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Developmental specialization and geographic structure of host plant use in a polyphagous grasshopper, *Schistocerca emarginata* (= *lineata*) (Orthoptera: Acrididae)

Received: 4 June 1998 / Accepted: 10 March 1999

Abstract Host plant use and availability were determined in early nymphal and adult-stage *Schistocerca emarginata* (= *lineata*) (Orthoptera: Acrididae) populations at six localities in Texas, USA. Early instar nymphal populations were feeding almost exclusively on either *Ptelea trifoliata* (Rutaceae) or *Rubus trivialis* (Rosaceae). This study represents the first demonstration of a geographic structure of host plant specificity in a polyphagous grasshopper. Recognizing this geographic structure required investigations of both developmental and geographical variation in host plant use. Nymphal diet breadths were significantly less than adult diet breadths at four of six localities and smaller overall when pooled nymphal and adult diet breadths were compared among sites. Neither restricted nymphal mobility nor host plant availability accounted for the observed differences in host plant use between developmental stages and among localities. Evidence suggests that the differences in host use among populations are due to host-plant-associated genetic differentiation.

Key words *Schistocerca emarginata* · Grasshopper · Host plant · Developmental variation · Geographic structure

Introduction

The restricted diets of phytophagous insects have long been of interest to ecologists. Even species considered to be generalist feeders often exist as locally specialized populations (Fox and Morrow 1981). Mounting evidence suggests this phenomenon is much more prevalent than was previously believed. Thompson (1994) summarized examples of geographic structure of host plant

use in the Lepidoptera, Homoptera, Coleoptera, and Diptera. Notably missing from this summary were any phytophagous Orthoptera, specifically the grasshoppers.

An overall majority of phytophagous insects restricts host plant use to a closely related group of plant species, sometimes even single species (Bernays and Chapman 1994). Grasshoppers are thought to be an exception. In general, grasshoppers are polyphagous, meaning they feed selectively on plants from multiple plant families. Polyphagy has been demonstrated at the species, population, and individual levels. Chapman (1990) and Chapman and Sword (1997) provide reviews of host plant use and the relative extent of polyphagy in grasshoppers. Examples of monophagy, diets restricted to a single or closely related group of plant species, are relatively rare but do occur. Rowell (1978) has suggested that this view of grasshopper polyphagy may be the result of a temperate zone bias and that further studies of tropical acridids may reveal an increased degree of host specificity. Marquis and Braker (1994), in a comparison of tropical and temperate grasshopper diet breadths, lend support to this idea.

A geographic structure of host plant specialization in which a generalist species exists as a series of host-specific populations has not been demonstrated in grasshoppers as it has in other phytophagous insect lineages. Does such a pattern not occur, or has it been overlooked? Insect diets may vary both temporally and spatially. The recognition of local specialization is facilitated by studies of host use which account for temporal variation within populations and spatial variation among populations (Fox and Morrow 1981). Only 4 of 61 surveyed studies of grasshopper diet in the field present both temporal and spatial host use data (refs. in Chapman 1990; Chapman and Sword 1997). Unfortunately, none of these studies contain the data necessary to determine the presence or absence of localized dietary specialization. Mulkern et al. (1962) presented host use data for the specific developmental stages of multiple species, but grouped data from 12 localities for analysis. Mulkern et al. (1969) studied the host use of numerous

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species at four localities, but grouped nymphal and adult host use data for analysis. Banfill and Brusven (1973) also investigated the diets of numerous species, but pooled data for various developmental stages from 15 localities and provided only anecdotal accounts of nymphal host use. Bernays and Chapman (1970) investigated host use at four localities, but only investigated temporal variation at a single site.

This study demonstrates that a geographic structure of host plant specificity can occur in a polyphagous grasshopper. Importantly, elucidating this pattern required investigating the combined effects of developmental and geographic variation in host plant use.

Materials and methods

Schistocerca emarginata

The grasshopper, *Schistocerca emarginata* (Scudder 1872), is often erroneously referred to as *S. lineata* (Scudder 1899) (Hubbell 1960). Male genital structures in all of the populations we studied were consistent with those ascribed to *S. lineata* by Hubbell (1960). He argued in favor of using the name *S. lineata* due to its popular acceptance, but here we use the proper name *S. emarginata* because the results of this study suggest that further taxonomic revision is likely. This species is considered to be polyphagous, very polymorphic, and widespread, ranging from southern Canada through central USA, and into northern Mexico (Hubbell 1960).

Localities

Host plant use was sampled in six Texas, USA, localities spanning a range of approximately 42,300 km². These localities are listed here and mapped in Fig. 1: (1) Brazos Bend State Park (BBSP), (2) Altair, (3) Lake Whitney State Park (LWSP), (4) University of Texas, Brackenridge Field Laboratory (BFL), (5) Pedernales Falls State Park (PFSP), and (6) Kerrville. Two study sites were utilized in Kerrville: Louise Hays City Park (LHCP) and Kerrville-Schreiner State Park (KSSP).

The sampled localities were distributed across several distinct vegetational areas in Texas. Detailed descriptions of their floras are given in Correll and Johnston (1970). BBSP is in the Gulf Prairies region, Altair in the Post Oak Savannah, and LWSP in the Cross Timbers and Prairies. BFL, PFSP, and Kerrville are all in the Edwards Plateau region.

Population-level diets

Each locality was sampled twice, once while the insects were in the early nymphal stages and again as adults. No adults were present at Kerrville (KSSP), thus only nymphal data were collected at this site. At Kerrville (LHCP), host use data were collected independently for two nymphal forms differing in their coloration and distribution on and near their respective host plants. The genetic relationship between these forms is currently under investigation. Adults of the two forms could not be distinguished. Therefore, adult host plant use data from Kerrville (LHCP) likely represents the diet of both forms. Sample sizes and sampling dates are summarized in Table 1.

Population-level diets were estimated by microscopic fecal analysis. The technique is described in Sword and Chapman (1994) and numerous examples of its application in studies of grasshopper diet are given in Rowell (1985a). Nymphs were collected directly off

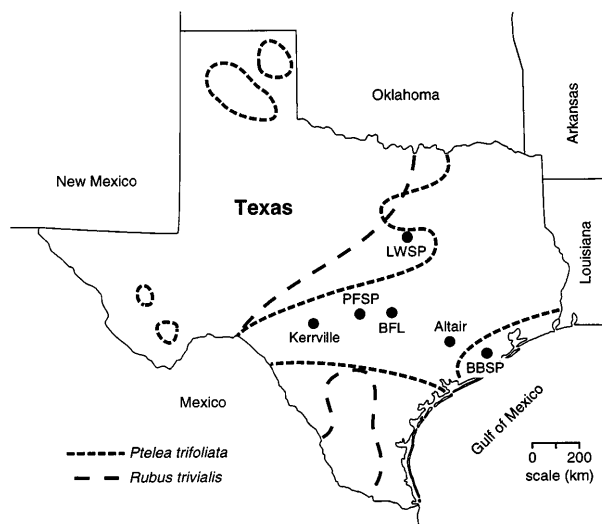


Fig. 1 Distributions of *Rubus trivialis* (Rosaceae) and *Ptelea trifoliata* (Rutaceae) in Texas, USA, mapped with *Schistocerca emarginata* sampling localities

Table 1 Sample sizes and sampling dates for nymphal and adult *Schistocerca emarginata* populations at six Texas localities

Locality	<i>n</i>	Developmental stage (instar)	Date
Altair	23	Nymphs (I–IV)	18 May 1995
	22	Adults	15 September 1996
BBSP	17	Nymphs (I–III)	19 May 1995
	17	Adults	15 September 1996
LWSP	30	Nymphs (I–III)	15 June 1995
	34	Adults	12 October 1996
BFL	43	Nymphs (I–IV)	10 May 1994
	20	Adults	12 September 1993
PFSP	26	Nymphs (I–III)	12 May 1996
	22	Adults	1 September 1996
Kerrville (KSSP)	32	Nymphs (I–III)	12 May 1996
Kerrville (LHCP)	32 (<i>Ptelea</i>)	Nymphs (I–III)	10 June 1997
	29 (<i>Rubus</i>)	Nymphs (I–III)	10 June 1997
	20	Adults	12 October 1996

plants and into clean glass vials for feces collection. Although the nymphs were commonly associated with specific plants, all potential host plants in the nymphal habitat were systematically searched to avoid sampling bias. Adults were flushed into glass vials, captured into nets, and transferred into glass vials. Three fecal pellets per individual were analyzed microscopically. The proportions of each type of plant material present in each pellet were recorded. These proportions were summed for each plant species and divided by the total number of pellets examined to obtain an estimate of the percentage of each plant in the population level diet. Plant availability in the grasshopper habitats, measured as percentage of total cover in the habitat, was assessed by sampling at ten random points along ten randomly placed 30-m transects traversing the collection area. All green plants present directly beneath or above each point were recorded. Specimens of each were collected for use as fecal analysis reference material and subsequent identification.

Diet selectivity at each locality was analyzed using a χ^2 -test for goodness of fit between the frequency of plants found in the diet and their expected frequencies computed from the plant availability data.

Diet breadths

Population-level diet breadths were quantified using the Shannon-Weiner diversity index (H), where

$$H = - \sum_{i=1}^s (p_i)(\ln p_i)$$

and p is the proportion of the population-level diet of s plants comprised by plant i . H values account for both the total number of plant species eaten by the members of a population and their relative abundances in the diet.

To facilitate direct statistical comparison of nymphal and adult population-level diet breadths within localities, population-level data sets were subjected to a bootstrap analysis (Dixon 1993). Such comparisons are not possible with point estimates alone, because these lack an estimation of variance. Ninety-five percent confidence intervals around H values for each population were obtained via a bootstrap procedure programmed in BASIC. Each population-level data set was randomly resampled with replacement 30,000 times and new H values were calculated following each resampling iteration. Data were vectors containing the relative proportions of each plant present in an individual's diet. The upper and lower 2.5% of the resulting distribution of H values were removed to obtain the bounds of the confidence interval.

Survivorship experiments

To determine the acceptability and suitability of a range of host plants to nymphs at a single locality, survivorship experiments were conducted using five different diet treatments. Field-collected first-instar nymphs from BFL were offered diets of either *Ptelea trifoliata* (Rutaceae), *Cornus drummondii* (Cornaceae), *Vitis mustangensis* (Vitaceae), *Clematis drummondii* (Ranunculaceae), or a mixture of grasses. Plant species chosen were components of the adult diet or species upon which feeding had been observed in the field. Fifteen individuals per diet treatment were reared together in 10-l clear plastic tubs with wire-mesh-covered lids. Fresh cuttings of each plant species were collected daily from different plants at BFL and offered in a vial of water. Insects were maintained at 30°C under constant light in an environmental chamber.

Reciprocal survivorship experiments were conducted to determine the role of host plant availability in nymphal host plant selection between localities. In these experiments, field-collected first-instar nymphs from both BFL and Altair were reared on single-diet treatments of *P. trifoliata* and *R. trivialis*. These populations were selected because of their differences in nymphal host use (described in this study) and their geographical proximity (Fig. 1). Sample size, rearing conditions, and feeding regimes were identical to those described above. These experiments were conducted during May and June 1995.

An additional reciprocal survivorship experiment was conducted in late June and early July 1997 using the two nymphal forms occurring sympatrically at Kerrville (LHCP). In this experiment, diet treatment groups of 15 individuals were initiated with 5 first-, 5 second-, and 5 third-instar insects. Different developmental stages were used due to a lack of early instar insects in the field. All other procedures were identical to those described above.

Survivorship data were analyzed using Kaplan-Meier survival analysis (SPSS 7.5). The null hypothesis of all survival functions being equal was tested using the log-rank test. Pairwise differences between survival functions were assessed with the log-rank test following Bonferroni correction for multiple comparisons.

Results

Population-level diets

Population-level host plant use and plant availabilities are summarized in Fig. 2. Nymphal *S. emarginata*

populations were predominantly feeding on *R. trivialis* (Rosaceae) at Altair (where *Rubus* comprised 95% of the diet), BBSP (100%), and LWSP (80%), whereas nymphal populations almost exclusively feeding on *P. trifoliata* (Rutaceae) were found at BFL (93%), PFSP (97%), and Kerrville (KSSP) (95%).

Among populations utilizing *Rubus* as a primary nymphal host plant, only at Altair did adults continue to use *Rubus* as a primary host (67%). The most commonly utilized host plant by adults from BBSP was *Quercus virginiana* (Fagaceae) (46%). At LWSP, *Helianthemum georgianum* (Cistaceae) comprised a majority of the adult diet (74%) (Fig. 2a). Populations utilizing *Ptelea* as a primary nymphal host at BFL and PFSP continued to include *Ptelea* as a primary component of the adult diet, but in reduced proportions (52% and 81%, respectively; Fig. 2b). No data on host plant use by adults were gathered at Kerrville (KSSP).

Host plant use data for insects from Kerrville (LHCP) are presented separately (Fig. 2c). At this site, the two different nymphal forms were found to be host

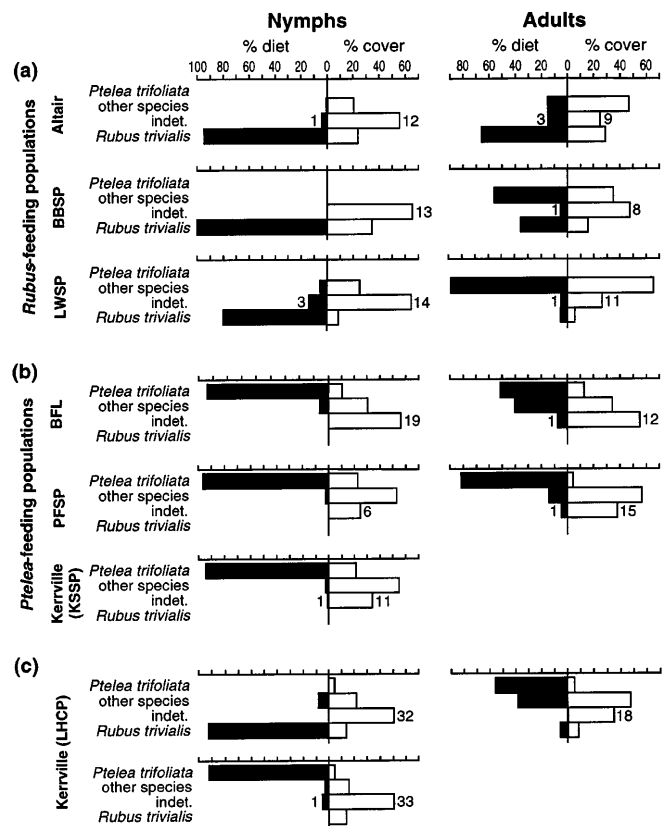


Fig. 2a–c *S. emarginata* nymphal and adult population-level host plant use and plant cover. Host plants other than *Ptelea trifoliata* (Rutaceae) and *Rubus trivialis* (Rosaceae) are grouped as *other species* and are listed in Appendix 1. Indeterminate fecal material and uneaten plants are categorized as *indet.* Numbers next to bars indicate the number of distinct types of unidentified fecal material and number of uneaten plant species. **a** Populations utilizing *Rubus* as a primary nymphal host plant. **b** Populations utilizing *Ptelea* as a primary nymphal host plant. **c** *Rubus*- and *Ptelea*-feeding nymphs occurring sympatrically at Kerrville (LHCP)

plant associated, one feeding primarily on *Rubus* (93%) and the other on *Ptelea* (92%). Patterns of host plant use for the *Rubus* and *Ptelea*-feeding nymphs closely resembled nymphal host plant use found in the other *S. emarginata* populations where the two forms did not co-occur (Fig. 2a, b). Both *Rubus* and *Ptelea* were fed upon by adults at this locality, but the adult diet was dominated by *Ptelea* (55%). Grass, *Juglans major* (Juglandaceae), and *Q. virginiana* were also substantial components of the adult diet (Fig. 2c).

Both nymphal and adult *S. emarginata* populations were highly selective in choosing their diets from among the plants present in their respective habitats (Fig. 2). Host plant frequencies in the diet differed significantly from their expected frequencies at all localities [χ^2 -values ranged from 49.8 ($df = 6$) to 1825 ($df = 2$); $P = 0.0001$ for all comparisons].

Diet breadths (*H*)

Nymphal population-level diet breadths (*H*) were less than adult diet breadths at all localities. Intrapopulation comparisons of nymphal and adult diet breadths yielded significant differences in all but the LWSP and PFSP populations (Fig. 3). When pooled and compared across all localities, the difference between the observed nymphal and adult diet breadths was highly significant (Mann-Whitney test, $z = -2.969$, $p = 0.0015$).

Survivorship experiments

S. emarginata nymphs from BFL failed to survive on diets of *V. mustangensis*, *Clematis drummondii*, and a mixture of grasses. *P. trifoliata* and *Cornus drummondii* were both suitable host plants and supported 80% and 53% survivorship, respectively (Fig. 4). The difference in survivorship between these two treatments was not significant.

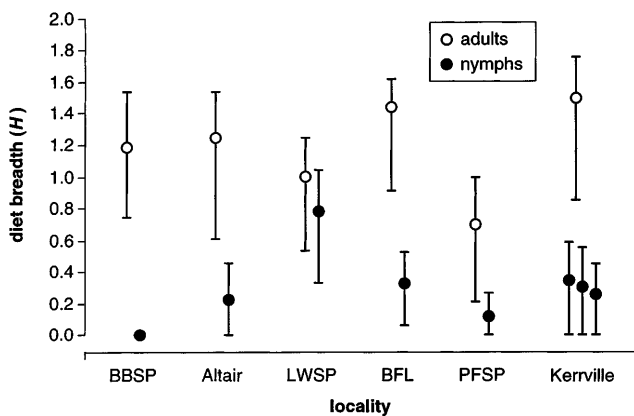


Fig. 3 Population-level diet breadths (*H*) for nymphal and adult *S. emarginata* populations at six Texas, USA localities. Bars represent 95% confidence intervals around observed *H* values

Reciprocal survivorship experiments using nymphs from BFL, a *Ptelea*-feeding population, and from Altair, a *Rubus*-feeding population, yielded significant differences in relative survivorship on the two host species ($P < 0.0001$; Fig. 5a). Insects from BFL were able to survive on both *Ptelea* and *Rubus*, while insects from Altair could survive only on *Rubus*, suffering 100% mortality on *Ptelea* within 6 days. In contrast, BFL insects reared on *Rubus* survived much better than the Altair insects on *Ptelea* ($P = 0.0054$). Differences in survivorship between the three best-performing treatment groups were not significant (Fig. 5a).

Reciprocal survivorship experiments using *Rubus*-feeding and *Ptelea*-feeding nymphs occurring sympatrically at Kerrville (LHCP) also yielded significant differences in relative survivorship on the different hosts ($P < 0.0001$) (Fig. 5b).

Discussion

Geographic structure of specialization

This study demonstrates that geographic differentiation of host plant specialization is present in *S. emarginata*. Sampled populations exhibited substantial developmental variation in host use between the early nymphal instars and adult stages (Figs. 2, 3). When this type of developmental variation was recognized and host use among localities compared, a geographic structure of host plant specificity emerged. Populations were specializing on either *P. trifoliata* or *R. trivialis* in the early nymphal stages. Failure to recognize either developmental or geographic variation in host use could have led to different conclusions. The combined effects of developmental stage and geographic scale on interpretations of *S. emarginata* host plant use are summarized in Fig. 6.

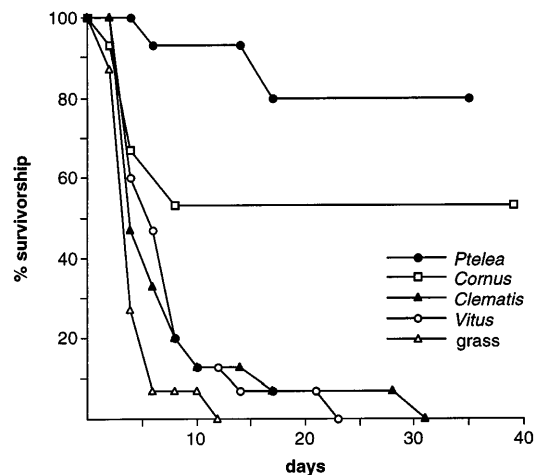


Fig. 4 Survivorship of *S. emarginata* from BFL, a *Ptelea*-feeding population, on five different diet treatments

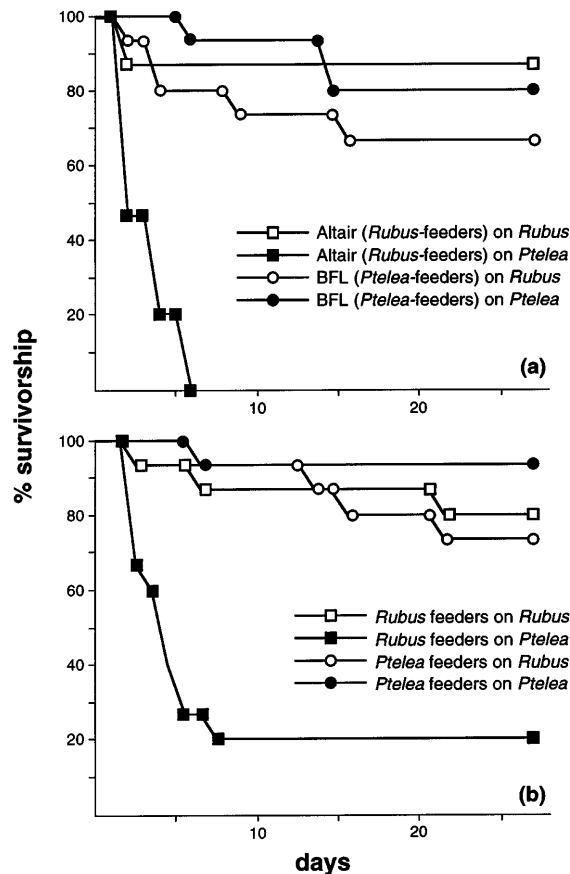


Fig. 5a,b Reciprocal survivorship curves for nymphs. **a** From Altair, a *Rubus*-feeding population, and BFL, a *Ptelea*-feeding population, reared on single-plant diets of either *Ptelea* or *Rubus*. **b** The same experiment utilizing *Rubus*- and *Ptelea*-feeding nymphs occurring sympatrically in Kerrville (LHCP)

Developmental variation in host use

Temporal variation in grasshopper diets, characterized in this study as developmental changes in host use occurring within a population, has been well documented in field studies (Mulkern et al. 1962; Bernays and Chapman 1970; Bailey and Riegert 1971; Banfill and Brusven 1973; Pfadt and Lavigne 1982; Braker 1986). Developmental changes in host use have primarily been attributed either to relatively low mobility of the early instars (Mulkern et al. 1962; Banfill and Brusven 1973) or to temporal changes in host plant availability (Bernays and Chapman 1970; Banfill and Brusven 1973; Bernays et al. 1976). Field studies lacking plant availability data make differentiating between these two factors difficult, if not impossible. In addition, nymphal and adult host plant use in hemimetabolous insects are commonly assumed to be similar (Samways and Sergeev 1997). Thus, developmental variation in host plant use has likely been ignored in many studies.

In *S. emarginata*, a shift occurs from specialized (monophagous) to relatively generalized (polyphagous) feeding at the population level during development (Figs. 2, 3). The design of this study did not allow

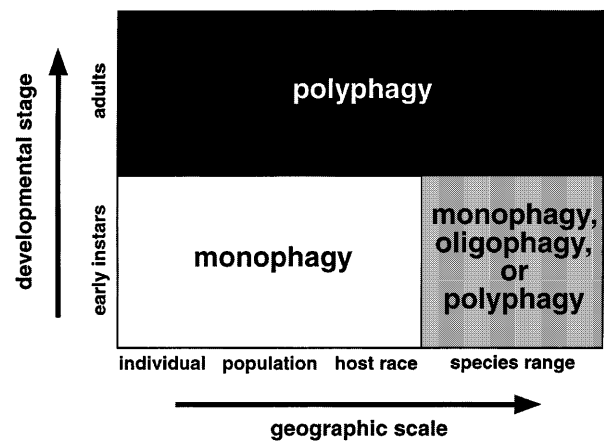


Fig. 6 Interpretation of host plant use in *S. emarginata* is a function of the combined effects of developmental stage and geographic scale. Determination of species-level monophagy, oligophagy, or polyphagy as early instars requires further investigation on a larger spatial scale and could be affected by taxonomic revisions

changes in the diets of individuals to be tracked and quantified, but the proportions of individuals with more than one type of plant material in the feces were greater in adult than in nymphal populations (Mann-Whitney test, $P = 0.008$, $z = -2.585$). The numbers of different plants in the adult population-level diets were also greater than in the nymphal diets (Mann-Whitney test, $P = 0.004$, $z = -2.862$). This suggests that the increase in population-level polyphagy was due to increased individual polyphagy rather than individual monophagy on different host plants. A primary focus in the study of insect-plant interactions has been the search for proximate and ultimate mechanisms that should promote either restriction or expansion of diet breadth (Jaenike 1990; Bernays and Bright 1993; Singer 1994). The shift in *S. emarginata* from monophagy to polyphagy during development offers the unique opportunity to investigate the ecology and evolution of these different strategies in a single species.

Restricted nymphal mobility cannot account for the observed specificity of nymphal host plant use in *S. emarginata*. *S. emarginata* oviposits in the soil and hatchlings are not spatially restricted to a single host plant. Specificity of nymphal host use would not have been observed if posthatching dispersal and feeding were random. Alternative host plants were acceptable and suitable for nymphal survival in *Ptelea*-feeding populations (Figs. 4, 5). Thus, differential mortality as a result of differences in host plant chemistry and morphology is not likely to be an exclusive explanation for the observed patterns of host use. Nymphs were not feeding on host plants in proportion to respective availabilities (Fig. 2), which suggests that host plants were being actively selected. Use of the same host plant at multiple localities supports this idea.

Changes in host plant availability do not account for the observed shift in *S. emarginata* feeding strategy, as the frequency of *Ptelea* and *Rubus* in each habitat

remained relatively constant over time (Wilcoxon signed-ranks test, $P = 0.237$; Fig. 2). Temporal changes in the relative acceptability or suitability of host plants were not investigated and cannot be ruled out as a factors affecting the observed changes in host plant use.

Generalist predators are thought to be an important factor in the evolution and maintenance of restricted host ranges in phytophagous insects (Bernays and Graham 1988). Predation appears to account for host specificity in *S. emarginata*, at least among *Ptelea*-feeding populations. Feeding on *Ptelea* confers gut-content-mediated unpalatability to predators and *S. emarginata* nymphs in *Ptelea*-feeding populations exhibit a density-dependent color polymorphism which results in aposematism at high population densities (Sword 1999). *Rubus* feeding does not confer unpalatability to *S. emarginata* (Sword 1998, 1999), but it may provide mechanical protection against predators. *Rubus* plants have branch thorns as well as surface stipules and can occur in dense low-lying thickets. The notion that *Rubus* represents "enemy-free space" (Jefferies and Lawton 1984) for *S. emarginata* nymphs warrants further investigation.

Why then, should *S. emarginata* switch from monophagy to polyphagy during development? The advantage of polyphagy to individual grasshoppers appears to be due to the mixing of plants in the diet, though the mechanisms resulting in such a mix may be quite varied (Simpson and Simpson 1990; Bernays and Bright 1993). Grasshoppers, as opposed to Lepidopterans and Hemipterans, grow better on a mixture of plants (Bernays and Minkenberg 1997). Polyphagy in grasshoppers is thought to be facilitated by their relatively large size and mobility (Chapman 1990), as well as a large number of chemosensory sensilla which allows them to discriminate among a broad array of plants (Chapman 1982). The shift from monophagy to polyphagy in *S. emarginata* may reflect a developmentally dependent trade-off between the advantage of monophagy (protection from predators in this case) and that of polyphagy, improved growth.

Geographic variation in host use

Geographic variation in grasshopper diets has been demonstrated numerous times (Mulkern et al. 1962; Blackith and Blackith 1966; Mulkern et al. 1969; Bernays and Chapman 1970; Banfill and Brusven 1973; Otte and Joern 1977; Boys 1978; Joern 1979; Boutten et al. 1980; Rowell 1985a; Howard et al. 1994; Sword and Chapman 1994). Differences in host use among localities are generally attributed to differential host plant availability (Banfill and Brusven 1973; Boutten et al. 1980; Rowell 1985a). Local adaptation might also play an important role in grasshopper host plant selection. Sword and Chapman (1994) provided evidence from *S. shoshone* suggesting that observed variation in host use was due to genetic differentiation between popula-

tions, rather than to the availability of a particular host. In addition, Rowell (1985b) concluded that *Rhachicreagra nothra* and *Rhachicreagra anchidiphalara* have evolved preferences for the most abundant available host plant in their respective habitats.

The *Ptelea* and *Rubus* availability data (Fig. 2) would initially seem to indicate that the observed geographic structure of nymphal host plant specificity is accounted for by the presence or absence of either *Rubus* or *Ptelea* in each habitat. The results of reciprocal survivorship experiments between first-instar nymphs from Altair, a *Rubus*-feeding nymphal population, and BFL, a *Ptelea*-feeding nymphal population, clearly demonstrate that host plant availability alone does not account for the observed differences in host use. The insects from Altair were unable to survive on *Ptelea* (Fig. 5a). The possibility of induction of host plant preference (Jermy 1987) has not been eliminated, but seems unlikely as an explanation for these results. No evidence for the presence of induction was found in the closely related *S. shoshone* (Sword and Chapman 1994). Additionally, nymphs and adults of numerous *Schistocerca* species (*S. americana*, *S. damnifica*, *S. obscura*, and *S. nitens*) will not accept *Ptelea* in the laboratory (G.A. Sword, personal observations). Otte (1975) found similar results in the acceptability of *Ptelea* to *S. obscura* and *S. emarginata* nymphs. These results suggest that populations of *S. emarginata* utilizing *Ptelea* as a host plant are specifically adapted to feed on *Ptelea*.

Host-plant-associated genetic differentiation

Studies of diet in polyphagous, phytophagous insects often seek to uncover genetically based trade-offs in performance across hosts to account for plant fidelity (reviewed in Futuyma and Peterson 1985; Jaenike 1990; Via 1990). Under the trade-off hypothesis, an evolutionary increase in fitness experienced by a genotype using one plant results in fitness reductions on alternatives. Herbivores are thought to experience greater costs from using plants other than their normal hosts because they are not adapted to deal with non-host plant selective pressures such as predation and parasitism (Brown et al. 1995), competition (Feder et al. 1995), and plant morphology/chemistry (Futuyma and Philippi 1987). Theoretical investigations have found that host specialization may occur in the absence of performance trade-offs (Fry 1996; Kawecki 1998).

Survivorship experiments in *S. emarginata* suggest that costs exist for non-host plant feeding (Figs. 4, 5). Costs are unapparent, however, for *Ptelea*-feeding nymphs reared on *Rubus* (Fig. 5). Undetected fitness reductions in laboratory settings should not be embraced as a lack of evidence for performance trade-offs (Rausher 1988). Nymphal coloration normally associated with *Ptelea*-feeding *S. emarginata* nymphs may be deleterious for non-host plant feeding in the field (Sword 1999). In the sympatric population at Kerrville (LHCP), the three

surviving individuals in the *Rubus* feeders reared on *Ptelea* (Fig. 5b) were predicted to survive a priori because their coloration resembled that of *Ptelea*-feeding *S. emarginata*. This suggests that a small number of nymphs commonly associated with *Ptelea* were feeding on *Rubus* at this locality. Conceivably, nymphal collection for this study occurred prior to selection. The presence of these nymphs in a sympatric population also offers the possibility for introgression of *Rubus* host preference alleles into *Ptelea* forms or genetic variation for host preference among *Ptelea*-associated *S. emarginata*.

Along with host-plant-associated differences in both performance (Fig. 5) and nymphal coloration (Sword 1998), mtDNA sequence data (E.B. Dopman and G.A. Sword, unpublished data) also suggest genetic differentiation between populations of *S. emarginata* utilizing *Rubus* and *Ptelea*. Depending on the degree of genetic isolation, these host-associated populations may represent host races (Diehl and Bush 1984) or distinct sibling species. Although differentiation may have occurred in allopatry, *Rubus*- and *Ptelea*-feeding nymphs occur sympatrically and genetic differences between them have implications for sympatric speciation via host race formation.

If selection is strong enough to establish a genetic correlation between loci governing performance and host preference traits prior to a host switch, adaptation to a new host plant can effectively reduce gene flow between host forms (Via 1990). In the absence of strong selection, reproductive isolation between sympatric populations is facilitated by resource-specific mating (Bush 1994). In *S. emarginata*, nymphs exhibit extreme resource specificity while adults do not. Adults are strong flyers and mating is not restricted to specific host plants. In sympatric localities such as Kerrville (LHCP), adults of the two forms would be expected to come into contact frequently and potentially mate. If genetic differentiation between these two host-associated forms is occurring in sympatry, we will be forced to re-evaluate our assumptions about the preconditions

for sympatric divergence. Studies of mate choice, host preference, and hybridization in contact areas will be essential in distinguishing between these two host-associated forms as host races with the genetic potential for sympatric speciation, or reproductively isolated sibling species.

Geographic structure of host use in other grasshoppers

It appears as though some New World *Schistocerca* species have a tendency to form associations with specific host plants (Hubbell 1928; Mulkern et al. 1969; Chambers et al. 1996; Sword and Chapman 1994). Therefore, it is not unlikely that a geographic structure of host specificity was found in *S. emarginata*. Host plant use in this study was sampled across a relatively small portion of *S. emarginata*'s range. Only further study will show if a similar geographic structure of host specificity exists throughout the entire range of *S. emarginata*.

Are grasshoppers really more similar to the other phytophagous insects in terms of host plant use than was previously believed? The results of this study are suggestive, but certainly not conclusive. To answer this question definitively, we need replicated field studies of grasshopper diet that adequately document both developmental and geographic variation in host plant use.

Acknowledgements Special thanks to R.F. Chapman and E.A. Bernays who introduced G.S. to insect ecology and kindly commented on an early version of this manuscript. M.C. Singer and L.E. Gilbert provided help and guidance throughout this project. Additional thanks to members of the Gilbert Lab Discussion Group, R. Dudley, P. Stiling, and three anonymous reviewers for comments that improved this paper. T. Wendt of the UT Plant Resources Center, L.E. Gilbert and J. Crutchfield assisted with the plant identifications. Permission to work in Texas State Parks was granted by Texas Parks and Wildlife Department Permit nos. 44-94, 26-95, and 13-96. This project was supported by grants from the Lorraine I. Stengl Endowment to the UT Department of Zoology.

Appendix 1 Host plants other than *Rubus trivialis* (Rosaceae) and *Ptelea trifoliata* (Rutaceae) in *Schistocerca emarginata* population-level diets

Locality	Stage	Percent diet	Percent cover	Plant	
Altair	Nymphs	1	20	<i>Vitus mustangensis</i> (Vitaceae)	
	Adults	5	2	<i>V. mustangensis</i>	
		5	20	<i>Baccharus neglecta</i> (Asteraceae)	
		4	19	Grass	
		2	3	<i>Cissus incisa</i> (Vitaceae)	
BBSP	Nymphs			<i>Lythrum alatum</i> (Lythraceae)	
	Adults			No other plants eaten	
		46	2	<i>Quercus virginiana</i> (Fagaceae)	
		8	4	<i>Lechea mucranata</i> (Cistaceae)	
		1	2	<i>Ambrosia psilostachya</i> (Asteraceae)	
LWSP	Nymphs	1	28	grass	
		3	1	<i>Rudbeckia hirta</i> (Asteraceae)	
	Adults	2	25	Grass	
		74	17	<i>Helianthemum georgianum</i> (Cistaceae)	
		8	44	Grass	
		3	2	<i>A. psilostachya</i>	
		3	2	<i>Celtis reticulata</i> (Ulmaceae)	
BFL	Nymphs	1	1	Indeterminate Fabaceae	
		5	18	Grass	
		2	2	<i>Ratibida columnifera</i> (Asteraceae)	
	Adults	<1	3	<i>Croton fruticulosus</i> (Euphorbiaceae)	
		<1	8	<i>V. mustangensis</i>	
		18	10	<i>V. mustangensis</i>	
		10	1	<i>Cornus drummondii</i> (Cornaceae)	
PFSP	Nymphs	7	5	<i>Croton lindheimerianus</i> (Euphorbiaceae)	
		5	15	Grass	
		<1	5	<i>Celtis laevigata</i> (Ulmaceae)	
	Adults	<1	2	<i>Heterotheca latifolia</i> (Asteraceae)	
		3	47	Grass	
		<1	5	<i>Solanum elaeagnifolium</i> (Solanaceae)	
		9	2	<i>Prosopis glandulosa</i> (Fabaceae)	
Kerrville (KSSP)	Nymphs	5	3	<i>S. elaeagnifolium</i>	
		<1	53	Grass	
		2	7	Grass	
	Kerrville (LHCP)	Nymphs (<i>Rubus</i>)	1	47	<i>Lonicera japonica</i> (Caprifoliaceae)
			6	6	<i>R. hirta</i>
		Nymphs (<i>Ptelea</i>)	2	17	Grass
			3	17	Grass
Adults	11	30	Grass		
	10	2	<i>Juglans major</i> (Juglandaceae)		
	8	4	<i>Quercus virginiana</i> (Fagaceae)		
	5	3	<i>C. lindheimerianus</i>		
	3	4	<i>Salvia texana</i> (Lamiaceae)		
	1	6	<i>S. elaeagnifolium</i>		

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