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How foraging tactics determine host-plant use by a polyphagous caterpillar

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Abstract The use of multiple host-plant species by populations of insect herbivores can result from a variety of possible ecological and behavioral mechanisms. An understanding of the foraging mechanisms determining polyphagy in relation to local ecological conditions is therefore essential to understanding the evolutionary ecology of polyphagy. Here, we evaluate patterns of host-plant use by the polyphagous caterpillar *Grammia geneura* (Lepidoptera: Arctiidae) in relation to host-plant availability and foraging tactics of individuals. Field surveys of caterpillar feeding and plant abundance carried out across several sites, seasons, and years showed that: (1) *G. geneura* consistently preferred forbs to grasses and woody plants, (2) forb-feeding was opportunistic, supporting the idea that caterpillars sample locally available host-plants, and (3) there were consistent patterns of host-plant use that were not explained by host-plant availability (electivity). An independent set of 7-h observations of 11 caterpillars showed that electivity for a subset of caterpillar-host associations could be explained by variation in the probability of initiating feeding and the average duration of feeding bouts on different hosts but not by variation in the probability of encountering different hosts, thus providing a behavioral basis for the observed variation in host-plant use. The use of detailed foraging tactics by larvae to explain host-plant use at the population level is a novel contribution of this study.

Keywords Feeding preference · Foraging tactics · Host-plant use · Sampling · Selective feeding

Introduction

Ecological patterns of host-plant use by insect herbivores have figured prominently in developing and testing theory in population biology (Ehrlich et al. 1980; Kuussaari et al. 2000), community ecology (Gilbert 1979; Strong et al. 1984), and coevolution (Ehrlich and Raven 1964; Gilbert 1979; Bécerra 1997). In many cases, however, the mechanisms generating such patterns are not well understood. This is particularly the case for oligophagous and polyphagous insect herbivores, for which a variety of behavioral and ecological mechanisms may result in observed patterns of multiple host-plant use (Singer 1983; Singer et al. 1989; Singer and Parmesan 1993). With respect to behavioral mechanisms for example, polyphagy at the population level may result from either monophagous individuals associated with multiple host-plant species, or from polyphagous individuals. Different foraging strategies exist even among species with polyphagous individuals (Chambers et al. 1996; Bernays and Minken-berg 1997; Bernays and Singer, unpublished manuscript) resulting in different patterns of host-plant use.

Ultimately, any thorough explanation of the evolution or ecology of polyphagy requires study of the foraging by individuals in nature. Ideally, this should be done under a range of local conditions because interactions between individual foraging tactics and the local environment are the source of variation in host-plant use at the population level. Variation in local conditions can alter patterns of host-plant use even when individual herbivores are behaviorally identical (Singer and Parmesan 1993). However, individual behavioral variation in foraging may interact with variation in local conditions to produce other possible patterns of host-plant use (Singer et al. 1989). For example, Singer et al. (1989) found Edith's checkerspot butterflies in one population to vary in their preference ranking of several host species, but no such difference among individual insects in another population. In this case, differences in the plant communities interacted with foraging tactics to produce similar patterns of host use between these populations. The neuro-

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physiological mechanisms involved in foraging behavior may be important as well. For example, host-plant preference may be fixed or subject to change with experience (Papaj and Prokopy 1989), possibly resulting in different patterns of host use in response to the same environment.

Among taxa of insect herbivores, Lepidoptera have perhaps the best characterized patterns of host-plant use. Despite the predominance of dietary specialization within this group, diverse foraging tactics of individuals are known for both specialist and generalist species. In many species, the behavioral tactics of host-plant location and selection employed by adult female butterflies largely determine patterns of host-plant use because the foraging behavior of individual caterpillars is often confined to the individual plant selected by their mothers (Thompson and Pellmyr 1991). However, in some species (e.g., many Arctiidae), caterpillars are relatively mobile and perform some or all host-plant location and selection (e.g., Dethier 1988). In contrast to butterflies that typically have relatively sedentary, stenophagous larvae, the foraging tactics of relatively mobile, polyphagous larvae and their influence on patterns of host-plant use are not well known. The goal of this study is to characterize the patterns of host-plant use by populations in relation to host-plant availability and the shared foraging tactics by individual larvae of the polyphagous moth, *Grammia geneura* (Arctiidae) in nature. Variation in foraging tactics among individuals will be addressed elsewhere.

Materials and methods

Study system

Grammia geneura (Strecker) (Arctiinae; Arctiini) ranges throughout arid grasslands of the southwestern USA and northwestern Mexico (M. S. Singer 2000). Adults fly prior to rainy seasons (late spring and early autumn in southeastern Arizona) for only a short period (adults possess a poorly developed proboscis and cannot feed). Females deposit clutches of eggs on the ground under litter in the dry season before many host plants germinate. After hatching, solitary “woolly bear” larvae locate and select host plants on their own. Possible host-plants in their habitat include annual and perennial grasses and forbs, as well as woody plants that range in stature from prostrate species to 10-m-high trees. Forbs and grasses typically cover 60–90% of the ground in relatively dense patches in which the foliage of multiple species interdigitates or occurs in close proximity (M. S. S. unpublished data). *G. geneura* tends to be most prevalent in savanna and grassland associated with hill-sides and flats along gently sloping drainages (ca. 1,100–1,600 m elevation) in southeastern Arizona, where all data presented here were gathered (Table 1).

Data collection

To determine patterns of feeding across time and space, we sampled feeding events of late instar caterpillars for six seasons: spring and summer of 1996–1998 at the various field sites listed. We recorded feeding events by collecting any caterpillar observed to be feeding within a designated plot (72×80 m²) at each site. This ensured independence of the feeding records. Whenever possible, species of host plants were identified. However, a small proportion (<5%) of badly damaged hosts precluded specific identifi-

Table 1 Southeastern Arizona field sites of *Grammia geneura*

Site	Mountain range	County	Elevation (m) ^a
Oracle	Santa Catalina	Pinal	1,375
Arivaca	San Luis hills	Pima	1,075
Ash Creek	Rincon	Pima	1,225
Redington Pass	Santa Catalina	Pima	1,275
Gardner Creek	Santa Rita	Pima	1,225
Box Canyon Road (at Arizona Trail)	Santa Rita	Pima	1,525
Patagonia	Santa Rita	Santa Cruz	1,275
Pena Blanca Cyn	Atascosa	Santa Cruz	1,125

^aElevations are rounded to the nearest 25 m

cation. Sites were sampled more than once (usually twice) during each season. All feeding records from a given site during a given season were pooled.

To determine patterns of host-plant availability across time and space, the above sites were sampled during the same season for abundance of plant species. We used stratified random transects (ten in spring, eight in summer samples) across the plots described above to sample ground coverage of plant species available to populations of caterpillars. Forty-five points were systematically sampled (every 1.6 m) along each transect line (72 m long), giving a total of 450 points in spring and 360 points in summer samples. All green parts of plant species in contact with a “point” (an approximate 5×5 cm² area) were recorded. Plant density tended to be higher during the summer, thus each point included more individual plants on average, and yielded similar numbers of plants as the spring samples. Measures of plant availability were restricted to ground coverage (up to ca. 2 cm in height) because caterpillars forage by walking on the ground or on low plants. Our observations and evidence from a related species suggest that woolly bear caterpillars find food by meandering and randomly contacting hosts (Dethier 1993). *G. geneura* larvae frequently contact plants (and other objects) with their mouthparts (M. S. S., personal observation). Feeding may follow contact immediately or may occur after a caterpillar ascends the plant following contact. Therefore, our method of sampling should represent the plants available for contact by foraging *G. geneura* caterpillars.

On separate occasions, we observed the feeding behavior of individual caterpillars at Ash Creek (spring 1996) to identify behavioral contributions to feeding patterns obtained from the sampling scheme described above. Eleven individual final instars of *G. geneura* were monitored continuously for 7 h. All encounters with host plants, occurrences of feeding, and durations of activities were used to calculate encounter frequencies, feeding probabilities, and feeding bout durations with respect to host-plant species.

Data analysis

Only samples with 20 or more feeding records were used in analyses (n=15: 11 spring, four summer samples). We used χ^2 tests to determine if caterpillars fed on three different vegetation types (grasses, forbs, woody plants) in relation to their abundance. We used simple linear regressions to determine if the relative frequency of feeding on particular host species depended on local availability (relative ground coverage). Proportions used in regression analyses were angularly transformed (Zar 1984).

To determine the behavioral basis of feeding frequency on different host species, we performed a stepwise multiple regression analysis of “electivity” (Ivlev 1961 in M. C. Singer 2000). Electivity is defined as the relative degree to which a host species is eaten in relation to its relative abundance. As M. C. Singer (2000) explains, this parameter is not necessarily a result of behavioral preferences of individual insects, but rather a property of the insect-plant interaction. Formally, we calculated the electivity of the in-

sects' interactions with several hosts for which we had behavioral data in the following way. For each species, we determined the slope of the best-fit line (forced through the origin) that adequately described ($R^2 > 0.50$) the relationship between the relative proportion of feeds on the plant and its relative proportion of ground coverage across all samples. From this slope, we subtracted 1 (the slope of the line describing a null expectation, the relative proportion of feeds based entirely on the relative coverage of a host). Therefore hosts used in greater proportion than expected based on their abundance would have positive values (favored), and those used less than expected would have negative values (avoided).

The full regression model used to explain electivity (the response variable defined above) included the following explanatory variables derived from the observational data: (1) encounter bias (the difference between the relative frequency of encountering a host species and its relative ground coverage), (2) the probability of initiating feeding [the mean (averaged across individual caterpillars, $n=11$) of the frequency of feeds/frequency of encounters for each plant species], (3) the average feeding bout duration (the mean, i.e., $n=11$, of the median feeding-bout durations of individual insects), and (4) all possible two- and three-way interactions. Encounter bias reflects pre-contact behavioral preference and possible variation in dispersion among plant species; the probability of feeding indicates post-contact, pre-ingestive phagostimulation; and the average feeding-bout duration is a measure of combined pre- and post-ingestive phagostimulation (Simpson 1995). The probability of initiating feeding and average feeding bout duration together account for a host's acceptability. All three parameters together should account for all of the biological variation in electivity determined from population surveys. Ultimately the model was simplified to include only those main effects and interactions that explained significant amounts of variation in electivity. The model included nine host-plant species (*Plantago patagonica*, *Plagiobothrys arizonica*, *Erodium cicutarium*, *Machaeranthera gracilis*, *Astragalus nothoxys*, *Pectocarya platycarpa*, *Cirsium neomexicanum*, *Lotus humistratus*, and *Bromus rubens*) on which we observed feeding by multiple caterpillars. We used Statview 4.0 (Abacus Concepts 1992) to fit regression lines describing electivity, and JMP IN 3.2.1 (SAS Institute 1996) to perform all other statistical tests.

Results

Preference for forbs

Caterpillars fed preferentially (in some cases exclusively) on annual and perennial herbaceous dicots (forbs), which accounted for approximately 20–80% of the ground-level vegetation cover (Fig. 1; forb species listed in Appendix I). Grasses and woody plants received far fewer feeding records even though grasses, like forbs, accounted for 20–80% of the ground cover. In all samples, the distribution of feeding records for grasses, forbs, and woody plants differed significantly from the expected distribution based on the availability of those vegetation types (Table 2). In a few cases, frequent feeding on woody plants seemed associated with reduced forb abundance or flushes of young growth on certain low shrubs (e.g., *Acacia greggii*, *Eriogonum wrightii*).

Population responses to forbs

The number of forb species eaten by caterpillars increased with the number of forb species available

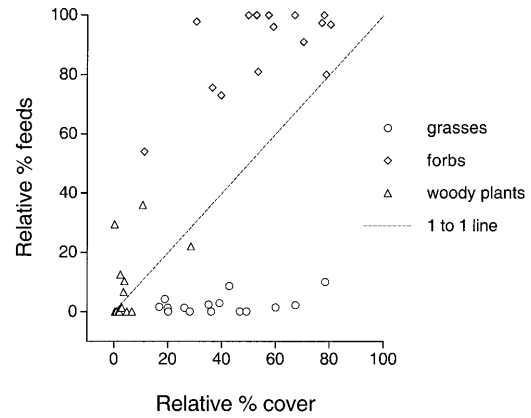


Fig. 1 Preference of *Grammia geneura* caterpillars for the three different vegetation types for each of 15 samples. The oblique, 1 to 1 line indicates a perfect correspondence between the relative abundance of vegetation types and the relative proportion of feeding on them. Each sampling occasion (15) is represented by one of each of three symbols

Table 2 Preference of *G. geneura* for different vegetation types. For each collection, the proportion of caterpillars feeding on grasses, forbs, and woody plants was compared with the proportions of these plant types available. Significance indicates that caterpillars fed disproportionately on grasses, forbs, and woody plants in relation to their relative abundance. In each case, the proportion of forb-feeding was higher than expected, based on the proportion of forb cover

Date	Location	N feeds	χ^2	df
March 1996	Arivaca	58	30.63**	2
March 1996	Gardner Cyn	63	11.12**	2
March 1996	Ash Creek	74	1,830.2**	2
April 1996	Pena Blanca	46	98.58**	2
March 1996	Redington	50	142.05**	2
March 1997	Ash Creek	78	69.57**	2
April 1997	Oracle	41	30.49**	2
March 1997	Patagonia	27	7.61*	2
March 1997	Redington	45	22.15**	2
April 1998	Ash Creek	134	135.11**	2
March 1998	Redington	151	35.69**	2
August 1996	Gardner Cyn	24	12.39**	2
August 1997	Ash Creek	103	61.53**	2
August 1998	Ash Creek	45	33.49**	2
August 1998	Box Cyn	78	26.90**	2

* $P < 0.05$, ** $P < 0.01$

($R^2 = 0.72$, $P < 0.001$) (Fig. 2a). The same relationship was observed for rare forbs (those accounting for <1% cover) ($R^2 = 0.51$, $P < 0.01$) (Fig. 2b). In 13 of 15 samples, the frequency of feeding on particular forb species was positively associated with their abundance as well (Table 3).

However, caterpillars consistently favored certain forb species: they ate them in greater frequency than that expected based on their abundance (Fig. 3). *Plantago patagonica* and *P. virginica* (Plantaginaceae), *Plagiobothrys arizonica* (Boraginaceae), *Erodium cicutarium* (Geraniaceae), and *Phlox gracilis* (Polemoniaceae) were some of the most favored spring forbs, while *Bidens leptoccephala* (Asteraceae) and *Eriogonum poly-*

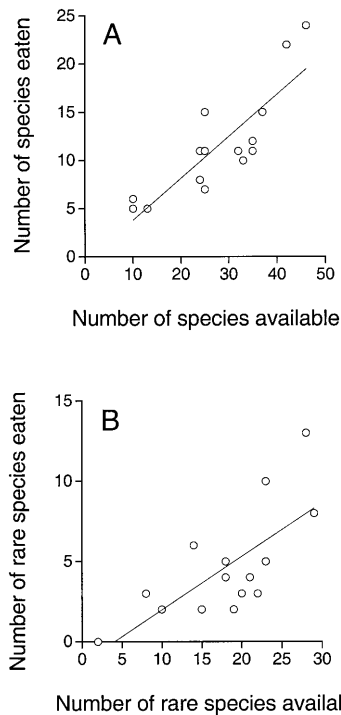


Fig. 2 Relationship between **A** the number of forb species available (the majority were rare: accounting for <1% cover) and the number eaten by *G. geneura* caterpillars at all 15 samples and **B** the same relationship for only the rare forb species

Table 3 Relationship between feeding frequency and forb abundance. On each occasion the relative abundance of each forb species was compared with the relative frequency with which it was eaten. *NS* Not significant

Date	Location	<i>N</i> species	R^2	<i>P</i>
March 1996	Arivaca	24	0.69	<0.01
March 1996	Gardner Cyn	10	0.03	NS
March 1996	Ash Creek	24	0.70	<0.01
April 1996	Pena Blanca	13	0.64	<0.01
March 1996	Redington	11	0.42	<0.05
March 1997	Ash Creek	24	0.73	<0.01
April 1997	Oracle	24	0.53	<0.01
March 1997	Patagonia	31	0.23	<0.01
March 1997	Redington	35	0.30	<0.01
April 1998	Ash Creek	37	0.56	<0.01
March 1998	Redington	42	0.33	<0.01
August 1996	Gardner Cyn	32	0.33	<0.01
August 1997	Ash Creek	27	0.30	<0.01
August 1998	Ash Creek	32	0.22	<0.01
August 1998	Box Cyn	47	0.02	NS

cladon (Polygonaceae) were favored summer forbs. In contrast, two non-favored forbs (i.e., not eaten more or less than expected based on their abundance) were *Machaeranthera gracilis* (Asteraceae) and *Ambrosia confertiflora* (Asteraceae), ubiquitous plant species that occurred in both spring and summer. Feeding frequency on both favored and non-favored forbs depended on their abundance (Fig. 3).

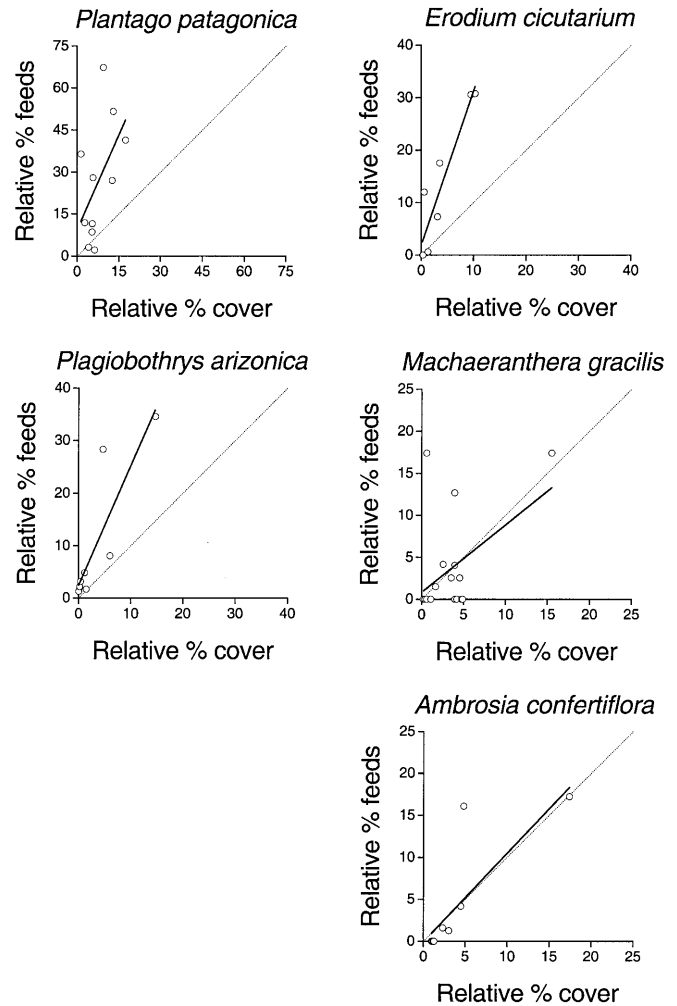


Fig. 3 Relationship between the relative abundance and the relative proportion of feeds on different preferred (*Plantago patagonica*, *Erodium cicutarium*, *Plagiobothrys arizonica*) and non-preferred forb species (*Machaeranthera gracilis*, *Ambrosia confertiflora*). The faint line is the 1 to 1 line, indicating the expected pattern if feeding and encounter probability were the same

Individual responses to forbs

The 11 individual caterpillars that were observed for 7-h interspersed periods of feeding with periods of locomotion within and between patches of multiple host-plant species. Because individual plants were in close proximity within patches, caterpillars often contacted dozens of individual plants over minutes or hours before initiating feeding. The behavioral basis of electivity was best explained by the probability of initiating feeding, the duration of feeding bouts, and their interaction (Table 4; adjusted $R^2=0.56$). Encounter bias did not explain significant amounts of variation as a main effect or in interactions with other parameters.

Table 4 Multiple regression analysis showing behavioral explainers of electivity of *G. geneura* and nine host-plant species. Note: adjusted $R^2=0.56$ for this model

Source of variation	df	F	P
Feeding probability	1	11.39	0.020
Feeding bout duration	1	7.71	0.039
Feeding probability \times feeding-bout duration	1	11.27	0.020

Discussion

Under a range of natural conditions, *G. geneura* caterpillars fed preferentially on forbs. In their habitat, the forb community is a locally abundant, high-quality resource, covering a large geographic area. Although woody plants and grasses in these habitats offer the same advantages of local abundance and wide geographic distribution, their tissues are relatively tough and nutritionally poor (Tabashnik and Slansky 1987). *G. geneura* rarely fed on woody plants, except when forbs were relatively scarce or when woody branches were near the ground and flushed with new growth (M. S. S. and J. O. S., personal observation). The ground-dwelling habit of *G. geneura* normally makes the softest tissues of woody plants (i.e., new leaves and shoots) less accessible than tissues of grasses and forbs. Despite the accessibility of grass tissues, *G. geneura* avoided feeding on them under a variety of ecological conditions. Grasses may be especially low in protein (Tabashnik and Slansky 1987) and may contain silica crystals that wear down the mouthparts of non-adapted herbivorous insects (Djamin and Pathak 1967). That chemical or physical characteristics of grass discourage feeding by *G. geneura* is suggested by observation that tough, fibrous C4 grasses were never eaten; all grass-feeding was confined to annual C3 grasses (e.g., *Bromus rubens*), especially young blades (M. S. S., personal observation). It has recently been argued that physical characteristics differ more than chemical (nutritional) characteristics between C4 and C3 grasses (Scheirs et al. 2001). In contrast to grasses, forbs possess softer tissues and contain relatively high concentrations of nutrients, especially protein and water (Tabashnik and Slansky 1987). Laboratory studies with *G. geneura* demonstrated large performance differences among insects reared on different host-plant species (M. S. Singer 2000), with the annual forbs tested offering higher food quality than the perennial forb and woody plant species used in those experiments.

However, forbs additionally contain a variety of secondary metabolic chemicals that may be deterrent or toxic to generalist herbivores. Conventional wisdom holds that forbs are more acutely toxic to non-adapted herbivores than are woody plants in temperate and sub-tropical regions (Feeny 1976; Gilbert 1979). The foraging tactics of *G. geneura* may help it cope with plant toxins. Individual caterpillars mix foods or graze from a variety of forb species, perhaps allowing the intake of a relatively nutritious diet with low concentrations of diverse phyto-

toxins (M. S. Singer 2000) even when host-plant species are individually unsuitable for complete development.

Results of surveys at the population level suggest that *G. geneura* caterpillars feed opportunistically by sampling the locally available forbs. The positive association between the number of both total and rare forb species available and the number fed upon indicates that caterpillars extensively sampled the local forb community. The general finding that feeding frequency increased with forb abundance is consistent with such sampling by caterpillars as well. Under some conditions, the opportunistic feeding of *G. geneura* may impose frequency-dependent selection on its host plants and perhaps promote forb species diversity (Huntly 1991).

Some of the variation in feeding frequency on different forb species that is unexplained by host-plant availability (electivity), however, can be attributed to the insects' behavioral preferences. That is, the probability that our population samples would include feeding on a given forb was determined both by the forb's abundance (chance of being encountered) and its acceptability to *G. geneura*. Certain forb species (e.g., *Plantago patagonica*, *Plagiobothrys arizonica*, *Erodium cicutarium*) were consistently eaten in greater proportion than would be expected based on their abundance. This resulted from more time spent feeding on such species (either through an increased probability of initiating feeding, prolonged feeding events, or both), suggesting their relatively high acceptability (Table 4). The significant interaction term in the regression model indicates the importance of combined effects of the probability of initiating feeding and feeding-bout duration. This is consistent with the idea that a plant species may be phagostimulatory at one level but not at the other. Indeed, behavioral and physiological evidence show that the probability of initiating feeding is determined primarily by close-range olfactory or gustatory stimuli from the plant surface (Chapman 1995), while the duration of a feeding bout is additionally determined by post-ingestive physiological feedbacks from ingesta in the gut (Simpson 1995).

Individual polyphagy, selective feeding, and sampling behavior are important behavioral components of multiple host-plant use by populations of *G. geneura*, as is the case for a variety of other herbivores. The polyphagy or grazing behavior of individual caterpillars is similar to the foraging of mammalian herbivores (Stephens and Krebs 1986) and numerous grasshopper species (Bernays and Bright 1993), but rather unusual among Lepidoptera. Further work on the detailed behavioral responses of individual caterpillars to host-plants and synthetic foods specifically shows similarity in foraging behavior between *G. geneura* and grasshopper species with forb-mixing individuals (Bernays et al. 1992; Chambers et al. 1996; M. S. Singer 2000). It is not yet clear, however, if forb-mixing behavior has the same function for caterpillars and grasshoppers (Bernays and Minkenbergh 1997). The selective feeding exhibited by *G. geneura* in the present study is another characteristic shared with a wide variety of grazing animals (e.g., Kitting 1980; Chandra

and Williams 1983; Rathke 1985; Parsons et al. 1994; Guglielmo et al. 1996), allowing ingestion of a high-quality diet. Sampling the plant community is also common to a variety of grazers (e.g., Rockwood 1976; Jenkins 1978; Owen-Smith and Novellie 1982; Clark 1982; Illius and Gordon 1990). Such behavior allows an herbivore to respond rapidly to variation in resource quality.

Together, these foraging tactics of *G. geneura* would be expected to give individuals the flexibility to forage successfully under a range of ecological conditions. This flexibility may be critical when key resources change quantitatively and qualitatively in an unpredictable way. Drastic unpredictable variation in the abundance and distribution of host-plant species over space and time is typical of the habitat of *G. geneura* (M. C. Singer 2000) because most host-plant species are desert ephemeral annuals with species-specific germination and survival responses to stochastic abiotic factors (e.g., Pake and Venable 1996).

A contrast between the foraging tactics of *G. geneura* and the oviposition behavior of several butterfly species suggests two general foraging strategies of forb-feeding within the Lepidoptera [individual polyphagy vs. dietary specificity (Futuyma 1976) related to life history constraints (larval vs. adult host location)]. The high spatio-temporal variation in the availability of forb species on a small scale means that specialists would require efficient tactics of host location. Although forb-feeding butterfly species [e.g., *Euphydryas editha* (Singer 1983), *Melitaea cinxia* (Kuussaari et al. 2000), *Pieris rapae* (Root and Kareiva 1984), *Papilio zelicaon*, *P. oregonius* (Thompson 1988)] may vary considerably in their landscape-scale mobility and tactics of host-plant selection, individual butterflies of these and most other species are highly mobile over a large spatial scale relative to individual *G. geneura* caterpillars, and are thus expected to locate host-plants relatively efficiently. Unlike *G. geneura* larvae, adults of such species also perform some host-plant selection prior to contacting plants (pre-alighting host selection) (Papaj and Rausher 1983), further facilitating their efficiency. These differences may allow (but not necessarily determine) the relatively specialized host-plant use by species in which adults locate hosts, and maintain more generalized host-plant use by species with larval host location. The limited mobility and capacity to locate preferred host-plant species may be important constraints of larvae that proximately prevent evolution towards efficient tracking and specialization on the highest quality hosts.

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Appendix I

Forb species recorded as hosts for *Grammia geneura* during sampling

Species	Family
<i>Trianthema portulacastrum</i> L.	Aizoaceae
<i>Allium macropetalum</i> Rydb.	Alliaceae
<i>Amaranthus</i> spp. <i>Guilleminea densa</i> (Willd.) Moq.	Amaranthaceae
<i>Lomatium nevadense</i> (Wats.) <i>Spermolepis echinata</i> (Nutt.) <i>Bowlesia incana</i> Ruiz and Pavon	Apiaceae
<i>Ambrosia confertiflora</i> (DC.) Rydb. <i>Bidens leptoccephala</i> Sherff. <i>Cirsium neomexicanum</i> A. Gray <i>Conyza canadensis</i> (L.) Cronquist <i>Erigeron</i> sp. <i>Gnaphalium purpureum</i> L. <i>Heterosperma pinnatum</i> Cav. <i>Hymenothrix wislizenii</i> A. Gray <i>Lasthenia chrysotoma</i> (Fisch. and C.A. Mey.) Greene <i>Machaeranthera gracilis</i> (Nutt.) Shinnars <i>Machaeranthera tanacetifolia</i> (Kunth) Nees <i>Malacothrix stebbensii</i> W.S. Davis and P.H. Raven <i>Melampodium strigosum</i> Stuessy <i>Uropappus lindleyi</i> (DC.) Nutt.	Asteraceae
<i>Cryptantha barbiger</i> (A. Gray) Greene <i>Cryptantha micrantha</i> (Tory.) I.M. Johnst. <i>Heliotropium fruticosum</i> L. <i>Lithospermum cobrense</i> Greene <i>Pectocarya platycarpa</i> Munz and Johnst. <i>Plagiobothrys arizonicus</i> (A. Gray) Greene ex A. Gray <i>Plagiobothrys tenellus</i> (Nutt. ex Hooker) A. Gray	Boraginaceae
<i>Lesquerella gordonii</i> (A. Gray) S. Watson <i>Schoenocrambe linearifolia</i> (A. Gray) Rollins <i>Sisymbrium irio</i> L. <i>Thysanocarpus curvipes</i> Hook.	Brassicaceae
<i>Triodanis</i> sp.	Campanulaceae
<i>Cerastium vulgatum</i> L. <i>Stellaria nitens</i> Nutt.	Caryophyllaceae
<i>Chenopodium</i> sp. <i>Salsola tragus</i> L.	Chenopodiaceae
<i>Cuscuta</i> sp. <i>Evolvulus alsinoides</i> L. <i>Ipomoea costellata</i> Torr. <i>Ipomoea</i> spp.	Convolvulaceae
<i>Crassula squarrosa</i> Nutt.	Crassulaceae
<i>Tragia laciniata</i> (Torn) Mull. Arg. <i>Acalypha</i> spp. <i>Euphorbia dentata</i> Michx. <i>Euphorbia heterophylla</i> L. <i>Euphorbia</i> spp. <i>Jatropha macrorrhiza</i> Benth.	Euphorbiaceae
<i>Astragalus nothoxys</i> A. Gray <i>Crotolaria pumila</i> Ortega	Fabaceae

Species	Family
<i>Desmanthus cooleyi</i> (Eaton) Trel.	
<i>Lotus humistratus</i> Greene	
<i>Lotus oroboides</i> (Kunth in H.B.K.) Ottley	
<i>Lupinus concinnus</i> Agardh.	
<i>Erodium cicutarium</i> (L.) L'Her. ex Aiton	Geraniaceae
<i>Nama</i> sp.	Hydrophyllaceae
<i>Phacelia arizonica</i> A. Gray	
<i>Phacelia distans</i> Benth.	
<i>Mentzelia albicaulis</i> Dougl.	Loasaceae
<i>Anoda cristata</i> (L.) Schldl.	Malvaceae
<i>Rhynchosida physocalyx</i> (A. Gray) Fryxell	
<i>Sida abutiloides</i> Jacq.	
<i>Sphaeralcea laxa</i> Woot. and Standl.	
<i>Boerhaavia coccinea</i> Mill.	Nyctaginaceae
<i>Boerhaavia</i> spp.	
<i>Oenothera primiveris</i> A. Gray	Onagraceae
<i>Eschscholtzia mexicana</i> Greene	Papaveraceae
<i>Plantago patagonica</i> Jacq.	Plantaginaceae
<i>Plantago virginica</i> L.	
<i>Eriastrum diffusum</i> (A. Gray) H. Mason	Polemoniaceae
<i>Linanthus aureus</i> (Nutt.) Greene	
<i>Phlox gracilis</i> (Douglas ex Hooker) Greene	
<i>Eriogonum polycladon</i> Benth.	Polygonaceae
<i>Talinum aurantiacum</i> Engelm.	Portulacaceae
<i>Androsace occidentalis</i> Pursh.	Primulaceae
<i>Diodia teres</i> Walt.	Rubiaceae
<i>Castilleja exsertum</i> (A. Heller) T.I. Chuang and Heckard	Scrophulariaceae
<i>Veronica peregrina</i> L.	
<i>Physalis crassifolia</i> Benth.	Solanaceae
<i>Physalis</i> sp.	
<i>Solanum eleagnifolium</i> Cav.	
<i>Plectritis ciliosa</i> (Greene) Jeps.	Valerianaceae

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