Individual advantages to ecological specialization: insights on cognitive constraints from three conspecific taxa

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The information-processing hypothesis (IPH) posits that specialist herbivores should make host-associated decisions more effectively than generalists and thus enjoy associated fitness advantages that may help explain the evolutionary prevalence of host-specific insects. This is because generalists must evaluate a greater diversity of host plants/cues than specialists and thus face a cognitive challenge that is predicted to constrain the efficiency and accuracy of their choices. Here, we present the first individual-level evaluation of this hypothesis. This involved experimentally quantifying the specificity, efficiency, and accuracy of host selection, as both larvae and adults, for many individuals representing each of three 'host forms' of *Neochlamisus bebbianae* leaf beetles. These experiments provided several significant findings: host forms differed in larval specificity, with the more specialized host forms more efficiently and accurately selecting optimal hosts as both larvae and adults. Positive correlations between larval specificity and both efficiency and accuracy across test individuals provided the most direct evidence to date for a biological association between these variables. Our results thus provide strong and consistent support for the IPH at the level of both populations and individuals. Because individual *N. bebbianae* make many host-associated decisions in nature, our results suggest that cognitive constraints may play a major role in the evolutionary dynamics of ongoing ecological specialization and diversification in this species.

Keywords: Chrysomelidae; diet breadth; foraging behaviour; insect–plant interactions; neural constraints; niche width

1. INTRODUCTION

Potential selective advantages to ecological generalism are easily imagined. For example, generalists will often have access to a greater resource base, a more nutritionally balanced diet, and a greater capacity to confront variable environments than ecological specialists (e.g. Bernays & Minkenberg 1997; Bernays *et al.* 1994; Funk & Bernays 2001; respectively). Nonetheless, in the most species-rich animal taxa—the herbivorous insects—most species are quite ecologically specialized, using host plants from a single plant family, genus, or even species, while ignoring most locally available plant taxa (Futuyma & Moreno 1988; Jaenike 1990; Bernays & Chapman 1994). The phylogenetic finding that transitions from herbivore generalism to specialization occur at higher rates than the alternative (Nosil 2002) offers a historical accounting for this pattern and underscores long-standing interest in its evolutionary causes.

Many hypotheses have been offered to explain the somewhat counterintuitive prevalence of herbivore specialization as an evolved ecological strategy (Jaenike 1990). One hypothesis that has only recently come under empirical test despite the age and esteem of its conceptual origins (Levins & MacArthur 1969) is the 'neural constraints' or 'information-processing' hypothesis (IPH; Bernays & Wcislo 1994; Bernays 2001). This hypothesis is based on two assumptions that generate a specific prediction. The first assumption is that constraints exist

on the amount of information that can be processed and the number and accuracy of decisions that can be made in a given period of time. The second assumption is that generalist herbivores encounter more host-associated information/decisions than specialists. The prediction is that specialists should thus exhibit greater efficiency and accuracy in host selection. If this prediction holds, then specialists should enjoy efficiency/accuracy-associated fitness advantages over generalists that promote the evolution of ecological specialization through natural selection.

The first assumption of the IPH is essentially a truism as no information-processing system can be infinitely efficient. That such cognitive constraints have biological consequences is reflected, for example, in the prevalence of the phenomenon of 'selective attention', an aspect of behavioural specialization, across animal taxa (Dukas 2004). All animals exist in a complex and stimuli-rich environment and this strategy allows them to filter out most stimuli while focusing on and more effectively processing those that are most important, with consequences for fitness (e.g. Lemmon 1991). This strategy would be of no advantage if all stimuli could be simultaneously processed with maximum efficiency.

The second assumption reflects herbivore biology. When a specialist evaluates whether or not plant-associated stimuli indicate the presence of its host, this decision might be based on the presence/absence of a particular chemical profile or even a single chemical that is diagnostic of its particular host plant (Bernays & Chapman 1994). Thus, in

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anthropomorphic terms, this specialist can afford to pay attention to and evaluate a small set of relevant cues while ignoring most plant-associated stimuli. By contrast, when a generalist encounters a plant, it must be attentive to, and evaluate the possible existence of, each of a broader array of stimuli associated with its broader array of acceptable hosts. (Importantly, even the most generalized insects will use only a fraction of locally available hosts. Thus, no generalist has the cognitively simplest option of all—accepting all plants without evaluation.)

The prediction of the IPH has received support from several recent experimental studies on insect herbivores. One approach has involved manipulative experiments of conspecific individuals whose foraging efficiencies were evaluated either as a function of the number of hosts (multiple versus single) encountered in behavioural trials (Bernays 1999; Bernays & Bright 2001) or after a period of conditioning on specialist versus generalist diets (Bernays 1998). In each of these studies, the lab-created specialists foraged more efficiently. Other studies have treated interspecific comparisons between naturally generalist versus specialist species. These have shown specialists to be more efficient (Oppenheim & Gould 2002), more accurate (Janz & Nylin 1997), or both (Bernays *et al.* 2004) in their selection and use of host plants. Two studies that compare conspecific populations exhibiting divergent degrees of specificity have similarly demonstrated the greater efficiency (Bernays & Funk 1999) and accuracy (Janz & Nylin 1997) of more specialized forms. An additional study of conspecific populations evaluated, and found no evidence for, a possible trade-off between host-use efficiency and accuracy (Janz 2003). Such conspecific comparisons are particularly valuable as they control for the evolutionary history of the evaluated entities and provide direct insights about ongoing evolution in the traits of interest (e.g. Funk & Bernays 2001).

The present study compares three conspecific taxa in the first individual-level analysis of the IPH. Here, we quantify host-use specificity, efficiency, and accuracy for each of many individuals of each study taxon as both larvae and adults. We use these data to evaluate the relationship between host specificity and both the efficiency and accuracy (hereafter collectively referred to as 'efficacy') of host-use at both the population and individual levels. This individual-level approach allowed us to test whether patterns of variation among individuals within populations support the interpretations of population- and species-level differences described above, and also evaluated here. Specifically, positive correlations between the degrees of specificity and efficacy across individuals would provide evidence supporting a biological relationship between these variables and thus further corroborate the plausibility of the IPH.

2. MATERIAL AND METHODS

(a) *Study taxa*

Our study system for these investigations is *Neochlamisus bebbianae* (Brown), an eastern North American species of chrysomelid leaf beetle that uses particular tree species from six genera as host plants (Karren 1972; Funk 1998). These six types of host-associated *N. bebbianae* populations (hereafter referred to as 'host forms') most readily use,

grow, and survive on foliage from the plant they use in nature (the 'native host'), but accept the native hosts of other host forms to a lesser degree (Funk 1998; D. J. Funk, unpublished data). The three *N. bebbianae* host forms associated with particular alders (*Alnus rugosa/incana*, *A. serrulata*; Betulaceae), red maple (*Acer rubrum*; Aceraceae), and Bebb's willow (*Salix bebbiana*; Salicaceae) are the focus of the present study. These host forms are sympatric in much of northeastern North America, where their hosts commingle in the same habitats. These beetles exist at modest densities (D. J. Funk, personal observation) and have a single generation per year. All life activities occur on the native host, and adults will fly among individual plants.

(b) *Test animals and conditions*

Experiments were conducted at Vanderbilt University. All test animals were reared from eggs collected on host plants in New York, New England, and southern Quebec. All foliage used for beetle rearing and testing was regularly collected and shipped in coolers from Oswego, New York, where these host forms naturally occur. When not being assayed, test animals were individually maintained in 5 cm Petri dishes with a fragment of native host foliage (e.g. alder foliage for the alder host form) and a moistened filter paper, both of which were replaced every other day. Petri dishes were stacked in clear plastic boxes lined with damp paper towels and sealed with plastic wrap and the box lid. These boxes were stored in incubators at 24 °C with a 14 : 10 h light–dark photoperiod. Eggs and pupae were checked daily for emergence of larvae and adults. Experiments (see below) were initiated with 50 hatchling larvae of each host form. These larvae participated in efficiency/accuracy assays on the day of their emergence, and participated in the specificity assays the following day. Upon development into adults, these individuals participated in specificity assays the day they emerged and participated in efficiency/accuracy assays upon the accumulation of sufficient test animals, always within three weeks of emergence. The same individuals assayed as larvae were also assayed as adults. These 'Petri dish assays' yield patterns of host use highly similar to those from assays involving longer-term beetle responses to sapling trees (Funk *et al.*, unpublished data). They thus provide an accurate yet efficient and highly controlled means of evaluating host-associated behavioural variation.

(c) *Specificity assays*

To estimate degree of host specialization, individual test animals participated in 24 h no-choice feeding trials. For these trials, each individual was placed in a 5 cm Petri dish lined with moistened filter paper and provided with leaf discs removed from foliage using a standard hole-punch tool. Following each trial, total feeding damage on leaf discs was scored under a dissecting microscope fitted with a 20×20 gridded ocular. Magnification was set so that one disc was the width of the grid and thus represented 314 grid units. Each test animal participated in three consecutive feeding trials, with each trial using discs from a different test plant (alder in one, maple in another, willow in another). Order of test plant presentation across the three trials was systematically varied across replicates to avoid possible bias due to effects of prior testing. Data from larvae consuming <10 units of foliage and from adults consuming <50 units were discarded to avoid including results from non-vigorous individuals.

The three raw feeding scores for each test individual were converted into the three proportions of total feeding exhibited on each test plant. We used an angular transformation of the variance in these proportions as a metric of individual host specificity. Using this metric, individuals that feed a comparable amount on all three plants have low specificity values while those that feed largely on one plant to the exclusion of the others have high values.

(d) *Efficiency/accuracy assays*

These behavioural assays were performed in an environmental chamber at 28 °C and >75% humidity and employed 5 cm Petri dishes with moistened filter papers to which one disc from each of the three test plants was added. These trials were initiated by the addition of a single test animal to each Petri dish. Over these 2 h trials, the location of each test individual (on alder, maple or willow discs, or the test arena) was recorded at 5 min intervals. An individual was considered to be 'on' a disc when at least two legs were in contact with it. Data from individuals that were observed on discs for ≤ 2 of the 24 observations were discarded prior to analysis.

Our index of individual efficiency (i.e. speed) was the number of observations remaining in the trial when the individual was first observed on its native host. This value thus varied between zero (if an individual was never observed on the native host disc) and 23 (if the individual reached the native host by the first observation). Our index of individual accuracy was the number of observations of a beetle on its native host divided by the total number of observations on any of the three plant discs. Here, accuracy refers to the choice of the test plant yielding highest fitness, which for each of these host forms is its native host, on which growth and survivorship are greatest (Funk 1998; D. J. Funk, unpublished data).

(e) *Statistical analyses*

Owing to deviations from normality, we primarily used non-parametric methods. To test for differences among host forms in mean individual specialization, efficiency, and accuracy, data were converted to ranks and analysed using a Kruskal–Wallis ANOVA followed by Dunn's non-parametric means comparisons for unequal sample sizes (Dunn 1964; Zar 1996). Additionally, a non-parametric two-way ANOVA (the Scheirer–Ray–Hare extension of the Kruskal–Wallis test; Sokal & Rohlf 1995) on host form and life stage (larva versus adult) was used to isolate the effect of life stage on degree of specificity. To test for associations between individual-level specificity and efficacy while controlling for differences among host forms, ANCOVAs were applied to both the larval and adult datasets. Both parametric ANCOVAs (on angular-transformed data) and non-parametric ANCOVAs (on data converted to ranks; Conover & Inman 1982) were conducted. The host form term in these ANCOVAs does not bear on the major questions addressed here and is not further discussed. Because the IPH makes *a priori* predictions of a positive association between individual specialization and efficacy, one-tailed hypothesis testing was employed.

3. RESULTS

(a) *Host form comparisons*

Mean larval specificity varied significantly among host forms ($H_{d.f.=2} = 16.6$; $p < 0.001$), with the alder host form exhibiting the highest specificity and the maple host form

proving to be least specialized (figure 1c). Host forms also varied significantly in larval efficiency ($H_{d.f.=2} = 61.7$; $p < 0.0001$) and accuracy ($H_{d.f.=2} = 21.3$; $p < 0.001$). For both of these latter metrics, the two more specific host forms exhibited significantly higher values than did the more generalized maple host form (figure 1e,g). Mean adult specificities were highly homogeneous among host forms ($H_{d.f.=2} = 2.1$; $p = 0.35$; figure 1d) and significantly higher than those of larvae ($H_{d.f.=2} = 23.16$, $p < 0.001$).

These latter results do not reflect the intuitive explanation—a tendency of adults from each host form to feed only during the trial with their native host. Indeed, plotting the feeding data as mean proportions of total feeding exhibited on each plant across individuals of each host form (figure 1a,b) demonstrates that adults fed as much on alternative test plants as did larvae, and that adults and larvae exhibited highly similar patterns of divergence among host forms in feeding tendencies. Thus, adults did not exhibit stronger preferences than larvae for their native hosts. Our data do reflect an increased tendency to feed during only one of the three feeding trials—only 5% of test larvae entirely restricted their feeding to a single trial while 35% of adults did so. However, the trial during which an adult fed was often not the trial featuring its native host. For our metric, feeding entirely on a non-host will yield specificity values equivalently high to feeding entirely on a native host, hence our results. These observations suggest that adults were not sufficiently motivated to feed in each of the three trials but instead satiated themselves on the first acceptable test plant, then largely discontinued feeding. These assays thus failed to provide biologically accurate estimates of each individual's intrinsic willingness to feed on all test plants and yielded erroneous estimates of individual-level adult specificity that ensured non-significant results in the ANCOVAs that employed these data (below). Future adult experiments will incorporate starvation periods between feeding trials to ensure continued motivation and accurate results.

In contrast to the specificity estimates, adult efficiency ($H_{d.f.=2} = 7.0$; $p < 0.05$) and accuracy ($H_{d.f.=2} = 20.6$; $p < 0.0001$) did significantly vary among host forms, exhibiting patterns similar to those of the larvae (figure 1f,h). The apparent appropriateness of these assays and the correspondence of their findings with larval results offer them as further, adult, support for the IPH.

(b) *Individual-level correlates of specificity*

ANCOVA revealed a significantly positive association between individual-level specificity and efficiency for the larval data (table 1; figure 2a). The association between larval specificity and accuracy was significant in the parametric analysis and marginally non-significant in the non-parametric analysis (table 1; figure 2b). Analyses of these relationships for adults provided no significant effect of specificity (efficiency, $F_{1,75} = 0.88$, $p = 0.35$; accuracy, $F_{1,75} = 0.06$, $p = 0.81$).

4. DISCUSSION

(a) *Hypotheses on the evolution of ecological specialization*

Why should a species shun most available resources and evolve to use just a few? Many hypotheses have been

Figure 1. Results from assays of host use behaviours in alder-, willow- and maple host forms of *N. bebbianae* as larvae and adults. (a, b) Raw population-level results from no-choice feeding trials, (c, d) mean individual host specificity, (e, f) mean individual host location efficiency, and (g, h) mean individual host use accuracy (see text for definitions of terms). (c) to (h) employed Kruskal–Wallis ANOVA followed by Dunn’s non-parametric means comparisons (see table 1). Different letters indicate significant differences ($p < 0.05$).

offered as potential explanations for the existence of such ecologically specialized taxa and especially for their predominance among herbivorous insect species. Various hypotheses invoke chemical coevolution, tradeoffs, the exploitation of enemy-free space, escape from interspecific competition, the capacity to reliably find mates at habitat-

specific sites, and so on as potential explanations for host specificity (Ehrlich & Raven 1965; Futuyma & Moreno 1988; Jaenike 1990).

The present study treats an additional and potentially complementary hypothesis. The IPH suggests that cognitive constraints entail that generalists, forced to

Table 1. ANCOVAs on rank-transformed (non-parametric) and angular-transformed (parametric) data testing the effect of individual specialization on efficiency and accuracy of *N. bebbianae* larvae in host-associated decisions. (Overall ANCOVA on efficiency: non-parametric $r^2=0.12$; parametric $r^2=0.15$; Overall ANCOVA on accuracy: non-parametric $r^2=0.17$; parametric $r^2=0.19$ (N, non-parametric; P, parametric).)

variable	analysis	source	d.f.	SS	F	p
efficiency	N	host form	2	17019.9	5.50	0.005
		specificity	1	5017.7	3.24	0.037
	P	host form	2	643.0	4.37	0.014
		specificity	1	516.7	7.02	0.009
accuracy	N	host form	2	28483.0	8.86	0.0002
		specificity	1	4371.2	2.72	0.101
	P	host form	2	2.887	9.82	<0.0001
		specificity	1	0.598	4.09	0.045

evaluate more varied host-associated stimuli, exhibit reduced behavioural efficacy compared to specialists, which enjoy higher relative fitness as a result. For insect herbivores, the fitness advantages of more *accurately* choosing optimal host resources are readily appreciated. Eggs laid on plants yielding superior larval growth and survivorship promote maternal fitness. Feeding on such plants may further increase individual fitness through elevated longevity and fecundity. The fitness advantages of *efficiently* finding, selecting, and using host resources are probably twofold. First, elevated efficiency increases rates of such activities as feeding, oviposition, and mate-finding, thereby increasing growth rates (and potentially generations per year), realized fecundity, and opportunities for reproduction, respectively. Second, by decreasing the time required for activities (such as host location) that leave an insect vulnerable to predation, increased efficiency may reduce susceptibility to predators and the need to maintain vigilance against them. The fitness consequences of exposure to predators are illustrated by the high mortality that natural enemies can inflict on herbivore populations (e.g. > 90%: Hochberg & Ives 2000; Mira & Bernays 2002). Notably, predation rates have been shown to be 100 fold greater when caterpillars are actively foraging rather than at rest (Bernays 1997). In sum, if specialists make faster, more accurate decisions, it seems biologically likely that selection should favour alleles promoting greater specificity, other things being equal.

(b) Support for the information-processing hypothesis from *Neochlamisus bebbianae*

The present study tests the IPH in three host forms of the leaf beetle *N. bebbianae*, thus presenting the third test of this hypothesis in conspecific herbivore populations. This work differs from prior investigations in additionally adopting an individual-level approach and in evaluating both larval and adult life stages. Results demonstrated that our study taxa differ significantly in their mean level of individual specificity, with the more specific host forms exhibiting significantly greater efficiency and accuracy than the most generalist host form as both larvae and adults. The individual-level specificity of larvae also proved to be positively and significantly correlated with individual efficiency as well as with individual accuracy. This first finding of the IPH-predicted relationship among individuals within populations lends important support to earlier inferences based on coarser-scale comparisons of

Figure 2. Association between individual specificity and (a) efficiency and (b) accuracy for each host form. Data and best-fit lines are plotted separately here for illustrative purposes. See table 1 for quantitative and statistical data summaries.

populations or species. In sum, our findings provide strong support for the IPH across intraspecific taxa, life stages, and individuals. In doing so our study adds to a small but growing body of evidence indicating that cognitive constraints contribute to the evolution of specialization in herbivorous insects (Bernays 2001).

(c) Neural constraints and *Neochlamisus*

Even if the cognitive constraints on behaviour predicted by the IPH are taxonomically general, their actual fitness consequences will vary across species. For example, these will depend on the frequency of host selection events and thus the number of opportunities for the efficacy of associated behaviours to affect fitness. In the case of *Neochlamisus*, such opportunities seem modest for larvae,

which generally develop entirely on their natal plant and thus do not commonly evaluate alternative plants. By contrast, adults must repeatedly locate and select host plants. Females lay dozens of eggs (Funk 1998) but typically only one egg per leaf, and often change plants between oviposition events (Brown & Funk 2005; D. J. Funk, personal observation). Furthermore, these beetles mate on their host plants and with multiple individuals (Funk 1998). These animals exist at sufficiently low densities that movement between plants must generally be required for each such mating. Because host plants commonly intermingle in the same habitats, adults will commonly encounter alternative hosts in making their many host-use decisions.

In combination with this study's support for the IPH and intrinsic individual-level variation, these observations suggest that degree of host specificity is likely to have important consequences for the fitness of *N. bebbianae* leaf beetles and for the evolutionary dynamics of ecological specialization among its host forms.

This research could not have been conducted without the consistent contributions of host plant foliage provided by Richard and Judith Funk. We thank Patrick Abbot, Elizabeth Bernays, Manuel Leal, Michael S. Singer, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. Chris Brown, Eric Janson, and Mark Mandel helped in beetle maintenance. S.P.E. was funded by Vanderbilt University and D.J.F. by the National Science Foundation (DEB0221262) during this study.

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