Potential and Realized Feeding Niches of Neotropical Hispine Beetles (Chrysomelidae: Cassidinae, Cephaloleiini)

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ABSTRACT Accurate descriptions of feeding habits are essential to understanding the evolution of dietary preferences and the high levels of diversification within the Chrysomelidae. Both primary observations and summaries suggest that the cassidine beetle tribe, Cephaloleiini, is a species-rich group of feeding specialists on monocot hosts. However, accurate host ranges are poorly defined for most hispine beetle species. To better document occurrence and feeding, we censused the Cephaloleiini associated with rolled leaves of five species of Marantaceae and six species of Heliconiaceae (Zingiberales) in lowland Central Panama. Additionally, we conducted choice and no-choice feeding tests on a subset of both the plants and beetles encountered in the censuses. Both types of data suggest that most species of Cephaloleiini feed on a greater variety of related plant species than has previously been reported.

KEY WORDS Hispinae, Cassidinae, Zingiberales, feeding niches, trophic selection

Summaries of tropical insect feeding based on field observations generally conclude that most species are restricted to a narrow set of host plants (Erwin 1982, Barone 1998, Odegaard 2000). However, more recently, Novotny et al. (2002) have reported that many tropical insects are less specialized than was previously thought. There are several reasons to believe that field observations of insect feeding associations, which reflect the realized feeding niche (Futuyma and Moreno 1988), could be biased toward specialization. First, the geographic range of a particular insect species can be quite broad, and within this range, the composition of plant communities may change dramatically. As a consequence, the list of host plants an insect species actually uses across its entire range may not be adequately sampled by regionally restricted field observation, leading to an underestimation of the actual number of host plants used by a particular insect. This will be a more serious bias for species with specific associations that occur in only certain regions and not others. Second, factors such as plant habitat, plant structure, and predator and parasitoid pressures may constrain diet to a subset of plant species on which the insect is capable of feeding and developing successfully (Fox and Morrow 1981). Third, insects visit plants not only to feed, but also to rest or find mates, and if such activities are not separated from feeding, they may tend to skew host plant lists. For all these reasons, simple field observations and records may not give an accurate indication of the diet range of an herbivorous insect and mass records are essential to increase the probability of obtaining the most complete description of host plant–insects associations.

In the unrealistic case of a completely exhaustive and nonbiased list of plant–phytophagous associations, we would observe what is called the realized feeding niche (Futuyma and Moreno 1988). Thus, the results of choice and no-choice tests by presenting potential food items may provide a method to estimate feeding flexibility of insects without the biases inherent in the field observations. Moreover, because the insects are not exposed to extrinsic factors that can narrow their choice, their feeding response can thus be associated to the fundamental feeding niche, which is more the result of genetic properties of the species (Futuyma and Moreno 1988). Nonbiased dietary information and comparison of realized and fundamental feeding niches are essential to accurately interpret the nature of plant–herbivore evolutionary relationships.

Our knowledge of trophic selection in the "rolled-leaf" hispine beetles (also called "hispoid Cassidinae"; principally the tribe, Cephaloleiini), is based on field observations and collecting notes made by investigators with differing priorities and access to well identified botanical and entomological collections (Strong 1977, Maes and Staines 1991, Windsor et al. 1992, Staines 1996, 2004, Flowers and Janzen 1997, Hespenheide and Dang 1999, McKenna and Farrell 2005). Most of these studies conclude that species of hispoid Cassidinae feed within a single family of host plants and that nearly all used plant families fall within the

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Monocotyledonae (Jolivet 1997, Jolivet and Hawkeswood 1995). Furthermore, the list of hispine species used by McKenna and Farrell (2005) indicates that the majority of Cephaloleiini are associates of Zingiberales, whereas a smaller number of species at the base of the phylogeny is associated with Arecaceae. The extent to which Cephaloleiini species feed on related plant species within or even among those families is less well documented.

Our aim was to better define the range of host plants accepted by cassidine leaf beetle species in the tribe Cephaloleiini, by recording their presence on monocot hosts, and by conducting feeding tests in the laboratory. The tribe Cephaloleiini contains >380 Neotropical species placed in 18 genera, which are best differentiated from other Cassidinae by their flat "onisciform" larval stage (Seeno and Wilcox 1982, Jolivet and Hawkeswood 1995, Staines 2002). The majority are considered "rolled-leaf hispines" and are found in tightly rolled apical leaves of monocots. Adults and juvenile forms of some taxa are principally found in leaf axils of palms (e.g., *Cephaloleia lata* on *Chamaedorea* spp.) or are surface feeders on the fully expanded leaves of some *Calathea* species (Marantaceae) and the newest expanded, nongreened leaves of several palm species (e.g., *Demotispa* sp. on *Oenocarpus mapori*). The host plants of many Cephaloleiini species remain poorly documented because they have only been identified to genus or family, and fertile vouchers have rarely been deposited (Flowers and Janzen 1997).

Materials and Methods

Field Sampling

Observations were made within forests bordering the Panama Canal area (Fig. 1) including a site near Gamboa (Pipeline Road) in Parque Natural Soberania (9°7′ N, 79°43′ W), along the trail system of the field station of the Smithsonian Tropical Research Institute (STRI) on Barro Colorado Island (BCI; 9°9′ N, 79°51′W) and within Parque Nacional San Lorenzo (9°17′ N, 79°58′ W). Sampling was performed during December 2001, from May to September 2002, from March to June 2003, and from August to September 2003.

Our study is based on observations recorded from Heliconiaceae and Marantaceae (Zingiberales) families containing 8 and 11 species, respectively, in the lowland areas of the Isthmus (Croat 1978). We surveyed hispoid Cassidinae on six Heliconiaceae and five Marantaceae species, chosen because of their greater abundance in the study sites (Croat 1978, D.W. and C.M., unpublished data) and because they were known to have a diversified hispoid Cassidinae fauna (Strong 1977, Staines 2004). Native to the tropical regions (Croat 1978), the Marantaceae and Heliconiaceae are characterized by large and colorful bracts and by young leaves rolled into long tubes opening after periods from a few days to a few weeks into large mature leaves with transverse venation and long pet-
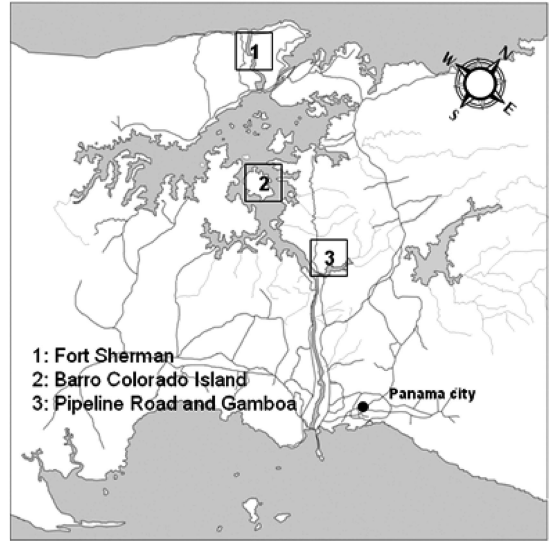

Fig. 1. Sampling sites of hispine beetles in areas bordering the Panama Canal area.

ioles (Williams and Harborne 1977, Berry and Kress 1991). The scroll-like immature leaves are the typical habitat for numerous species of "rolled-leaf" Cassidinae (Strong 1977, Jolivet 1997, McKenna and Farrell 2005). These two host plant families occur in a range of habitats from old forest to highly disturbed areas (Croat 1978, Berry and Kress 1991). All of the host plant species are native to Panama (Croat 1978), but most occur elsewhere in Central and South America as well.

For each individual plant that was surveyed, a single mature or rolled leaf was carefully inspected, the number and species of adult hispine beetles were recorded, and the beetles were returned to the plant. Beetles were collected without replacement only when their identification was in doubt. Plants occurring along trails were surveyed inside young (60–120 yr old) and old (400 yr old) forest on BCI and in mainland forests (Parque Soberania and Fort Sherman). Hispine species were identified based on the plates in the Biologia Centrali-Americana (Baly 1885); descriptions and key given by Staines (1996 and 2002) and by comparison with identified specimens in the STRI insect collection.

During the sampling periods, sites were partially visited once a week. Because leaf-rolls had to be destructively removed from plants, each individual plant marked with flagging tape was surveyed only once in a field season to minimize disturbance to beetle assemblages. The scroll-like immature leaves (rolled leaves) were only included in the study if they were closed at the bottom (watertight), thereby maintaining a high degree of humidity, which seems to be an important factor for "rolled-leaf" hispoid Cassidinae communities (Strong 1977).

Feeding Tests

The seven most frequent Cephaloleiini species in this study were *Cephaloleia belti* Baly, *C. sallei* Baly, *C. dilaticollis* Baly, *C. erichsonii* Baly, *C. instabilis* Baly, *C. pretiosa* Baly, and *Aslamidium semicircularum* Borowiec. Larvae of six of these species fed within the unexpanded leaves of Zingiberales, mainly on Heliconiaceae and Marantaceae (Strong 1977). The seventh species, *Aslamidium semicircularum*, an open leaf scraper, fed on open mature leaves of various species of Marantaceae. Eight plant species were selected for the feeding trials, each belonging to the Heliconiaceae (*Heliconia latispatha* Bentham, *H. mariae* Hooker, *H. vaginalis* Bentham, *H. irrasa* R.R. Smith, *H. catheta* R.R. Smith) or the Marantaceae (*Calathea latifolia* Klotzsch, *C. inocephala* H. Kenn. and Nicolson, and *Ischnosiphon pruinosus* Petersen). These species are known to shelter some species of Cephaloleiini (Strong 1977) and were the most abundant species of Marantaceae and Heliconiaceae in the study area.

Adult insects and the fresh plant leaves used during feeding trials were collected daily near the town of Gamboa. Individuals were maintained in the laboratory, at 24°C, on the host plant on which they were initially collected within 3-liter plastic bags. Adult beetles were placed in a petri dish containing a moistened filter paper and two circular leaf discs (one facing upward and the other downward) of each of the plant species in the choice test. A cleaned, 12-mm-diameter cork borer was used to punch disks from the outer margin of the internal side of rolled leaves or from mature leaves, according to hispine species feeding habits. For no-choice tests, the same procedures were followed but with only one plant species per petri dish (two disks from open leaves and two from rolled leaves, one disk facing upward, the other downward). After 24 h without food, beetles were introduced and allowed to feed for 24 h. After the tests, the area (mm^2) of the disk consumed was quantified using Scion Image software after picture transformation (Adobe Photoshop 5.0 LE) in binary color. Consumption was measured by calculating the eaten area of leaf disk such as suggested by Peterson and Renaud (1989), which minimizes biases caused by autogenic changes during the test.

A qualitative feeding response, accepted or rejected, was scored for each disk. When only bitten once, disks were considered rejected because this slight damage results from probing or tasting behavior, which is the first step of the trophic-selection process (Schoonhoven 1991). Each test was replicated at least 10 times with naïve beetles.

Statistical Analysis

Quantitative Analyses. Statistical analyses were performed using SAS Enterprise Guide v 8.02.

Mean areas consumed by each hispine species were tested for homogeneity of variance with Levene's test before performing analysis of variance (ANOVA).

Welch's correction was used in cases of non homogeneity.

Because of the design of choice tests, the factor *hispine individual* must be taken into account. Because individual physiological state could influence the feeding response differentially between replications, the factor *hispine individual* was crossed to *consumed plant species* thus making a two-way ANOVA. Although there was only one replicate for each level of the factor *hispine individual,* this has little impact because we were only interested in testing the significance of the *consumed plant species* factor.

No-choice tests were analyzed by one-way ANOVA, with *consumed plant species* as fixed factors.

Qualitative Analyses. χ^2 tests (Yates correction for 1 df) were used in qualitative analyses where responses were limited to plant accepted or plant rejected.

Voucher specimens were deposited in the insect collection of the Unité d'Écologie et de Biogéographie of the Université catholique de Louvain (Belgium) and in the voucher collections of the Smithsonian Tropical Research Institute in Panama.

Results

Field Sampling

A total of 2,045 individuals belonging to 19 hispine species were found on 2,399 surveyed plants (Table 1). The more abundant hispine species were *Cephaloleia belti, Aslamidium semicircularum, C. erichsonii,* and *C. sallei. C. belti* and *C. erichsonii* were each found on 9 of the 11 plants species in the study, whereas *C. dilaticollis, C. pretiosa,* and *C. instabilis* were found on 4 plant species. *A. semicircularum* and *C. dilaticollis* were mainly present on species of Marantaceae, *C. pretiosa,* and *C. instabilis* on Heliconiaceae and *C. erichsonii, C. belti,* and *C. sallei* on both families, but not always on all species of each plant family.

Feeding Trials

Choice Tests. Definite feeding responses (more than one bite) were recorded for all beetle species except *A.semicircularum,* which responded weakly to all plant species. The maximum percentage of individuals of a particular species feeding on a host plant species was 73% (*C. instabilis* on *H. latispatha*) during choice tests.

The average area of leaf disks eaten did not vary significantly among plant species for six of the seven beetle species tested (Table 2). Only *C. instabilis* consumed significantly different areas of leaf ($F = 3.36$; df = 5,50; $P = 0.01$), preferring the leaf disks of *H. latispatha* and *H. irrasa* above the other six plant species. Although heterogeneity in *C. pretiosa* feeding responses was not significant, average acceptance of Heliconiaceae was higher than Marantaceae ($\chi^2 = 14.83$; $P < 0.0001$). Moreover, Marantaceae were preferred by *C. dilaticollis,* which did not feed on Heliconiaceae. There was no significant difference in the

Table 1. Field sampling results of hispine beetles on plants of Marantaceae and Heliconiaceae

Hispoid Cassidinae species	Plant species	Number of inspected plants[a]	Number of hispine adults found
Aslamidium semicircularum Borowiec	*Calathea inocephala*	726	68
	C. insignis	182	149
	C. latifolia	286	22
	C. lutea	33	101
	Ischnosiphon pruinosus	225	75
Cephaloleia belti Baly	*C. latifolia*	123	42
	C. lutea	3	2
	I. pruinosus	22	2
	Heliconia catheta	37	121
	H. irrasa	27	5
	H. latispatha	103	289
	H. mariae	74	85
	H. vaginalis	25	2
	H. wagneriana	12	34
C. dilaticollis Baly	*C. inocephala*	105	103
	C. insignis	5	4
	C. lutea	3	2
	I. pruinosus	22	1
C. erichsonii Baly	*C. inocephala*	105	220
	C. insignis	5	1
	C. latifolia	123	4
	C. lutea	3	3
C. erichsonii Baly	*H. catheta*	37	1
	H. latispatha	103	5
	H. mariae	74	70
	H. vaginalis	25	2
	H. wagneriana	12	1
	C. latifolia	123	5
C. instabilis Baly	*H. catheta*	37	8
	H. latispatha	103	44
	H. mariae	74	2
C. pretiosa Baly	*H. catheta*	37	26
	H. latispatha	103	53
	H. mariae	74	12
	H. wagneriana	12	9
C. sallei Baly	*C. inocephala*	105	1
	C. latifolia	123	200
	C. lutea	3	4
	I. pruinosus	22	7
	H. catheta	37	2
	H. latispatha	103	12
	H. mariae	74	1
	H. vaginalis	25	1

[a] The no. plant species observed corresponds to the no. of inspected plants with rolled leaves for rolled leaf hispines and to the no. plants with only open leaves for *A. semicircularum,* which is an open leaf scraper.

average acceptance of *C. belti, C. sallei, C. instabilis,* and *C. erichsonii* on Marantaceae and Heliconiaceae.

No-Choice Tests. The performance of three hispine species was evaluated in no-choice tests, *A. semicircularum, C. belti,* and *C. sallei,* and each accepted a slightly broader array of food items than in choice tests (Table 3). *A. semicircularum* included *Ischnosiphon pruinosus* in its diet under no-choice conditions. Similarly, *C. sallei* fed on *H. catheta* and *H. irrasa,* and *C. belti* on *I. pruinosus* only during no-choice tests. The maximum percentage of individuals of a particular hispine species feeding on a host plant species was 80% for *C. sallei* on *C. inocephala.*

There were significant differences among plants in the mean areas *C. sallei* consumed under no-choice tests (ANOVA, $F = 2.21$; df $= 7{,}76$; $P = 0.04$). Neither *A. semicircularum* nor *C. belti* preferred any particular plant species ($F = 0.96$ and $F = 2.20$; df $= 3{,}36$ and df $= 7{,}81$; $P = 0.42$ and $P = 0.06$, respectively). No-choice

Table 2. Results of choice tests

		C. inocephala	*C. latifolia*	*I. pruinosus*	*H. catheta*	*H. irrasa*	*H. latispatha*	*H. mariae*	*H. vaginalis*	n[a]	P[b]	Favorite family[c]
A. semicircularum	mm²±SD	0.09±0.3	0.30±0.8	0	0	0	0	0	0	10	0.23[e]	M
	Eaten disks[d]	1	2									
C. belti	mm²±SD	20.28±33.3	4.79±7.2	0	0.66±1.3	13.49±15.0	13.80±21.4	2.69±4.0	4.63±7.5	10	0.13[e]	M+H
	Eaten disks[d]	3	4	0	3	7	5	4	3			
C. dilaticollis	mm²±SD	19.63±36.9	8.77±22.6	5.42±16.4	0	0	0	0	0	14	0.21[e]	M
	Eaten disks[d]	8	4	3								
C. erichsonii	mm²±SD	28.75±51.9	9.35±22.0	0	2.21±6.0	0	0	33.28±48.8	1.97±5.0	12	0.07[e]	M+H
	Eaten disks[d]	5	2	0	2	0	0	5	2			
C. instabilis	mm²±SD	0.24±0.8	6.95±15.8	0	1.94±5.0	13.28±16.6	18.91±17.6	0	4.90±9.8	11	0.01[f]	M+H
	Eaten disks[d]	1	5	0	3	6	8	0	5			
C. pretiosa	mm²±SD	0.81±2.5	0	0.47±1.5	4.41±5.0	10.14±14.0	7.07±10.4	10.14±13.5	10.09±17.7	10	0.10[e]	H
	Eaten disks[d]	4	0	1	7	6	5	6	4			
C. sallei	mm²±SD	1.79±5.0	19.24±39.8	4.36±9.4	0	0	0.22±0.7	9.88±17.0	17.42±28.1	11	0.18[e]	M+H
	Eaten disks[d]	2	6	3	0	0	1	4	5			

The mean quantitative (mm² ± SD) and qualitative measures of the amount of leaf area consumed by each hispine species presented simultaneously with equal areas of leaf disks taken from eight plant species (ANOVA II, consumed plant species and individual as factors).

[a] n = no. of replication.
[b] Calculated for consumed plant species factor.
[c] M, Marantaceae; H, Heliconiaceae.
[d] Number of eaten disks represents qualitative answers.
[e] Not significant.
[f] P < 0.01.

Table 3. Results of no-choice tests

	C. inocephala	C. latifolia	I. pruinosus	H. catheta	H. irrasa	H. latispatha	H. mariae	H. vaginalis	P^a	Favorite family[b]
A. semicircularum	1.03 ± 2.6	0.60 ± 2.0	0.64 ± 2.1	0	0	0	0	0.027 ± 0.1	0.40[c]	M
C. belti	10.15 ± 32.9	1.48 ± 6.8	0.30 ± 1.0	5.15 ± 17.6	3.66 ± 7.6	11.60 ± 32.4	3.43 ± 8.1	18.47 ± 45.7	0.11[c]	M+H
C. sallei	9.26 ± 13.0	18.60 ± 31.6	1.80 ± 3.4	0.09 ± 0.3	1.00 ± 3.6	5.00 ± 20.6	12.39 ± 28.5	3.25 ± 7.1	0.01[d]	M

The mean quantitative (mm² ± SD) and qualitative measures of the amount of leaf area consumed by each hispine species when given leaf disks of a single plant species (ANOVA II, consumed plant species and leaf type as factors, $n = 10$).

[a] Calculated for consumed plant species factor.
[b] M, Marantaceae; H, Heliconiaceae.
[c] Not significant.
[d] $P < 0.01$.

tests also revealed that *C. sallei* consumed Marantaceae more often than Heliconiaceae ($\chi^2 = 4.56$; $P = 0.03$). Similar results were seen with *A. semicircularum* which gave only one positive response on Heliconiaceae. In contrast, *C. belti* consumed equally the two plant families ($\chi^2 = 1.84$; $P = 0.17$).

Discussion

The eight species of Cephaloleiini recorded in monocot leaf scrolls in Panama were associated with from 4 to 9 of the 11 plant species included in this study. Furthermore, three of the eight beetle species were recovered from hosts in both of the families (Zingiberales) included in this study. Both of these observations suggest that the list of hosts used by Cephaloleiini is larger than has typically been reported in the literature and may well be even larger if all Heliconiaceae and Marantaceae occurring regionally had been included. Earlier reviews of occurrence data focusing on Heliconiaceae feeding beetles have generally concluded that Cephaloleiini are associated with a small number of host plant species within a single family (Staines 2004). By including host plants from more than one family, we are able to see that some Cephaloleiini species include numerous related host plant species in their diet and that hosts may come from more than one plant family (Table 4).

Although previous reports indicated *Cephaloleia belti* occurs on five *Heliconia* species, we found it associated with 9 of the 11 species in the survey and in our choice experiments. Morrison and Strong (1981) have suggested that hispines could be strongly specialized explaining that "*C. consanguinea (Hispinae)*, [which] *is a monophagous herbivore of H. imbricata (Zingiberales: Heliconiaceae) in wet lowland of eastern Costa Rica.*" Later, Staines (2004) redescribed *C. consanguinea* as *C. belti*, which is one of the least host specific species in lowland Panamanian forest. Another example is *C. erichsonii*, which is reported from four plant species (Staines 2004), whereas we found it on nine host plant species.

The preferences expressed during the feeding tests (Tables 2 and 3) by *A. semicircularum* and *C. dilaticollis* for Marantaceae and by *C. pretiosa* for Heliconiaceae correspond to "first-degree oligophagy" as defined by Jolivet (1998). The absence of obvious specific preferences corresponds to Jolivet's "second-degree oligoph-

agy." We found no indication of monophagy among any of these nine beetle species. The results of choice and nonchoice feeding tests at the plant family level corresponded generally to preferences observed in the field. However, there were greater differences in the abun-

Table 4. Comparison between the present census of hispine—host plant associations and the previous review of Staines (2004)

Hispine species	Field host plant species (this study)	Field host plant species (Staines 2004)
Aslamidium semicircularum Borowiec	C. inocephala C. insignis C. latifolia C. lutea Ischnosiphon pruinosus	Calathea. sp.
Cephaloleia belti Baly	C. latifolia C. lutea H. catheta H. irrasa H. latispatha H. mariae H. vaginalis H. wagneriana I. pruinosus	Heliconia imbricata H. latispatha H. pogonantha H. mariae H. tortuosa
C. dilaticollis Baly	C. inocephala C. insignis C. lutea I. pruinosus	C. insignis
C. erichsonii Baly	C. inocephala C. insignis C. latifolia	C. gymnocarpa C. inocephala C. leucostachys
C. erichsonii Baly	C. lutea H. catheta H. latispatha H. mariae H. vaginalis H. wagneriana	
C. instabilis Baly	C. latifolia H. catheta H. latispatha H. mariae	H. latispatha H. imbricata H. wagneriana
C. pretiosa Baly	H. catheta H. latispatha H. mariae	No data
C. sallei Baly	C. inocephala C. latifolia C. lutea H. catheta H. latispatha H. mariae H. vaginalis I. pruinosus	No data

dances of hispines observed on different host plants in the field. *C. erichsonii* was mainly found on *C. inocephala* and *H. mariae, C. sallei* on *C. latifolia*, and *C. instabilis* on *H. latispatha*, whereas other hispine species were more equally distributed among plant species (Table 1). However, choice tests revealed no such preferences. Defining the host range of hispines requires a large and time-consuming survey, which may nevertheless underestimate host ranges as shown in Table 4. The review of Cassidinae associations with Zingiberales by Staines (2004) seems to considerably underestimate actual numbers of host plant species used by hispine beetles as indicated by our studies in Panama. Furthermore, feeding tests as a complementary tool may provide an even better indication of the range of acceptable hosts. Indeed, specialization can vary spatially and temporally in nature as a function of food availability and other extrinsic factors such as predators and parasitoids pressure (Fox and Morrow 1981). The larger diets recorded in no-choice tests, where tested beetles fed on one more plant species than in choice tests, is a good example. As suggested by Barone (1998), a broader range of feeding in no-choice tests could be the consequence of starvation, where individuals do not have the possibility to focus on preferred rather than secondary host plants (Zwölfer and Harris 1971). Essentially, this is analogous to a different habitat with different host-species composition, which would also affect insect choice. In this way, feeding tests can be useful in defining the potential or fundamental feeding niche, whereas field observations correspond to the realized niche (Futuyma and Moreno 1988).

Acknowledgments

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