata*, plant secondary compounds, Lepidoptera, specialization, tropics

INTRODUCTION

Faced with a deluge of special cases that often appear to be a morass of contradictions and confusion, ecologists frequently attempt to generalize about predominant forces or patterns that are manifested by specific experiments and observations. A few prominent examples in research on lepidoptera include: attempts to use specific studies of oviposition patterns (particularly those of lepidopteran pest species) to construct a diet-choice theory for all phytophagous insects (e.g., Courtney and Kibota 1990); attempts to identify the most important processes which organize communities by examining particular systems of predators, herbivores and plants (e.g., Karban 1989); and attempts to explain the high incidence of dietary specialization in lepidopteran larvae by examining known feeding patterns (e.g., Ehrlich and Raven 1964). These generalizations, which arose from

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multiple-species pattern analyses as well as from reductionist (single-species or single-system) approaches, have contributed significantly to a theoretical framework for a large number of studies on lepidoptera.

In light of these and many other studies which provide good data for generalizations, it is surprising that there is a dearth of attempts to characterize important components of lepidopteran larval defenses, either by conducting multiple-species experiments or through literature reviews (Witz 1990, Dyer and Floyd 1993, Dyer 1995; also for adult Lepidoptera see Maclean et al. 1989). While multiple-species approaches are generally not as thorough as experiments examining the effectiveness of a particular defense in one species, they allow for different generalizations on insect defenses which can ultimately provide a framework for both basic and applied research questions with specific systems. For example, Bernays and Cornelius (1989) demonstrated that a number of species of leaf rollers were extremely palatable to ants; their generalization that trade-offs could exist between chemical defense and concealment from predation provides an impetus for quantitative genetics experiments examining the potential for such trade-offs in specific systems.

Two important groups of general hypotheses about larval defenses which I attempt to address in this study are: 1) hypotheses about the effectiveness of a suite of defenses against specific predatory guilds or against single species, and 2) hypotheses about effectiveness of specific defenses against a suite of predatory guilds or against multiple species. A related question which I address involves generalizations about the importance of biotic interactions (particularly natural enemies: Brower 1958, Bernays and Graham 1988) and plant chemistry (Dyer 1995) in influencing herbivores' diet breadths. Recent studies have demonstrated that certain specialist herbivores are better protected than certain generalists against various invertebrate predators (Bernays 1988, Bernays and Cornelius 1989, Dyer and Floyd 1993, Dyer 1995), which suggests that natural enemies could be important in the maintenance of narrow diet breadth or could be a selective force in the evolution of dietary specialization. In this study, I further test this natural enemy hypothesis, and I also explore the possibility that plant chemistry mediates the evolution of differences in defensive capacity between specialists and generalists. Chemistry might provide such a mechanism if specialized herbivores tend to evolve the ability to sequester plant defensive chemicals and use them as defenses against their natural enemies.

In order to generalize about the efficacies of various defenses against different predators and about the importance of biotic interactions and plant chemistry in the evolution of dietary specialization, I offered specialist and generalist lepidopteran larvae (caterpillars) with a wide variety of potential defensive qualities to three predators representing different predatory guilds: an assassin bug, *Apiomerus pictipes* (Reduviidae); a paper wasp, *Polistes instabilis* (Vespidae); and the giant tropical ant, *Paraponera clavata* (Formicidae). Specifically, I asked the following questions: 1) Are different predator guilds deterred by different types of defenses? 2) What are the most

effective defensive mechanisms of lepidopteran larvae against a suite of predators? 3) Are specialist herbivores better protected than generalists against a suite of predators? 4) Are noxious prey chemicals effective defenses against a suite of predators?

The prey used in my experiments were larvae in 13 different families of Lepidoptera that were native to a variety of micro-habitats in Costa Rica. These caterpillars exhibited a wide variety of antipredator mechanisms which could be compared. *Apiomerus pictipes* is a common sit-and-wait predator that ranges from Colorado (USA) to Columbia (Johnson 1983). It is solitary, visually oriented, and quickly kills prey by inserting its mouthparts and sucking, leaving behind a dry carcass. *Polistes instabilis* is a common foraging predator found from Costa Rica to Southern Brazil and Argentina (Richards 1978). It is a solitary (i.e., it does not recruit), visually-oriented predator, and it kills prey by biting rather than stinging. Each wasp extensively chews the prey before returning to the nest to distribute ingested fluids and solid caterpillar remains to the other adults and larvae (West-Eberhard 1983). *Paraponera clavata* is a foraging predator common in lowland rainforests and found from Nicaragua to the Amazon (Janzen and Carroll 1983). It is a chemically-oriented predator that forages independently or in groups and that kills prey by using its powerful sting, using its mouthparts and cooperating with nestmates (pers. obs.). All three predators commonly prey on caterpillars (pers. obs., West-Eberhard 1983, Johnson 1983) and are sympatric with all the caterpillars used in my study.

MATERIALS AND METHODS

I conducted all experiments and most collecting in June and July, 1993 at the following sites in Costa Rica: Palo Verde National Park, Lomas Barbudal National Park, and private land near Lomas Barbudal. These sites are located in the Guanacaste province of Costa Rica and are characterized by dry forest (sensu Holdridge et al. 1971) and marsh (at Palo Verde).

Collecting

I collected most caterpillars at Palo Verde and Lomas Barbudal. I also bought several species of caterpillars that are known to occur in Guanacaste from *Finca Mariposa*, a commercial butterfly farm in La Guacima.

I either identified caterpillars to the lowest taxon possible using Stehr (1993), or if sufficient numbers of caterpillars were available, I reared them to the adult stage for identification. I deposited voucher specimens of most caterpillars and adults at both the Instituto Nacional de Biodiversidad (INBio) in Costa Rica and the University of Colorado Entomology Museum, Boulder (Table 1).

For host plant data, I identified plant families on which I found caterpillars and held the caterpillars in captivity for several days to verify that they actually were using their presumed host plants as food resources. If possible, I collected enough plant material for identification to lower taxa by park naturalists or I dried and pressed them for identification by other tropical botanists. Voucher specimens for some host plants are at the University of Colorado Herbarium, Boulder (Table 1).

Table 1a. Generalist caterpillars offered to *P. clavata*, *P. versicolor*, and *A. pictipes* and the host plants upon which the caterpillars were found.

Caterpillar ^a	Predators ^b	Host Plants ^c
Arctiidae (5, 5, 3) CU:LS93GAT	A(Y), B(Y), W(Y)	(Annonaceae)* <i>Costus</i> sp. (Costaceae) <i>Siparuna pauciflora</i> (Monimiaceae) <i>Welfia georgii</i> (Palmae) <i>Adiantum</i> sp. (Polypodiaceae) <i>Myriocarpa longipes</i> (Urticaceae)*
Arctiidae (5, 5) CU:PV93AWB	A(N), B(Y)	<i>Protium panamense</i> (Burseraeae) (Compositae) <i>Hernandia</i> sp. (Hernandiaceae) <i>Nectandra hypoleuca</i> (Lauraceae) <i>Colubrina spinosa</i> (Rhamnaceae) (Rubiaceae)
<i>Eois</i> sp. (Geometridae) (3, 3) CU:TBG92	A(N),B(N)	(Araceae)* (Leguminosae) <i>Piper urostachyum</i> (Piperaceae) <i>Sabicea</i> sp. (Rubiaceae)
<i>Pero</i> sp. (Geometridae) (5, 3, 5) CU:LS93ATB	A(N), B(N), W(N)	(Annonaceae)* <i>Diffenbachia</i> sp. (Araceae) <i>Costus</i> sp. (Costaceae) <i>Erythrina</i> sp. (Leguminosae) <i>Pentaclethra maculosa</i> (Leguminosae) <i>Hampea appendiculata</i> (Malvaceae)
Geometridae (5, 3, 5) CU:BTB92	A(N), B(N), W(N)	<i>Richeria dressleri</i> (Euphorbiaceae) <i>Ardisia</i> sp. (Myrsinaceae) <i>Passiflora</i> spp. (Passifloraceae)* <i>Colubrina spinosa</i> (Rhamnaceae) <i>Citrus</i> spp. (Rutaceae) (Solanaceae) (Violaceae)
<i>Gonodonta</i> sp. (Noctuidae) (5, 3, 3) IN:GON92	A(N),B(N),W(N) TASTY	(Brassicaceae) (Compositae) <i>Wissadula excelsior</i> (Malvaceae) <i>Calathea</i> sp. (Marantaceae) <i>Pithecellobium</i> sp. (Mimosaceae) <i>Ficus</i> sp. (Moraceae) <i>Solanum</i> sp. (Solanaceae) <i>Myriocarpa longipes</i> (Urticaceae)*
<i>Pantographa limata</i> (Pyralidae) (5, 3, 5) CU:LS93SIM	A(N),B(N),W(N) TASTY	<i>Costus</i> sp. (Costaceae) <i>Manihot esculenta</i> (Euphorbiaceae) <i>Hamelia patens</i> (Rubiaceae) <i>Paullinia pterocarpa</i> (Sapindaceae) <i>Cestrum</i> sp. (Solanaceae)* (Solanaceae) <i>Goethalsia meiantha</i> (Tiliaceae)* <i>Luehea seemannii</i> (Tiliaceae)* <i>Myriocarpa longipes</i> (Urticaceae)*

<i>Antheraea polyphemus</i> A(N),W(Y) (Saturniidae) (3, 3) IN:SAT92		<i>Godmania aesculifolia</i> (Bignoniaceae)* <i>Solanum</i> sp. (Solanaceae)* <i>Luehea</i> sp. (Tiliaceae)* [Plus 18 additional families reported in Tietz 1972]
<i>Automeris rubescens</i> A(N),W(Y) (Saturniidae) (3, 3) CU:PV93IOT		<i>Cordia alliodora</i> (Boraginaceae) <i>Rourea glabra</i> (Connaraceae) <i>Cassia</i> sp. (Leguminosae)* <i>Inga</i> sp. (Leguminosae) [Plus 5 additional families reported in Janzen 1984]
<i>Automeris zugana</i> A(N),W(Y) (Saturniidae) (5, 3) CU:93IOM		<i>Cydista heterophylla</i> (Bignoniaceae)* <i>Cassia</i> sp. (Leguminosae)* <i>Lonchocarpus</i> sp. (Leguminosae)* (Sapindaceae) <i>Solanum hazenii</i> (Solanaceae) [Plus 2 additional families reported in Janzen 1984]
<i>Citheronia lobesis</i> A(N),B(Y),W(Y) (Saturniidae) (5, 3, 3) CU:PV93HHD		(Anacardiaceae) <i>Cydista heterophylla</i> (Bignoniaceae)* <i>Godmania aesculifolia</i> (Bignoniaceae)* <i>Cochlospermum vitifolium</i> (Cochlospermaceae)* [Plus 4 additional families reported in Janzen 1984]
<i>Erinnyis ello</i> A(N),W(Y) (Sphingidae) (4, 3) CU:PV93ELL		(Bignoniaceae) <i>Manihot esculenta</i> (Euphorbiaceae) <i>Sapium</i> sp. (Euphorbiaceae) <i>Cissus microcarpa</i> (Vitaceae) [Plus 2 additional families reported in Tietz, 1972 and 1 additional family reported in Janzen, 1984]

Table 1b. Specialist caterpillars offered to *P. clavata*, *P. versicolor*, and *A. pictipes* and the host-plants upon which the caterpillars were found.

Caterpillar ^a	Predators ^b	Host Plants ^c
<i>Euchaetes</i> sp. (Arctiidae) (3,3) CU:PV93BOA	B(Y),W(Y)	<i>Asclepias curassavica</i> (Asclepiadaceae)*
Arctiidae (3) CU:PV93MHA	W(N)	<i>Cydista heterophylla</i> (Bignoniaceae)*
Hesperiidae (3) IN:PV93HES	W(Y)	<i>Solanum</i> sp. (Solanaceae)*
Limacodidae (3,3)	B(Y),W(Y)	<i>Quercus oleoides</i> (Fagaceae)

Lymantriidae (3, 3) CU:PV93040	B(Y),W(N)	<i>Cassia</i> sp. (Leguminosae)*
Lymantriidae (3, 3) IN:LS92LYM	B(Y),W(Y)	<i>Godmania aesculifolia</i> (Bignoniaceae)*
Megalopygidae (3, 3) CU:PV93MGT	B(Y),W(Y)	<i>Ceiba pentandra</i> (Bombacaceae)
<i>Azeta versicolor</i> (Noctuidae) (3, 3, 3) CU:PV93010	A(N),B(N),W(N)	<i>Siparuna pauciflora</i> (Monimiaceae)
<i>Diphthera festiva</i> (Noctuidae) (3) IN:PV93NOC2	W(Y)	<i>Solanum</i> sp. (Solanaceae)
<i>Caligo memnon memnon</i> (Brassolinae) (5, 3, 5) CU:LS93CAL	A(Y),B(Y),W(Y) NASTY	<i>Heliconia imbricata</i> (Heliconiaceae)
<i>Agraulis vanillae</i> (Nymphalinae) (3) CU:LS93AGV	W(Y)	<i>Passiflora</i> sp. (Passifloraceae)*
<i>Aeria eurimedia agna</i> (Ithomiinae) (4, 3, 3) CU:LS93AEA	A(N),B(N),W(Y)	(Apocynaceae)
<i>Morpho peleides limpida</i> (Morphinae) (5, 3, 4)	A(Y),B(Y),W(Y) NASTY	<i>Lonchocarpus oliganthus</i> (Leguminosae)*
<i>Adelpha fessonia</i> (Nymphalinae) (5, 3, 4) CU:LS93ADF	A(N),B(N),W(N) TASTY	<i>Randia armata</i> (Rubiaceae)*
<i>Marpesia petreus</i> (Nymphalinae) (5, 3, 3)	A(N),B(Y),W(Y)	(Anacardiaceae)
<i>Papilio cresophantes</i> (Papilionidae) (5, 3, 3) CU:LS93PAC	A(Y),B(Y),W(Y) NASTY	<i>Citrus limon</i> (Rutaceae)*
<i>Papilio anchisiades idaeus</i> (Papilionidae) (5, 3, 5)	NASTY	A(Y),B(Y),W(Y) <i>Citrus limon</i> (Rutaceae)*

CU:LS93PAP

Anteos clorinde (Pieridae) (5, 3, 3) A(N),B(N),W(N) NEUTRAL *Cassia fruticosa* (Leguminosae)*

CU:LS93ANT

Pyralidae (3, 3) B(Y),W(Y) *Bombacopsus quinatum* (Bombacaceae)

CU:PV93FNT

Saturniidae (3, 3) A(Y),W(Y) *Ceiba pentandra* (Bombacaceae)

CU:PV93013

Manduca sexta (Sphingidae) (5, 3, 3) A(Y),B(Y),W(Y) *Solanum* sp. (Solanaceae)

CU:LS93THW

Sphingidae (3) W(Y) *Piper* sp. (Piperaceae)

CU:PV93003

^aThose species that I could not identify past the family level are identified by the family. Sample sizes (number of caterpillars offered to ants, bugs, and wasps respectively) are indicated in parentheses underneath each species. Voucher specimen codes are included under those species for which I had appropriate replicates to keep a voucher. CU = University of Colorado Entomology Museum, Boulder; IN = Instituto Nacional de Biodiversidad, Costa Rica.

^bNot all caterpillar species were available for all predators; this column indicates to which predators each species was offered. A = ants, B = bugs, W = wasps. The predators' average responses (rejection) are indicated in parentheses after the letter indicating the predator. Y = Rejected more than half of the time, N = Not rejected more than half of the time. If extract data were available, the level of the "chemistry" category is also included in this column.

^cCaterpillars were reared on host plants on which they were found. Although there are other reported hosts for some species, none of them are known to feed on plants in more than 2 families. Asterisks (*) indicate those species for which voucher specimens are available at the University of Colorado Herbarium, Boulder.

Experiments with wasps

I offered caterpillars to wasps throughout the day and at 5 different sites. Three of the sites were areas where wasps were frequently found foraging along the side of a dirt road within and just outside of Lomas Barbudal. The other two sites were two different trees in Palo Verde which contained many wasp nests. Caterpillars offered to wasps foraging along the road were placed on the ground amidst vegetation where the wasps were foraging. Caterpillars offered to wasps in the trees were placed in small, clear plastic cups which were suspended with string from branches of the trees. If the caterpillars crawled out of the cups before being encountered by a wasp, they were placed back into the cup. Depending on availability, I offered 3–5 individuals of each caterpillar species (32 species) to the wasps (see Table 1), and each site received only 1 individual of each species. Each caterpillar was independently offered at a different spot along the road or in the tree, and the order of presentation was haphazard (often depending on when caterpillars were found). No site received more than 4 caterpillars in a single day.

I observed all caterpillar-wasp interactions until either most of an entire caterpillar was carried away by wasps or at least 3 wasps had encountered and rejected it. Rejections consisted of a wasp approaching the caterpillar and either touching it or coming within about 20 cm without attacking; 20 cm is a distance which is well within the field of vision of wasps (Spradbery 1973).

Experiments with bugs

Fourteen assassin bugs were collected at the 3 experimental sites and were kept in 17 cm by 13 cm by 7 cm plastic boxes containing paper towels and twigs. When not being used for experiments, twice a week the bugs were fed a drab, glabrous noctuid caterpillar (voucher: PV93NOT at the University of Colorado Museum, Boulder) which was abundant and which was palatable to various wasps, ants and mantids (*personal observations*).

Three to five replicates of 24 species of caterpillars were offered to the bugs (Table 1), and no bug received more than 6 total caterpillars or more than 1 replicate per species. Caterpillars were placed in the plastic boxes containing bugs and were left with the bugs for 24 hours. The bugs would either attack the caterpillar within an hour or they would ignore it, which constituted a “rejection.”

Experiments with ants

Data were used from caterpillars offered to *P. clavata* in a larger study (Dyer 1995). In that study, caterpillars were offered to 5 ant colonies, and the numbers of ants (within a colony) rejecting individual caterpillars were classified into the categories “no rejections” (0 ants rejecting the caterpillar), “some rejections” (fewer than 7 ants rejecting the caterpillar), and “completely rejected” (8 or more ants rejecting the caterpillar). Because the wasps and bugs either rejected or accepted prey as opposed to having inconsistent responses within a colony (hence, “some rejections”), I reclassified the ant rejection category to make it comparable to data for the bugs and wasps. Caterpillars receiving fewer than 5 rejections were considered to be “not rejected,” while caterpillars receiving 5 or more rejections were considered to be “rejected.” This was an arbitrary categorization, but it effectively split the “some rejections” category in half and made the *P. clavata* responses comparable to data for the bugs and wasps.

Statistical analyses

I scored each caterpillar species for the following categorical variables: a) caterpillar diet breadth — generalist or specialist; b) caterpillar coloration — brightly colored, visually cryptic, or other; c) caterpillar morphology — spines, hairs, or glabrous; d) caterpillar size — small, medium, or large; and e) caterpillar chemistry — palatable extract or deterrent extract.

For the diet breadth variable, I used a taxonomic definition of specialization. Caterpillars known to feed on fewer than 2 families of plants (according to Tietz 1972, Janzen 1984, DeVries 1987, Marquis 1991, and personal communication with various naturalists), or caterpillars of unknown diet breadth that were found feeding on only 1 plant species, were classified as “specialists” (22 species; 9 of which had unknown diet breadths). Since most herbivores at La Selva are monophagous or

oligophagous (Marquis and Braker 1994), I assumed that it was unlikely that unknown caterpillars would be erroneously classified as specialists. Caterpillars found feeding on plants in greater than 3 families were classified as “generalists” (12 species; most fed on plants in greater than 6 families).

The coloration and morphology variables were based on visual inspection of the caterpillars. “Spiny” caterpillars had sclerotized spines at least 2 mm long. Caterpillars with hairs or with hairs and spines were rated as “hairy” only if more than 50% of their cuticle was covered with secondary setae that were at least 5 mm long. “Glabrous” caterpillars had no hairs or spines.

The size statistic was based on the weight (in mg) of a caterpillar just before it was offered to a predator. Levels of size categories were: “small” (weight \leq 200 mg), “medium” (200 mg < weight \leq 1000 mg), and “large” (weight > 1000 mg). The size categories were pooled in the preceding manner based on examination of a frequency histogram of all the weights.

For the chemistry variable I used results from a bioassay done with crude caterpillar extracts offered to *P. clavata* (Dyer 1995). Data for this variable were only available for 8 caterpillar species (see Table 1). The levels of this variable were: “nasty” (caterpillars with deterrent extracts), “tasty” (caterpillars with extracts which attracted ants), and “neutral” (caterpillars with neutral extracts). This variable was included to examine the defensive efficacy (against all three predators) of chemicals found in caterpillars without the confounding effects of morphological and behavioral features.

I used logit analyses to study the relative importance of these caterpillar characteristics as determinants of predator rejections (see Christensen 1990 for a thorough discussion of logit models). All of the caterpillar characteristics which I examined may act as important anti-predatory traits (reviewed by Edmunds 1974, DeVries 1987, Evans and Schmidt 1990). For all logit models I used the maximum likelihood method for parameter estimation of linear models and Chi-square statistics for hypothesis testing (see SAS 1990). All of the models were nonhierarchical because I either obtained significant highest-order associations in the saturated models, or because I had specific hypotheses that I wanted to test. Since the models were nonhierarchical, I used the Newton-Raphson algorithm for parameter estimation and model testing (SAS 1990). I assigned values of 1×10^{-20} to cells that contained “sampling zeroes” (sensu Bishop et al. 1975), while cells that contained “structural zeroes” (sensu Bishop et al. 1975) were automatically deleted (see SAS 1990).

To avoid running a large model containing many cells with zeroes or small values, it was necessary to use more than one model. I chose variables for models that addressed specific questions which I wanted to ask with my experiments; in addition, examination of frequency tables for all combinations of variables helped form decisions for appropriate models (see Tabachnick and Fidell 1989). Variables that were not significantly associated with rejection in 2-dimensional frequency tables (using a conservative criterion of $P < 0.001$ because of the large number of tests) were not included in the models.

I ran two logit models which included data from all the predators. Model 1 addressed these questions: 1) Are caterpillars’ levels of rejections dependent on the type of predator?, 2) Are the presence of unpalatable chemicals in caterpillars likely

Table 2. Summary of two-dimensional tables with predictors versus rejections.

Predator	Predictor	χ^2	DF	P
ALL (n=287)	Chemistry	84.5	2	0.000
	Diet Breadth	29.6	1	0.000
	Predator	34.9	2	0.000
	Size	31.6	2	0.000
	Morphology	25.3	2	0.000
	Coloration	10.0	2	0.007
ANTS (n=103)	Chemistry	36.2	2	0.000
	Diet Breadth	17.8	1	0.000
	Size	1.9	2	0.386
	Morphology	11.3	2	0.003
	Coloration	0.97	2	0.617
BUGS (n=76)	Chemistry	24.0	2	0.000
	Diet Breadth	4.5	1	0.035
	Size	28.7	2	0.000
	Morphology	29.5	2	0.000
	Coloration	2.5	2	0.297
WASPS (n=108)	Chemistry	25.4	2	0.000
	Diet Breadth	4.5	1	0.033
	Size	24.6	2	0.000
	Morphology	0.24	2	0.885
	Coloration	16.7	2	0.000

to make predators reject them more frequently?, 3) Which predictor of rejection (chemistry or predator) is more reliable?, and 4) Are there interactions between rejections, type of predator, and extract palatability? Model 2 addressed these questions: 1) Are specialists rejected more frequently than generalists against a variety of predators?, 2) Is diet breadth a better predictor of rejection than type of predator?, and 3) Are there interactions between rejections, diet breadth, and type of predator?

For the wasps and bugs I also ran a logit model for data specific to each predator. Each model asked questions about associations between caterpillar characteristics and rejections by the predator. The bug model included morphology and size as predictors. The wasp model included coloration and size as predictors. Models examining predictors of ant rejections are reported elsewhere (Dyer 1995).

RESULTS

I used results from 108 individuals of 32 caterpillar species offered to the wasps and results from 76 individuals of 24 caterpillar species offered to the bugs. For the ant data, I only used data for caterpillar species that were also offered to either the wasps or bugs; this subset of the data included 103 individuals of 23 caterpillar species. χ^2 values from the 2-dimensional tables of defenses and rejections are summarized in Table 2.

Table 3. Summary of log-linear models.

Model ^a	Likelihood ratio probability ^b
Models using all predators	
1. Chemistry (5.38 ***)	0.589
2. Diet Breadth (-5.67 ***) Predator (5.56 ***)	0.905
Model for bugs	
3. Size (3.44 ***) Morphology (3.0 *)	0.594
Model for wasps	
4. Size by Coloration (-2.85 ***) Coloration (2.56 *)	0.290

^aThe variables shown are significant predictors of rejections from the most parsimonious model that fit the data. Predictor variables were ranked by standardized parameter estimates, which are given in parentheses along with asterisks to indicate significance of the estimate (* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.005$).

^bThe 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.

For the combined predators, Model 1 revealed a significant ($\chi^2 = 36.0$, $DF = 2$, $P < 0.0001$) chemistry effect on rejections. Chemistry was a more reliable predictor than type of predator, which was not significant ($\chi^2 = 0.41$, $DF = 2$, $P = 0.814$; Table 3). The predators rarely rejected caterpillars with neutral and tasty extracts, while 98% of caterpillars with nasty extracts were rejected (Fig. 1). There were no significant interactions between chemistry and predators—all predators were deterred by the caterpillars with observed chemical defenses.

Model 2 for the combined predators revealed a significant association between predator and rejection ($\chi^2 = 34.68$, $DF = 2$, $P < 0.0001$) and an association between diet breadth and rejection ($\chi^2 = 28.86$, $DF = 1$, $P < 0.0001$). Predator was a more reliable predictor than diet breadth (Table 3) and there were no interactions between the two predictors. Ants were the most likely to eat caterpillars, and the wasps were the most cautious (Fig. 2). The association between diet breadth and rejection reflects the fact that specialists were rejected more frequently than generalists (Fig. 3).

The logit model for the bugs revealed a significant association between size and rejection ($\chi^2 = 11.95$, $DF = 2$, $P = 0.0025$) and a significant association between morphology and rejection ($\chi^2 = 8.78$, $DF = 2$, $P = 0.012$). Size was a more reliable predictor than morphology (Table 3) and there were no interactions between the two predictors. As the mean size of caterpillars increased, the levels of rejection also increased (Fig. 4). Caterpillars with hairs were rejected more frequently than those with other morphologies—particularly caterpillars with spines which were never rejected (Fig. 5).

The logit model for the wasps revealed a significant interaction between size, coloration, and rejection ($\chi^2 = 17.43$, DF = 2, P = 0.0002) and a significant association between coloration and rejection ($\chi^2 = 8.05$, DF = 2, P = 0.0179). The interaction was a more reliable predictor than coloration (Table 3). Brightly colored caterpillars of all sizes were better protected than caterpillars with other colorations (Fig. 6); however, if the caterpillars were large, their coloration was not important (100% of the large caterpillars were rejected by the wasps — Fig. 4).

DISCUSSION

To some extent, the predators evaded characterization by generalizations such as, “hairs are a good defense against invertebrate predators.” Predators varied in their propensities to reject, and each predator was influenced by a different assemblage of caterpillar defenses. However, there were results which can be generalized for a variety of invertebrate predators (based on the wide behavioral and taxonomic differences between the three predators) and results that can be generalized for specific predatory guilds represented in this study.

The best generalizations about caterpillar defenses against invertebrate predators come from examining the results of the models that included all predators. Chemistry and diet breadth were both important predictors of rejections when considering the suite of predators and when including the variation in predators' inclination to reject prey. Specialists and caterpillars with deterrent extracts were rejected more frequently than other caterpillars by the predators, and since these predators represent very different guilds, it may be reasonable to conclude that these qualities would protect caterpillars against many different types of invertebrate predators. Examples of the guilds that were covered by these predators include: solitary predators (*P. instabilis* and *A. pictipes*), recruiting predators (*P. clavata*), sit-and-wait predators (*A. pictipes*), flying predators (*P. instabilis*), visually oriented predators (*P. instabilis* and *A. pictipes*), chemically oriented predators (*P. clavata*), sucking predators (*A. pictipes*), chewing predators (*P. instabilis*), stinging predators (*P. clavata*), nocturnal predators (*P. clavata*), and diurnal predators (*P. instabilis* and *A. pictipes*). One caveat to broad interpretation of these results is that these predators are not necessarily representative of their foraging guilds; *P. clavata*, for example, is much more likely to indiscriminately accept prey than other members of the tribe Ectatommini (Dyer and Folgarait, unpub. data). Thus, the results from this study do not indicate that prey protected against these three predators should be equally protected against any representatives of their respective foraging guilds, rather they illustrate the effectiveness of narrow diet breadth and defensive chemistry against very different types of predators.

The importance of diet breadth and chemistry as predictors of rejection for this group of predators are also consistent with another generalization: both predation and plant chemistry could affect herbivores' diet breadth. A scenario by which this could happen is as follows: 1) An herbivore overcomes

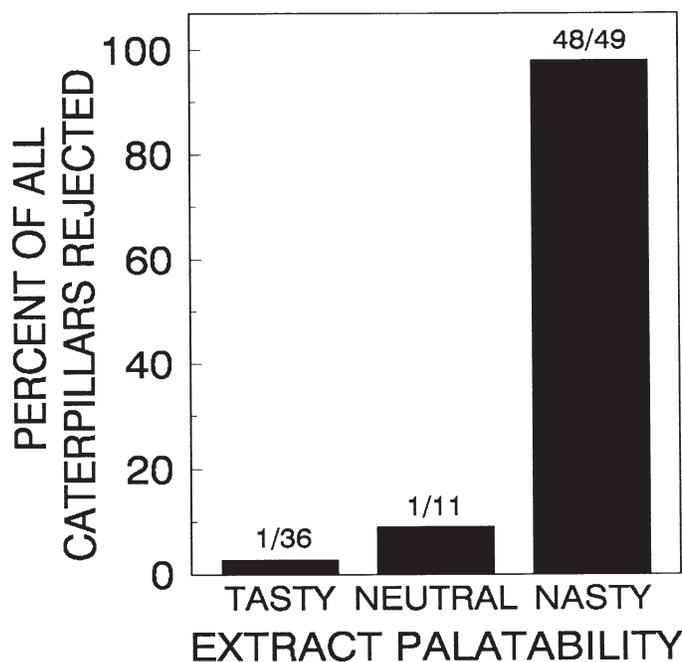


Fig. 1. The association between palatability of caterpillars' chemical extracts and percentage of rejections by all the predators. The y-axis represents the percentage of individual caterpillars ($n = 96$ individuals; 8 species) with specific palatabilities that were rejected by all 3 predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular palatability) is in the denominator.

a specific plant defense and in the process loses access to other plants because of trade-offs in physiological abilities to utilize plants with different chemical compounds (Ehrlich and Raven 1964). 2) As the herbivore becomes more specialized as a result of step 1, it also sequesters secondary compounds either casually (because it is eating fewer plants; Jones et al. 1989) or because of specific physiological adaptations (Bowers 1990). 3) Specialization is further maintained by predators because specialists are better chemically protected than more generalized herbivores (Dyer 1995). Steps 2 and 3 are consistent with results from these experiments because herbivores with specialized diets were better protected against a group of predators, chemistry was an important component of their defense, and there is evidence that some of the species used in my experiments sequester noxious compounds from their host plants (Dyer 1995).

The results unique to specific predators reveal prey preferences that could be common responses for their respective guilds. Size, for example, was important for the two solitary predators (the bugs and wasps) but not for the ants which could recruit other ants and easily subdue larger prey items. It is

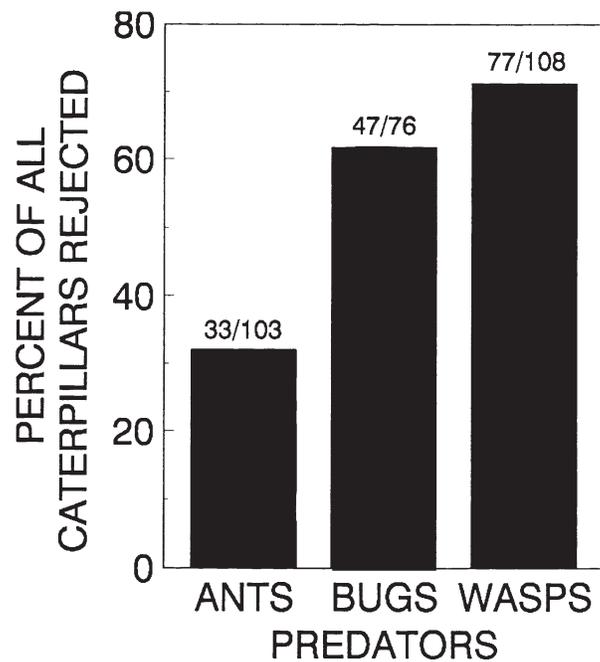


Fig. 2. Percentages of all caterpillars rejected by each predator. The *y*-axis represents the percentage of individual caterpillars ($n = 287$ individuals; 34 species) rejected by each of the 3 predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (to that particular predator) is in the denominator.

generally assumed that prey size is an important limitation for invertebrate predators (Cohen et al. 1993, Reavey 1993), but this assumption may vary with the degree of predators' social cooperation. The differences between the solitary (wasps and bugs) and recruiting (ants) foragers were actually quite dramatic; the bugs and wasps barely touched large prey items (many of which were generalists which probably were not otherwise defended very well), while the ants attacked them as voraciously as caterpillars of any other size. The size categories were not ambiguous, in that all of the predators would be in the same category as the "small" prey, since their mass varies from 50–200 mg, while the "large" caterpillars had masses over 9 g.

Hairs were an important deterrent for the bugs which have mouthparts specialized for sucking. Hairs are probably a significant deterrent for most hemipteran predators because they prevent insertion of a bug's proboscis (pers. obs., also see Bowers 1993). Alternatively, hairs may function by warning the caterpillar of a predator's advance before it actually has a chance to catch the caterpillar (Tautz and Markl 1978). Indeed, many hairy caterpillars (particularly arctiids) are fast, and an "early warning system" such as hairs extending far from the body may make it difficult for sit-and-

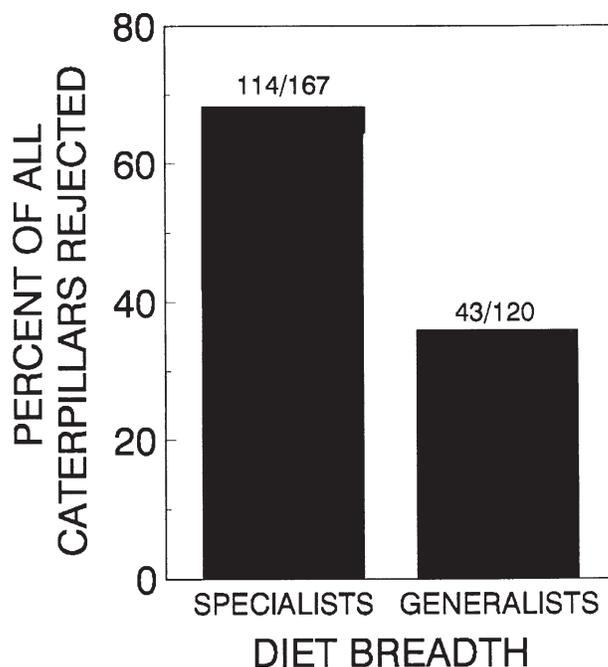


Fig. 3. The association between diet breadth and percentage of rejections by all the predators. The y-axis represents the percentage of all generalist or specialist caterpillars ($n = 287$ individuals; 34 species) that were rejected by the 3 predators (ants, bugs, and wasps). Although not all caterpillar species were offered to all predators, the predators are treated as a group. The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular diet breadth) is in the denominator.

wait predators to successfully attack them. It is not as clear, however, why the hairs were effective against the ants but not against the wasps. One explanation could be that wasps, which can fly and are more maneuverable, are able to pluck hairs (without the prey escaping) from caterpillars more effectively than ants (Bowers 1993). I have observed wasps and ants plucking hairs from prey with varying degrees of success.

Coloration was important for wasps, but it was not important for ants which are often chemically oriented. Wasps were deterred by brightly colored prey which supports general theories about aposematism (see Cott 1940). Bugs, on the other hand, which are also visually oriented (Johnson 1983), were not deterred by brightly colored prey. A correlation between palatability and coloration is widely assumed to exist in the animal kingdom (*e.g.* Cott 1940, Edmunds 1974, Harborne 1989), and coloration has even been used as an indicator of palatability (Sillen-Tullberg 1988). It is therefore noteworthy that for two of the three invertebrate predators used in my experiments, bright coloration is not correlated with unpalatability.

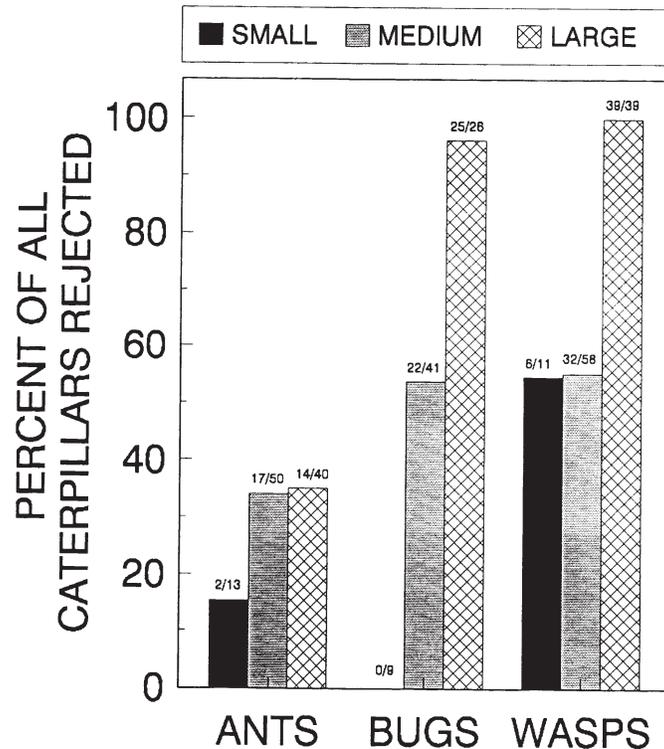


Fig. 4. The association between size and percentage of rejections by the 3 different predators. The y-axis represents the percentage of all caterpillars ($n = 287$ individuals; 34 species) of each particular size that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (of that particular size) is in the denominator.

As with most studies of community patterns, there were several major limitations to this study which prevent me from concluding with grand generalizations. With regard to questions about the relative effectiveness of various caterpillar defenses, I had to ignore many important defenses such as symbioses with ants (e.g., DeVries 1991), aggregation (Bowers 1993), and other behavioral defenses (Edmunds 1974, DeVries 1987, 1994, Evans and Schmidt 1990). It is therefore impossible to conclude that any defense examined in this study is the “most important.” Second, the relatively small taxonomic sample size (number of individual species representing each family) of this study makes it impossible to determine if a characteristic typically associated with a specific taxon is an effective defense or if some correlated trait of that taxon is responsible. For example, comparisons of hairy and glabrous caterpillars could just be comparisons of traits correlated with hairy and glabrous families (e.g., Arctiidae vs. Pyralidae), because not all the families used in my experiments included all of the possible mor-

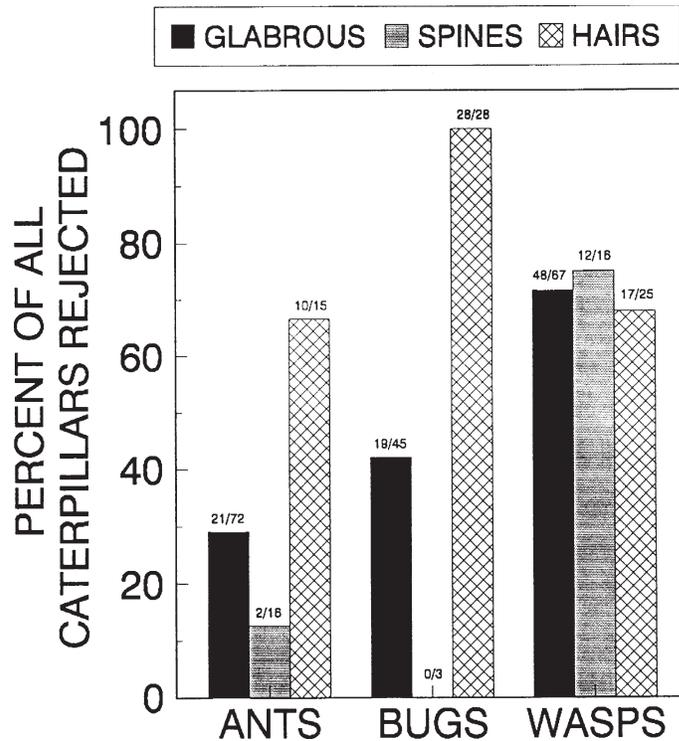


Fig. 5. The association between morphology and percentage of rejections by the 3 different predators. The y axis represents the percentage of all caterpillars ($n = 287$ individuals; 34 species) of each particular morphology that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular morphology) is in the denominator.

phologies. I addressed this problem to some extent in another study with larger sample sizes (Dyer 1995), and found that defenses were effective despite taxonomic affinity.

With regard to questions about the evolution of specialization, multi-species comparisons, such as this study, are not particularly useful in terms of providing evidence for natural selection on particular characteristics, since protection from natural enemies could be a consequence rather than a cause of specialization. Actual tests of predation as a selective pressure on diet breadth would require studying intraspecific variation (see Futuyma and Moreno 1988).

Despite these limitations, a few reasonable generalizations can be made which address my original questions. 1) Predators from different guilds are deterred by different defenses, but there are some antipredator mechanisms that may function against many different guilds. 2) Narrow diet breadth and the utilization of noxious chemicals are significantly associated with rejec-

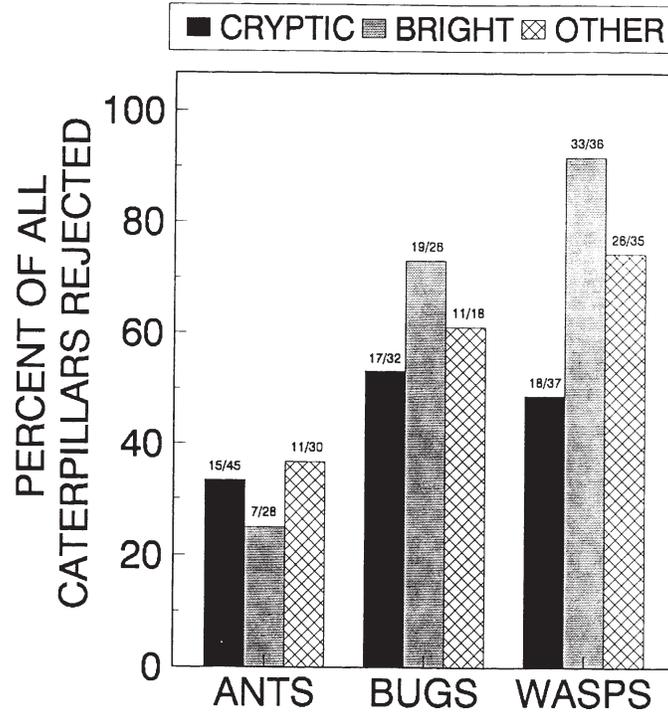


Fig. 6. The association between coloration and percentage of rejections by the 3 different predators. The y-axis represents the percentage of all caterpillars ($n = 287$ individuals; 34 species) of each particular morphology that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular coloration) is in the denominator.

tion by a suite of predators. 3) Generalist predators are probably important in the maintenance of narrow diet breadth in caterpillars.

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