

Variation of butterfly diet breadth in relation to host-plant predictability: results from two faunas

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Host-plant data for North American and Australian butterflies were used to test the hypothesis that larval diet breadth increases with decreasing resource predictability (where the latter was estimated by host-plant growth-form/duration). For each region in turn we compared the diet breadths of butterflies which utilise herbaceous host-plants with those of species having woody hosts. For North America alone we also compared the diet breadths of species having annual hosts with those utilising perennial hosts, and the diets of species having herbaceous-annual hosts with those using woody-perennial hosts. Studies of diet breadth may be biased by the host taxonomic level which contributes most to the diet index used. For example, the results of analyses which employ indices based on numbers of families of hosts utilised may differ from those using indices based on counts of host species or genera. To investigate this potential problem we performed cross-species analyses where diet breadth was defined in turn as the number of host species, genera, or families eaten. We found that using different taxonomic levels did give inconsistent results. To avoid this we employed phylogenetic diet breadth indices in comparative analyses of Independent Contrasts. The former incorporate information from the whole of the host-plant phylogeny, whilst the comparative method eliminates any confounding effects of butterfly phylogeny. The results indicated that there is a phylogenetic component to butterfly diet breadth. They also largely differed from those of the cross-species investigations, although there were similarities (i.e. results differed between regions and varied according to whether the whole fauna or just endemics were investigated). Our results suggested that in both regions, non-endemics which feed on herbaceous plants have wider diet breadths than non-endemics which utilise woody hosts. However, we found no consistent evidence that the diet breadths of endemics increase with decreasing resource predictability (as estimated here).

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Theoretical studies have mostly suggested that insect diet breadths will expand when host-plants are unpredictable in space and/or time (e.g. reviews by Jaenike 1990 and Mayhew 1997; but see Ward 1992) and this has been found in a number of cases (e.g. several orders of insects (Cates 1981); exopterygote sap sucking insects (Brown and Southwood 1983, Loye 1992); leafhoppers (Novotný 1994); *Drosophila* (Jaenike 1978); and acridids (Joern 1979; but see Rowell 1978)). In contrast, studies of Lepidoptera have produced contradictory

results, with even different analyses of the same fauna conflicting (cf. Futuyma 1976, Slansky 1976, Hayes 1982, Niemelä et al. 1982, Gaston and Reavey 1989, Janz and Nylin 1998). This may partly be due to differing definitions of diet breadth between studies (Jaenike 1990).

In this study we used surrogates for host-plant predictability in order to test the hypothesis that the diet breadths of butterflies increase as host predictability declines. To test the universality of any patterns we

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found, we analysed host data for the butterfly faunas of two distinct regions: North America and Australia. Annual and/or herbaceous plants are generally less predictable in space and time than are perennial and/or woody plants (see for example Feeny 1975, 1976, Cates 1981). Using new data and methods we therefore compared the diet breadths of butterflies which utilise herbaceous hosts (hereafter “herb feeders”) with those using woody hosts (“woody-plant feeders”). As host-plant duration data were available for North America, we also compared the diet breadths of a) butterflies which utilise annual hosts (“annual feeders”) with those having perennial hosts (“perennial feeders”), and b) species which utilise herbaceous-annual hosts (“herbaceous-annual feeders”) with those having woody-perennial hosts (“woody-perennial feeders”). Note that these categorisations are not statistically independent of one another: our rationale for performing separate analyses is given below.

Previous investigations of diet breadths (e.g. Joern 1979, Novotný 1994, Fiedler 1998, Janz and Nylin 1998) have generally employed indices which were based on numbers of host taxa utilised. However, it is likely that the results of such studies will differ according to the host taxonomic level which contributes most to the index, since two host taxa (e.g. two plant families) are not phylogenetically equivalent entities unless they happen to be sisters (Symons and Beccaloni 1999). We investigated this potential problem by performing cross-species analyses of diet breadths for the respective numbers of host species, genera and families used per butterfly species. We then compared these results with those of analyses employing phylogenetic diet breadth indices. The latter incorporate information from all levels of the host phylogeny: only these are likely to reflect the overall similarities (or differences) between hosts (e.g. Farris 1979). We employed three such indices as each one produced a single unequivocal and unbiased estimate of an aspect of diet breadth (see Symons and Beccaloni 1999 for a detailed discussion of these). The use of several different phylogenetic indices in concert makes it possible to determine whether diet breadth differences are due to variation in the number of species consumed, or due to the relative relatedness of hosts (see discussion below). It is also possible to determine the degree to which hosts cluster as nearest neighbours on the phylogeny (Symons and Beccaloni 1999).

Butterfly species may have similar diets simply as a result of shared ancestry, and not as a result of the selective regime they have experienced. It is therefore important to remove any possible confounding effects of butterfly phylogeny so as to make comparisons between statistically independent entities (Harvey and Pagel 1991). In order to do this we employed a comparative method in our analyses of diets as measured by phylogenetic diet breadth indices and by numbers of host species.

Non-native plants generally have fewer species of insect associated with them than native species (e.g. Southwood 1961). Thus, it is likely that the introduced component of the flora will not exhibit ecological patterns as clearly as the native flora which has been in the region for much longer. To investigate whether this is the case, we performed separate analyses of the native and introduced components of diets in addition to studying entire diets.

Finally, we made comparisons of endemic butterflies only in addition to conducting analyses of the entire fauna. We did this because the inclusion of non-endemics risks the omission of hosts which are only utilised by these species in areas outside the regions we investigated here and which therefore did not feature in our host data. Furthermore, endemics are more likely than non-endemics to reflect the ecology of a region since they will generally have spent a greater proportion of their evolutionary histories in or near it. For these reasons we feel that analyses of endemics’ diets give the most representative results.

Methods

Data sources and cross-species analyses

We considered only butterfly species native to the mainlands of America north of Mexico and Australia. In compiling host records the following were excluded: doubtful records; ‘oviposition’ records; records of hosts only known to be utilised in captivity; records where the plant or butterfly species name was not recorded or was in doubt; and host records for introduced butterflies (4 North American and 2 Australian species). We obtained a total of 2844 North American host records (441 butterfly species with 1532 hosts) and 1355 Australian host records (288 butterfly species with 815 host species). Our dataset included information for ca 81% of North American and ca 78% of Australian endemic butterfly species.

Only folivores were included in our analyses: all species with at least one record of feeding on other plant structures were excluded (64 North American and 42 Australian species), as were carnivores (1 North American and 5 Australian species). Herbivores which utilise plant parts other than leaves were excluded because they may represent a different guild (see Fiedler 1991) and because the plant parts eaten have different predictabilities and chemistries to leaves. Approximately 48% and 64% of these species in North America and Australia, respectively, were not recorded as using leaves at all; it is unclear what proportion of the remaining species’ diets is made up of leaves. Species thus eliminated belonged to the family Hesperidae (*Megathymus* and related genera) in North America and the family Lycaenidae in both regions.

Table 1. Numbers of species of butterflies and mean numbers of host taxa in each of the analyses conducted. Mean values are given for the following diet partitions: A = all hosts, N = native hosts alone, and I = introduced hosts alone.

Butterfly division	Number of butterfly species			Mean number of								
				Host families			Host genera			Host species		
	A	N	I	A	N	I	A	N	I	A	N	I
North America												
All herb feeders	205	197	77	1.4	1.3	1.3	3.9	3.1	3.1	6.9	5.6	4.0
All woody-plant feeders	119	112	28	1.6	1.6	1.5	2.3	2.1	2.0	4.5	4.2	2.3
Endemic herb feeders alone	109	106	29	1.2	1.2	1.1	3.1	2.7	2.1	5.7	5.2	2.6
Endemic woody-plant feeders alone	48	48	7	1.5	1.5	1.4	2.5	2.3	2.1	5.0	4.7	2.1
All annual feeders	25	21	16	1.3	1.3	1.1	4.6	3.6	3.1	7.9	6.3	4.1
All perennial feeders	330	316	95	1.4	1.4	1.4	3.0	2.6	2.4	5.5	4.8	3.1
Endemic annual feeders alone	10	9	6	1.0	1.0	1.0	4.7	3.7	2.5	8.1	6.9	3.2
Endemic perennial feeders alone	160	158	32	1.4	1.3	1.2	2.8	2.6	2.0	5.3	4.9	2.4
All herbaceous-annual feeders	23	21	14	1.3	1.3	1.1	5.0	3.6	3.4	8.5	6.3	4.5
All woody-perennial feeders	119	112	28	1.6	1.6	1.5	2.3	2.1	2.0	4.5	4.2	2.3
Endemic herbaceous-annual feeders alone	10	9	6	1.0	1.0	1.0	4.7	3.7	2.5	8.1	6.9	3.2
Endemic woody-perennial feeders alone	48	48	7	1.5	1.5	1.4	2.5	2.3	2.1	5.0	4.7	2.1
Australia												
All herb feeders	102	93	33	1.2	1.2	1.2	2.0	1.5	2.2	2.9	2.2	2.6
All woody-plant feeders	112	109	26	2.0	1.9	1.5	3.8	3.0	4.8	6.9	5.4	7.1
Endemic herb feeders alone	63	61	6	1.1	1.1	1.0	1.3	1.2	2.0	2.3	2.1	2.5
Endemic woody-plant feeders alone	51	51	4	1.6	1.6	1.3	2.8	2.2	8.8	5.9	4.9	12.8

Overall we analysed a total of 2210 North American host records for 377 butterfly species (123 genera in 5 families). These utilise 1279 host species in 473 genera and 85 families. Leaf feeders represented about 82% of the North American endemics for which we had records. The majority of North American records (i.e. 2075) were taken from Scott (1986); the remainder were obtained from 13 references, except four that were personal communications (Appendix A). One thousand one hundred and seventy-two host records were analysed for a total of 246 Australian butterfly species (93 genera in 5 families). These utilise 723 host species in 351 genera and 83 families. Leaf feeders represented ca 91% of the endemics for which we had records. Most of these records were taken from Common and Waterhouse (1981) and Dunn and Dunn (1991) (683 and 250 records, respectively), whilst the remainder were obtained from 61 references (Appendix A).

Host-plants were assigned to one of three groups as follows: “herbaceous plants” = forbs and grasses; “woody plants” = epiphytic shrubs, shrubs, shrubs/trees, and trees; and “unclassifiable” = growth-form unknown, epiphytes, “herb/shrubs”, and vines. Australian growth-form data were taken from the literature, whilst North American growth-form/duration data were taken from the PLANTS database (USDA NRCS 1997). The latter contained some obvious errors which we corrected (e.g. some trees are classified as being both trees and grasses). Butterflies were classed as herb feeders, woody-plant feeders or “unclassifiable” if greater than 50% of their hosts belonged to one of these groups (as defined above). Insects with “unclassifiable” diets were excluded from the analyses: these represent about 14% of North American and ca 13% of Australian species. In addition, North American butterflies were also divided into a) predominantly annual or perennial feeders and b) herbaceous-annual or woody-perennial feeders, according to the growth-form/duration of the majority of their hosts (Table 1). For the first of these divisions about 6% of species had “unclassifiable” diets, whilst for the second this figure was approximately 17%.

We identified the following sets of host-plants for each butterfly species: a) all hosts, b) natives alone, and c) introduced species alone. We performed cross-species comparisons using each of these host sets separately to determine how different definitions of diet breadth affected results. For each region and set of hosts, diet breadth was measured (in turn) as the numbers of host families, genera and species utilised per butterfly species. Host generic and family placements followed Brummitt (1992). We analysed endemics alone in addition to making comparisons across all butterfly species in each region. Diet breadth distributions for a) herb vs woody-plant feeders, b) annual vs perennial feeders, and c) herbaceous-annual vs woody-perennial feeders, were compared using Mann-Whitney two sample tests corrected for ties (Sokal and Rohlf 1995). Comparisons

b) and c) were made for North America only. We did not attempt to remove any confounding effects of butterfly phylogeny here since our object was to compare the effects of host taxonomy on diet breadth estimates: any bias introduced by the butterflies was constant across analyses.

Phylogenetic diet breadth indices

Phylogenetic diet breadth indices were calculated using a computer program written by F. B. S. and A. Rambaut (Oxford University). This program, named “MSST”, is available from F. B. S. on request. The three indices used were the Phylogenetic Diversity (PD) (Faith 1992a, b), the Per-Taxon Phylogenetic Diversity index (PTPD) which was obtained by dividing the PD index value by the number of species in a diet, and a novel Clade Dispersion index (CD). The latter is a branch-length independent measure of the degree to which taxa form a clade of nearest neighbours on the tree. It was calculated as the actual minimum number of branches traversed when travelling between species in a diet on the host phylogeny, divided by the theoretical minimum. Note that the latter value was estimated as $(2n-2)$, where n is the number of species in a diet (see Symons and Beccaloni 1999). We employed the PTPD in order to determine whether any differences in the PD values of diets were a consequence of the degree of relatedness of hosts or simply due to differences in the number of host species eaten across diets. Many butterflies only utilise a single plant species (approximately 28% and 35% of the North American and Australian faunas, respectively), and diet breadths indices for these species were assigned the value 1. Index values for other species were therefore: $(1 + \text{mean diet breadth index from 100 tree resolutions})$.

Host-plant phylogeny construction

We constructed host-plant phylogenies for each region in order to implement the phylogenetic diet breadth indices discussed above. We included all the hosts of the butterflies in a region (and excluded non-hosts). We justify this on the basis that current host-plants have a demonstrable ability to be colonised by butterflies (since they are utilised by at least one species) while plants which are not hosts may not be colonisable. Phylogenies were constructed using the “Matrix Representation with Parsimony” (MRP) method (Baum 1992, Ragan 1992). This allows topologies from studies with differing sets of taxa or types of characters to be combined to give an overall phylogeny estimate. Since MRP is node (or component) based, source trees may not have equal influence on the resultant phylogeny (Bininda-Emonds and Bryant 1998). We used this

Table 2. Mann-Whitney test results for North American and Australian cross-species comparisons of herb vs woody-plant feeder diets. Only significant results are given (other cells blank). A = analysis with all butterflies; E = with endemics alone. Quoted two-tailed probabilities are incorrect since the inherited component of butterfly diet breadth has not been eliminated. Subscript letters indicate the grouping with larger value of *U*: h = herb feeders, w = woody-plant feeders.

	North America			Australia		
	Plant families	Plant genera	Plant species	Plant families	Plant genera	Plant species
All plants	E _w ***	A _h ****	A _h ****	A _w ****	A _w ****	A _w ****
Native plants only	E _w ***	A _h ****	A _h **	E _w ****	E _w ****	E _w ****
				A _w ****	A _w ****	A _w ****
				E _w ****	E _w ****	E _w ****
Introduced plants only	A _w *					A _w *
						E _w *

* $p \leq 0.1$, ** $p \leq 0.05$, *** $p \leq 0.01$, **** $p \leq 0.001$.

method because the evolutionary relationships between plants are contentious and none of the available large scale molecular phylogenies gives species level resolution for all the hosts investigated here.

We combined the phylogenies implied by four recent supra-family level plant taxonomies with phylogeny estimates from 63 (North America) and 47 (Australia) references (Appendix B) to construct MRP matrices for the hosts of each region. We matched taxa at the generic level or at the lowest taxonomic level above this in cases where species in published phylogenies differed from those in the host lists. For example, if a published phylogeny did not include any of the species of Rosaceae in our data sets, we used the position of rosaceous species that were featured to place all rosaceous species in our host lists. This method was also necessary for those publications which assumed the monophyly of particular higher taxa and which did not give species names (especially cladistic morphological studies of the relationships between higher taxa). In this way we made a compromise between the conservative approach of only including studies which dealt with exactly those species in the host list, and making blanket assumptions of higher taxon monophyly. Since several traditional plant families may not be monophyletic (e.g. Labiatae and Asclepiadaceae: see Brummitt 1992) we avoided matching at this or at higher taxonomic levels unless required by a particular study (see above). Matrix components were not weighted since few phylogenies included clade support measures, and weighting according to parent tree size may not always be beneficial (Bininda-Emonds and Bryant 1998).

A hypothetical ancestor exterior to any of the in-group clades was assumed prior to parsimony jackknifing by the ‘‘Jac’’ programme of Farris (1995) (see also Farris et al. 1996). A jackknife support cut-off value of 50% was used and 1000 iterations were performed. Three hundred and eighty-four clades were obtained for North America (ca 25% of the total expected for a fully bifurcating tree), whilst 252 clades were obtained for

Australia (30.9% of expected). Phylogenies are available on request. We randomly resolved each tree 100 times before index calculation using MacClade version 3.0 (Maddison and Maddison 1992) on the assumption that recovered polytomies actually represent fully bifurcating regions where the data used were insufficient for tree resolution (‘‘soft’’ polytomies: loc. cit.). Since any two taxa in a polytomy remain only two branch lengths apart no matter how large the polytomy, true values of diet indices are progressively underestimated as polytomy size increases. Random tree resolution prevented this bias.

Our plant phylogenies did not have branch length estimates since the MRP method used to construct them does not incorporate this information. Since branch lengths (indicating genetic distances between taxa) are important when using phylogenetic diet breadth indices (see Faith 1992b), we modelled the resolved trees’ branch lengths in two different ways. This allowed us to determine how our results depended on branch length assumptions. In one group of analyses we gave phylogenies equal length branches. This mimics a punctuational evolutionary mode, where the actual time intervals between successive speciations are irrelevant. In another set of analyses, we generated branch lengths according to Grafen’s (1989) ‘gradualistic’ algorithm (hereafter ‘‘Grafen’’ branches). This makes the lengths of branches leading from ancestral taxa proportional to the number of their descendants; taxa which have more descendants are expected to be older or more divergent (these two things are equivalent under a Brownian motion model: see Felsenstein 1985). Here speciation is assumed to be a function of time and not decoupled from it as in the equal branch length model.

Butterfly phylogeny construction

Butterfly phylogenies were required for CAIC analyses (see below) and were constructed separately for each region. Matrix representation with parsimony was not

used here as only a few poorly resolved phylogeny estimates were available (e.g. de Jong et al. 1996, where intra-familial relationships are essentially unresolved). Therefore, the ‘phylogenies’ used were the combination of a taxonomy (presented in Scott 1986 or Common and Waterhouse 1981 for North American and Australian butterflies, respectively; only higher taxa present in both references were included to ensure a similar degree of phylogenetic resolution across the two regions) and two nodes from de Jong et al. (1996). Once again, true branch lengths were unavailable and so the two different branch length models described above were employed. The phylogenies used are available on request.

Comparative methodology

We used Felsenstein’s (1985) Independent Contrasts method (as realised by Pagel 1992 and implemented by the “brunch” algorithm of the CAIC 2.0 computer package: see Purvis and Rambaut 1995) to relate host types (categorical variable) and phylogenetic diet breadth index values (continuous variable). In addition, we examined the relationship between the number of host species utilised per butterfly species (continuous variable) and host type. The analyses performed involved the same comparisons as in the cross-species analyses (although we did not compare the numbers of host families or genera utilised). Variables and butterfly phylogeny branch lengths were not transformed since contrasts were approximately normally distributed. In any case, two-tailed sign tests were used for statistical comparisons (Siegel 1956).

Results

Cross-species results

The results of two-tailed tests of cross-species diet comparisons which were ‘significant’ at the $p \leq 0.10$ level are presented in Tables 2 and 3. These are considered by region below.

North American comparisons between herb and woody-plant feeders

Only two comparisons of the diets of endemic species indicated significant differences in diet breadth. In both cases, woody-plant feeders utilised more plant families and this was true when either entire diets or the native components of these were considered (Table 2). Rather different results were obtained for comparisons involving the whole fauna (endemics + non-endemics). Although woody-plant feeders utilised more families of introduced plants, in all other cases where a significant result was obtained herb feeders had larger diet breadths (Table 2). Differences between the results for the whole fauna and those for the endemics alone suggested that non-endemic herb feeders generally had wider diet breadths than non-endemic woody-plant feeders (note that this comparison was not made explicitly). The results for the endemics were very different to those for the whole fauna.

North American comparisons between annual and perennial feeders

In whole fauna comparisons involving either a) entire diets or b) the native host component of diets alone, annual feeders utilised more plant genera than perennial feeders. Similarly, comparisons of entire diets indicated that annual feeding endemics used more host genera than perennial feeders. Annual feeders also utilised more native plant species in whole fauna comparisons (Table 3). Thus, the results for the endemic portion of the fauna agreed only in part with those for the whole fauna.

North American comparisons between herbaceous-annual and woody-perennial feeders

Endemic woody-perennial feeders utilised more host families than endemic herbaceous-annual feeders in comparisons of either a) the entire diets or b) only the native host component of diets (see Table 3). However, in comparisons involving the whole fauna, butterflies with herbaceous-annual hosts generally used significantly more genera and species. This was largely independent of which diet component was examined

Table 3. Mann-Whitney test results for North American cross-species comparisons of annual vs perennial feeders, and herbaceous-annual vs woody-perennial feeders. Only significant results are given (other cells blank). A = analysis with all butterflies; E = endemics alone. Quoted two-tailed probabilities are incorrect since the inherited component of butterfly diet breadth has not been eliminated. Subscript letters indicate the grouping with larger value of U : a = annual feeders; h-a = herbaceous-annual feeders; w-p = woody-perennial feeders.

	Annual vs perennial			Herbaceous-annual vs woody-perennial		
	Plant families	Plant genera	Plant species	Plant families	Plant genera	Plant species
All plants		A _a *		E _{w-p} *	A _{h-a} ***	A _{h-a} ***
Native plants only		E _a *			E _{h-a} *	
Introduced plants only		A _a *	A _a *	E _{w-p} *	A _{h-a} ***	A _{h-a} **

* $p \leq 0.1$, ** $p \leq 0.05$, *** $p \leq 0.01$.

Table 4. Two-tailed sign test results for comparative analyses of North American and Australian herb vs woody-plant feeder diets. Capital letters indicate a significant value for a particular index (non-significant results are not shown): PD = Phylogenetic Diversity index, PTPD = Per-Taxon Phylogenetic Diversity index, CD = Clade Dispersion index, S = Number of host species. Numbers of contrasts used in significant comparisons were: 23 for North American whole-fauna analyses of entire diets or native host components of diets alone, and 14 or 15 for endemic butterfly comparisons of these diet components; 7 for North American whole-fauna analyses of the introduced component of diets; and 5 for all Australian analyses. Between 6 and 23 (North America) or 5 and 10 (Australia) contrasts were used for tests which were not significant. There were too few contrasts for statistical investigation of the introduced host component of either North American endemics' diets, or those of Australian butterflies (less than 5 in each case). h = herb feeders, w = woody-plant feeders.

Phylogeny branch type		North America			Australia	
Butterfly	Plant	All plants	Native plants only	Introduced plants only	All plants	Native plants only
All butterflies						
equal	equal	PTPD _h *		PD _h **		
equal	Grafen			PD _h **		
equal	any	S _h **	S _h **	S _h **		
Grafen	equal	PD _h *	PTPD _h *	PD _h **		
		PTPD _h *				
Grafen	Grafen					
Grafen	any	S _h *	S _h *	S _h **		
			CD _h *			
Endemics only						
equal	equal			Not testable	PD _w *	PD _w *
equal	Grafen			Not testable	PD _w *	PD _w *
					PTPD _w *	PTPD _w *
equal	any			Not testable	S _w *	S _w *
Grafen	equal			Not testable	PD _w *	PD _w *
Grafen	Grafen			Not testable	PD _w *	PD _w *
					PTPD _w *	PTPD _w *
Grafen	any			Not testable	S _w *	S _w *

* $p \leq 0.1$, ** $p \leq 0.05$.

(although there was no significant difference between numbers of introduced plant species utilised). Endemic herbaceous-annual feeding butterflies also had wider diet breadths when entire diets were compared by counting numbers of host genera. Once again, the results depended on whether the whole fauna or just the endemics were investigated: they also depended on which host taxon formed the basis of the diet breadth measure.

Contrasting the results for the endemics with those for the whole fauna suggested that non-endemic herbaceous-annual feeders generally had wider diet breadths than those utilising woody-perennial hosts (see above).

Australian comparisons between herb and woody-plant feeders

No significant diet breadth differences were detected when numbers of either introduced host families or genera were compared (Table 2). This is likely to be due to the small sample sizes involved. In all other cases woody-plant feeders had broader diet breadths than herb feeders. This was also true when the number of introduced host species in diets was compared (although the 'significance' was marginal). The results for the whole fauna and for endemics alone were similar in this region: in general they did not depend on which dietary component was investigated.

Comparative method results

The results of two-tailed tests of diet comparisons which were significant at the $p \leq 0.10$ level are presented in Table 4.

North American comparisons between herb and woody-plant feeders

Significant results were only seen in analyses which involved the whole butterfly fauna. In all these cases, herb feeding species had wider diet breadths than those feeding on woody hosts (Table 4). The results of comparisons were influenced by the branch length assumption employed by the host phylogeny, since fewer comparisons tended to be significant when phylogenies used Grafen branches. Note that although many comparisons did not show statistically significant differences, herb feeders had wider diet breadths in all but one comparison.

CD values differed significantly between herb and woody-plant feeders only when native hosts alone were considered and Grafen branches were used for the butterfly phylogeny. Numbers of host species in diets differed significantly in all comparisons. Significant differences in PD index values were evident in only four comparisons (one comparison of entire diets and three comparisons of introduced hosts: see Table 4), whilst the value of the PTPD index differed in only three. Two

of the latter involved entire diets where the host phylogeny was assigned equal branches.

It is likely that variation in the diets of non-endemics influenced the results for the whole fauna since there were no significant differences between the diets of endemic butterflies. These discrepancies emphasise the importance of partitioning species according to endemism.

Other North American comparisons

In many cases too few contrasts were available to compare the diet breadths of herbaceous-annual and woody-perennial feeders. The exceptions were whole-fauna analyses of entire diets and the native host components of these. However, no significant results were obtained for these comparisons, and they are therefore not presented. In annual vs perennial feeder comparisons the introduced components of endemics' diets could not be compared for the same reason. For the other comparisons involving these butterfly groupings no significant results were seen (results therefore not presented). This situation contrasts with the cross-species results.

Australian comparisons between herb and woody-plant feeders

Significant differences were all associated with comparisons of the diet breadths of endemic butterflies. Woody-plant feeding endemics had wider diet breadths when either their entire diets or just the native host component of these was considered. (Note that although the signs of the contrasts for introduced host comparisons mostly suggested that woody-plant feeders had wider diets, there were too few contrasts to perform sign tests.) Thus, the cross-species and comparative results for endemic butterflies were similar but the fauna-wide results differed. Once again, the comparative results for the endemic species contrasted with those for the whole fauna. Note that although many comparisons (of all butterflies or only endemics) did not show significant diet breadth differences, there was a general tendency for woody-plant feeders to be more polyphagous (seen in 65 of 72 comparisons; most comparisons where this was not the case involve the CD index).

The results for diet breadth indices were varied: PD values were significantly different in all comparisons; PTPD values only differed significantly when Grafen branches were assumed for the plant phylogeny; and CD values did not differ significantly in any analysis. Numbers of host species utilised differed significantly in all these comparisons (Table 4).

In summary, the comparative results differed from the cross-species results in that significant differences in diet breadth only existed for endemic butterflies. In both types of analysis endemic butterflies feeding on woody plants had significantly broader diet breadths than those feeding on herbaceous plants.

Discussion

Choice of regions and data

This study differs from previous investigations in several ways. Our datasets are the most comprehensive so far compiled for the regions in question, with host records for approximately 80% of all endemic species. Our data refer to species of hosts and butterflies so as to ensure that taxa utilised in phylogenetic index calculations and comparative analyses are phylogenetically equivalent entities. This contrasts with most other investigations where, for instance, lists of the higher plant taxa in diets constituted the host data (e.g. Janz and Nylin 1998). However, such an extensive treatment was only possible by restricting our focus to regions with well-known faunas. It is therefore possible that the results for one or both of our areas are not representative of those for the global fauna (see below). Note that although we excluded non-folivores from our analyses, a reanalysis of our data where all species were included (folivores + non-folivores) gave very similar results to those presented here (results not shown but available on request).

Across region patterns

The phylogenetically controlled comparisons of the diets of all North American herb and woody-plant feeding butterflies discussed above gave results which apparently conflict with earlier studies. Thus, Futuyma (1976) found that butterflies with woody hosts are more polyphagous, whilst Hayes (1982) found no difference in diet breadths. Our comparative results for the entire fauna contrasted in that they appeared to show that herbaceous plant feeding butterflies tend to have wider diet breadths than woody-plant feeding butterflies. However, we found no diet breadth differences between either a) annual and perennial feeders or b) herbaceous-annual and woody-perennial feeders. Given this, and since no analysis of endemic butterflies showed a diet breadth difference, we argue that there is no evidence that the diet breadths of North American butterflies are related to resource predictability. Our results therefore concur with those of Hayes (1982).

In contrast to the results for North America, endemic woody-plant feeding Australian butterflies had wider diet breadths than those feeding on herbaceous plants. Here, however, no dietary differences were apparent in fauna-wide comparisons. Thus, there was no consistent pattern of diet breadth with resource predictability across the two regions we considered for either whole faunas or endemic species alone. This suggests that Janz and Nylin's (1998) finding that on a global scale tree feeding butterflies have larger diet breadths than non-tree feeders may obscure significant regional variation.

Comparing results of analyses for endemics alone with those for all butterflies, we infer that non-endemic

herb feeders in both regions have wider diet breadths than non-endemic woody-plant feeders. This deduction, if correct, represents the only consistent across-region pattern. The non-endemics of both regions are mostly at the margins of their ranges, and their diets in these localities may reflect this. However, a complete explanation of this putative pattern is not possible because we do not have complete host data for these species: an in-depth study of the ecology of species at the edges of their ranges does not fall within the scope of this paper.

Unfortunately, relatively few endemic butterfly species utilise introduced hosts. This meant that we were unable to perform any comparisons of the introduced components of endemic butterflies' diets. A lack of sufficient contrasts also prevented whole-fauna comparisons of the introduced components of Australian butterflies' diets, and those of herbaceous-annual vs woody-perennial feeders in North America. Results differed for the introduced and native components of North American herb and woody-plant feeders' diets in whole fauna analyses (Table 4). However, no such difference existed between different diet components when the diets of North American annual and perennial feeders were compared (no results were significant). Our inability to compare the introduced components of endemics' diets meant that it was not possible to determine whether any real difference exists between native and introduced diet components. In contrast, the importance of partitioning the fauna according to endemicity is highlighted by differences between the results for endemic species alone and those for whole faunas. We repeat our belief that the results for the former are more indicative of ecological interactions in the regions for the reasons given above.

Phylogenetic conservation of diet breadth

The question of whether diets have been conserved within butterfly lineages can be assessed by comparing the results of cross-species and comparative analyses of the number of host species eaten. We note that the highly significant (and consistent) dietary differences apparent in cross-species analyses of the diets of Australian endemics were not seen in comparative analyses. In North America the two types of analysis gave fairly similar results for herb vs woody-plant feeder comparisons, but disparate results when diet comparisons were between either a) annual versus perennial feeders or b) herbaceous-annual versus woody-perennial feeders. It therefore appears that aspects of diet are conserved within lineages, thus highlighting the importance of controlling for butterfly phylogeny in studies of this kind (see also Janz and Nylin 1998).

Guild structure

In general, leaf feeding butterflies specialise on hosts having the same growth-form. Indeed, only about 13% of North American and 6% of Australian butterflies in our dataset fed on both herbaceous and woody hosts. The diets of 74% of North American and 50% of Australian species with hosts of both types comprised $\geq 75\%$ hosts of one growth-form when hosts with unknown growth-forms were excluded. Our data therefore corroborate the belief of Futuyma (1976) and Niemelä et al. (1982) that herb and woody-plant feeders represent distinct guilds (see also Janz and Nylin 1998).

In a similar way, the leaf feeding butterflies of each region appear to specialise on plants of a single duration. In our dataset only 20% of North American species utilised both annuals and perennials (when hosts with unknown duration were excluded, 49% of these species had diets which consisted of $\geq 75\%$ hosts with one duration). Six percent of American species included in the comparison between herbaceous-annual feeders and woody-perennial feeders utilised both host-plant categories: 75% of these species had diets where 75% or more of their hosts belonged to one of these categories (excluding hosts which could not be assigned to a category). It is not clear that the reason for the small overlap in the utilisation of the two host categories by these species is simply that the growth-form and duration of hosts tend to be related (see below).

The reason for the existence of the guilds discussed above may lie in adaptations required by differing host-plant defence strategies (e.g. Cates and Orians 1975, Feeny 1975, 1976, 1991, Futuyma 1976), in the temporal and/or spatial predictabilities of hosts (see references in Jaenike 1990 and Mayhew 1997; see also Southwood 1988); in floristic biases (see discussion below); or in differing host nutritional qualities (e.g. water and nitrogen contents of the two types of plant differ: Slansky 1993). Alternatively, guilds might have arisen as a consequence of differing host-plant locating strategies (Beccaloni 1995, 1997, Janz and Nylin 1998).

Choice of plant predictability surrogates

We chose plant predictability surrogates in the expectation that they correlate positively with the way that butterflies view constancy of resource. This may not, however, be the case (e.g. Courtney 1985). Only more detailed investigations at the population level can address this issue: such a study was not our aim here.

The surrogates used here are not statistically independent of one another since annuals are necessarily herbaceous whilst woody plants are necessarily perennial. To an extent therefore, evolutionary constraints cause correlations between plant growth-form and duration. Nonetheless, our results indicated that this cor-

relation is not perfect because we found no significant difference between the diets of North American annual and perennial feeders despite finding significant differences between the diets of herb and woody-plant feeders in the same region (comparative analyses of the whole fauna). We also note that within perennial feeding butterflies there was an excess of herb over woody-plant feeders ($p = 0.06$, binomial test), which may suggest that the insects respond differently to these two aspects of predictability. Two further reasons for performing separate analyses using different predictability surrogates were: first, that there may have been undetected errors in the North American growth-form/duration data (see methods section); and second, that the set of host species for which growth-form/duration information was available varied slightly according to the surrogate investigated. Given that higher plant taxa can include species which have a variety of different growth-forms/durations, we collected growth-form/duration information for each individual host species (cf. Janz and Nylin 1998).

Phylogenetic diet breadth indices

Our cross-species results suggested that using traditional diet breadth indices can give misleading results due to bias arising from the taxonomic level which contributes most to them (see North American results). Therefore, it is not valid to compare the results of two studies which employ different diet breadth indices. Using phylogenetic diet breadth indices avoids this problem. We discuss aspects of these indices below.

Significant differences in PD values can be due to differences in the relatedness of the hosts in diets, due to differences in the numbers of hosts used, or due to a combination of the two. However, significant differences between either the numbers of host species utilised, or the PTPD values of the diets of two groups of butterflies, may not be associated with significant differences in PD values (see Table 4). In these cases one can infer that differences in PTPD values are counterbalanced by differences in the numbers of host species utilised (or vice versa). This situation illustrates the importance of taking the entire branching structure of the hosts' phylogeny into account: a diet which comprises several very closely related species is arguably less diverse than one which consists of slightly fewer more distantly related hosts.

We only recorded a significant difference in CD index values in one comparison where Grafen branches were assumed for the butterfly phylogeny (Table 4). Since the statistical significance of the comparison was marginal and as no difference was seen when equal branches were assumed, it seems unlikely that CD values really did differ between diets. Hence, the hosts of any one group of butterflies in this study did not

cluster more closely on the plant phylogeny than did those of another. However, it is possible that our results were a consequence of the version of the index used in this study (see Symons and Beccaloni 1999), or possibly were due to the high proportion of monophagous species in our datasets.

Aspects of phylogeny construction

Phylogenetic diet breadth indices require the construction of a host phylogeny. However, all phylogeny estimates are very dependent on the number and identities of the taxa involved (e.g. Lanyon 1985). Our estimates only involved species which are butterfly hosts because it would have been impossible to include all plant species in each region, let alone all world plant species (note that the flora of North America consists of approximately 24441 plant species in 3525 genera and 334 families, whilst that of Australia comprises ca 17683 plant species in 2719 genera and 301 families). Therefore, there is a possibility that the values of diet indices for any one particular butterfly species were influenced by the diets (hosts) of other butterfly species in the region. In fact, the results of PD and PTPD comparisons would not be affected in this way if a) the topologies we recovered accurately reflect the phylogenetic relationships between hosts and b) the branch lengths we used accurately reflect genetic distances between taxa. We attempted to ensure the accuracy of our phylogeny estimates by combining trees from a wide range of sources (Appendix B). We feel that the absence of true branch lengths does not invalidate our results as we employed two contrasting branch length assumptions and yet obtained similar results for both in the majority of cases.

Differential effects of host chemistry

The apparency hypothesis of Feeny (1975) suggested that "apparent" plants (those which are easily discovered by herbivores) possess relatively large amounts of "quantitative" chemical defences (such as tannins or silica), whilst "unapparent" species (those which are relatively undetectable by herbivores) possess relatively small amounts of "qualitative" defences (such as glucosinolates and alkaloids). Systematic differences in chemistry of this kind between different plant growth-forms/durations could have biased our results. However, recent studies have suggested that the association between the different types of defence and the degree of apparency of the host-plant is by no means clear cut (Schoonhoven et al. 1998). In addition, Janz and Nylin (1998) concluded that plant growth-form is an even more conservative aspect of the interaction between butterflies and their host-plants than plant phylogeny,

suggesting that factors such as host chemistry are of lesser importance. In any case, in order to determine whether such biases exist, it would be necessary to have both comprehensive plant secondary compound data and information regarding how each species of butterfly responds to these chemicals (e.g. whether a species perceives a difference between the secondary compounds of different plants). Complete data of these kinds do not exist for our study regions thereby precluding an investigation of this issue.

Confounding effects of distributional differences

By measuring CD index values on a phylogeny of all regional hosts we implicitly assumed that all butterfly species have had an equal opportunity to colonise all regional hosts. In fact, habitat differences and larger scale geographical factors mean that the distributions of some butterflies and plants do not overlap (and, despite substantial changes in geographical ranges of both insects and hosts over geological time, may never have done so). Obviously, such plants can not be hosts for these butterfly species: their inclusion may artificially inflate CD values since the addition of extra branches to the host phylogeny will make hosts appear more disparate (see Symons and Beccaloni 1999 for a relevant discussion). It is therefore possible that different results will be obtained when fine scale data are available which allow the worker to restrict analyses to those hosts and butterflies known to be present in a given habitat and locale. In this case, CD values should be obtained from a phylogeny comprising all those plants present in a particular locality rather than all plants in the entire region. Note that the values of the PD and PTPD will not vary with phylogeny scope provided that true branch lengths are available (see above).

We draw attention to one possible source of bias which we did not address in our study: the underlying composition of the floras of the areas studied. Previous macroecological investigations of diet breadth in Lepidoptera have ignored the fact that the phylogenetic composition of regional floras might dictate the degree of dietary difference observed, even in the absence of differences in host chemistry or predictability. For example, phylogenetic diet index values for woody-plant feeders may be greater than those for herb feeders simply because the woody plants in the region are less closely related than the herbaceous plants. Note that this bias differs somewhat from that caused by disjunct butterfly/host ranges and will affect all diet indices, not just CD values. A possible way around this problem would be to obtain null values of diet breadth indices by estimating a mean value for each index over a large number of random 'diets' on the plant phylogeny, where each one contains the same number of hosts as in

a given real diet. Observed diet index values could then be divided by this mean value. In order to do this one has to make a priori decisions regarding which species of host-plants should be included in the phylogeny used to estimate random 'diets'. For example, phylogenies could contain only regional hosts (as here), or they could include non-hosts too. Given that herb and woody-plant feeders constitute different guilds, a case can be made for calculating random 'diets' using the subset of either woody or herbaceous hosts alone according to which growth-form makes up the bulk of a diet. We did not do this here as it was not clear a priori that such guilds existed.

We note that the question of whether woody (and/or herbaceous) hosts are more or less closely related than are non-hosts in the region which have the same growth-form/duration is a separate question which can be addressed in a similar way. Thus, index values for random 'diets' taken from the pool of actual hosts can be compared with similar values obtained from random 'diets' sampled from the set of all herbaceous or woody plants in the region (excluding those species which are hosts to ensure that samples are statistically independent).

Butterfly population variation and dynamics

In our study we treated each butterfly species as a homogenous entity whereas in fact there are likely to be differences between the diets of individual populations (see Thompson 1994). We justify this decision on the basis that the sum of the diets of individual populations represents those hosts which the species as a whole has a demonstrable ability to utilise.

Geographical distributions are not the only factors which determine whether a given plant species will become a host for a given butterfly in a given place. For example, plants which are rare in a given locale may be more difficult to colonise than common species due to reduced rates of encounter by butterflies, even in those cases where the species is a host in other locations. Any systematic differences in the abundances of species belonging to different host types (e.g. where individual tree species are rare whilst individual herb species are abundant, irrespective of the overall abundance of trees as a whole) could have biased our results. Unfortunately, a lack of relative abundance data prevented us from examining this. In future studies, biases arising from differences in abundances and/or range sizes might be removed by weighting the branch lengths of the host phylogenies (see below and Symons and Beccaloni 1999).

Lack of data also meant that we were unable to control for any variation in the degree of predation or competition experienced by the butterfly groupings used here. However, we recognise that such differences may have influenced our results.

Conclusion

In this study, we demonstrated the importance of using phylogenetic information from both host-plant and butterfly phylogenies in analyses of diet breadth. Prevailing taxonomy-based methods of measuring diet breadth (counts of numbers of host taxa utilised) were shown to be inconsistent, giving different results according to which host taxonomic level was considered. For this reason, phylogenetic diet breadth measures do not necessarily give the same results as analyses using taxonomy-based indices.

Our results suggested that there is an inherited component to butterfly diet breadths, and this finding underlines the importance of taking butterfly phylogeny into account in studies of this kind. We also demonstrated that analyses of the endemic portion of a fauna can give very different results to those where the entire fauna is considered.

No simple and consistent relationship between unpredictability of resource and the diet breadths of butterflies was found across the regions studied. However, it may have been that complicating factors such as regional differences in predation, in competition, in the composition of floras, in host chemistries, etc., served to obscure the true relationship between these variables. Further data from these and other regions, together with a resampling approach which eliminates the effects of underlying phylogenetic or abundance biases in the floras, may clarify the situation.

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Appendix A: References from which butterfly host-plant records were taken

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Appendix B: References used to construct phylogeny estimates for the host-plants of North American and Australian butterflies

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