

TRANSITION RATES BETWEEN SPECIALIZATION AND GENERALIZATION IN PHYTOPHAGOUS INSECTS

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Abstract.—Although most species of animals exhibit specialized patterns of resource use, it is unclear whether specialization evolves at a faster rate than generalization. To test this hypothesis, transition rates toward specialization and toward generalization were estimated using phylogenies from 15 groups of phytophagous insects. Among the groups studied, maximum-likelihood analyses showed that the forward transition rate from generalization to specialization was significantly higher than the reverse transition rate from specialization to generalization (mean ratio of forward to reverse transition rate = 1.47 using uniform branch lengths and 1.76 using Grafen branch lengths). Although phylogenetic conservatism of host-plant use is common, the results suggest that the evolution of specialization is a highly dynamic process. For example, higher transition rates both toward and away from specialization as well as equal transition rates were inferred. Collectively, the results reveal a tendency for directional evolution toward increased specialization but also indicate that specialization does not always represent an evolutionary dead-end that strongly limits further evolution.

Key words.—Diet breadth, insect-plant interactions, maximum likelihood, niche width, phylogenetic conservatism, resource use, specialization.

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Many animal species exhibit specialized patterns of resource use, using only a subset of all suitable and available resource types (for reviews see Futuyma and Moreno 1988; Jaenike 1990). However, generalist species that use a wide array of resources are by no means uncommon. A number of factors are thought to promote specialization, including genetically based trade-offs in performance between different habitats (e.g., habitat-specific adaptations, Via 1989, 1991; Schluter 1993, 1995; Sheck and Gould 1993; Sandoval 1994a,b; Joshi and Thompson 1995; Fry 1996; but see Rausher 1984; Futuyma and Philippi 1987; Keese 1998), competition for resources (MacArthur and Levins 1964; Dykhuizen and Davies 1980), resistance to predators (Bernays and Graham 1988; Bernays 1989; Dyer 1995), high costs of information processing (Bernays and Wcislo 1994; Bernays 1999; Bernays and Funk 1999) and mate-finding (Colwell 1986), low costs to searching for suitable habitat (Levins and MacArthur 1969; Southwood 1972), and deleterious mutations with habitat-specific expression (Kawecki 1994). In contrast, rare or unpredictable habitats (Southwood 1972; Wiklund 1974; Lacy 1984; Strong et al. 1984), difficulties with meeting nutritional requirements using a single food type (Bernays et al. 1997; Ballenbeni and Rahier 2000), and greater resource availability (Thompson 1982) all favor generalization.

Although selection for specialization is thought to be common and to result in directional patterns of evolution toward increased specialization, evidence that specialization tends to be a highly derived state or a dead-end that constrains further evolution is equivocal (Simpson 1953; Holloway and Hebert 1979; Moran 1988; Janz and Nylin 1998; Kelley and Ferrell 1998). Much research on ecological specialization has focused on phytophagous insects, which use discrete habitat types (i.e., different hosts; for review see Jaenike 1990) and often exhibit phylogenetic conservatism of host-plant use; related species use similar hosts and host shifts are often

constrained to taxonomically, chemically, or structurally similar host species (Miller 1987; Futuyma and Moreno 1988; Farrell et al. 1992; Farrell and Mitter 1994; Funk et al. 1995; Janz and Nylin 1998; Kelley and Farrell 1998; Crespi and Sandoval 2000; Janz et al. 2001). For example, a lack of genetic variation in the ability to use novel host plants can constrain the evolution of host range (Futuyma et al. 1995). Although the factors both favoring and constraining the evolution of ecological specialization have been well outlined, empirical data on the rates at which specialization versus generalization evolve are few.

In this study, I use previously published phylogenies and maximum-likelihood methods (Pagel 1994, 1999a,b; Schluter et al. 1997) to estimate the rate of evolution toward specialization and toward generalization for various groups of phytophagous insects, predicting that the evolutionary transition rate toward specialization will tend to exceed the transition rate toward generalization. These analyses represent the first attempt to assess variation in the rate at which specialization versus generalization evolve using a compilation of phylogenetic data.

MATERIALS AND METHODS

Data Collection

Published phylogenies and records of host-plant use for various groups of phytophagous insects were gathered from the literature. A total of 15 cases were found where: (1) a phylogenetic tree was available; (2) reliable host-records had been published; and (3) there was within-group variation in the degree of specialized host-plant use (Table 1). Using these data, extant groups of insects were coded as specialized or generalized in their patterns of host-plant use (see Table 1 for coding scheme). In fully resolved phylogenetic trees, branch lengths were set to one or assigned using methods

TABLE 1. Studies used to estimate transition rates between generalized (gen) and specialized (spec) host-plant use.

Taxon	Phylogeny	Number of spp. gen, spec	Criteria for specialization	Reference
<i>Timema</i> walking sticks	mtDNA	6, 11	feed on only one species of host plant	Sandoval et al. 1998; Crespi and Sandoval 2000
<i>Nymphalini</i> butterflies	mtDNA, nDNA	21, 9	feed on only one family of host plant	Janz et al. 2001; Nylin et al. 2001
<i>Uroleucon</i> aphids	mtDNA, nDNA	4, 5	feed on only one species of host plant	Moran 1984; Moran et al. 1999
<i>Oreina</i> leaf beetles	allozymes	6, 6	feed on only one plant tribe	Dobler et al. 1996
<i>Papilio</i> butterflies	mtDNA	12, 12	feed on only one tribe of host plant	Sperling 1992, 1993; Janz and Nylin 1998
<i>Ophraella</i> leaf beetles	mtDNA	5, 7	feed on only one species of host plant	Futuyma and McCafferty 1990; Funk et al. 1995; Futuyma et al. 1995
Elachistidae	morphology	2, 5	feed on only one host plant clade (clade identity from Janzen and Nylin 1998)	Berenbaum and Passoa 1999
<i>Chrysolina</i> leaf beetles	mtDNA, nDNA	10, 20	feed on only one genus of host plant	Garin et al. 1999
<i>Timarcha</i> leaf beetles	mtDNA, nDNA	14, 19	feed on only one family of host plant	Gómez-Zurita et al. 2000
<i>Dendroctonus</i> bark beetles	mtDNA	13, 6	feed on less than half of available hosts	Kelley and Farrell 1998
<i>Gonioctean</i> leaf beetles	mtDNA, allozymes	5, 10	feed on only one genus of host plant	Mardulyn et al. 1997
<i>Graphium</i> butterflies	morphology	5, 7	feed on only one family of host plant	Saigusa et al. 1982; Scriber 1984; Miller 1987
<i>Enchenopa</i> treehoppers	allozymes	2, 7	feed on only one species of host plant	Wood 1993
<i>Drosophila</i> flies	mtDNA, nDNA	9, 28	feed on only one family of host plant	Heed 1968; Montgomery 1975; Baker and DeSalle 1997; Kambysellis and Craddock 1997
Heliothinae butterflies	nDNA	11, 10	feed on only one family of host plant	Cho 1997

outlined in Grafen (1989; tips contemporaneous, depth of each node set equal to one less than the number of tip species that descend from it). These Grafen branch lengths were estimated using a program provided by T. Garland (PDTREE). Polytomies were resolved using branch lengths of infinitesimal size and arbitrarily in all possible topological combinations (only two trees contained polytomies: Gonioctean beetles, nine possible resolutions; Heliothinae, three possible resolutions; all branch lengths set equal to one). For cases where branch lengths of infinitesimal size were used, I also conducted analyses using the κ scaling parameter described in Pagel (1994).

Phylogenetic Trends: Tests for Directional Evolution

For each of the phylogenetic trees, I tested for directional evolution by comparing a model of evolution where the transition rate from generalization to specialization and the transition rate from specialization to generalization were free to vary to a model where these two rates were constrained to be equal (Pagel 1994, 1999a,b). Directional evolution is implied if the model where rates are free to vary provides a significantly better fit to the data than the model where the rates were forced to be equal. Whether these two models differed from one another was tested using a simple likelihood-ratio (LR) test with one degree of freedom. All analyses were run on a program provided by M. Pagel (Discrete ver. 4.01).

Using the results from all 15 phylogenetic trees, I also tested for an overall tendency for directional evolution toward increased specialization. Specifically, I examined whether the mean forward transition rate from generalization to specialization tended to be higher than the reverse transition rate from specialization to generalization by testing whether the ratio of these rates for each tree (forward rate/backward rate), summed across all trees, was significantly greater than one (using a one-sample, one-tailed *t*-test; Sokal and Rohlf 1995). Statistical analyses were conducted using SPSS ver. 10.1 (SPSS, Inc., Chicago, IL).

To determine the degree to which the relative number of specialists and generalists at the tips of each tree might influence the estimates of transition rates (i.e., the state of the root might influence the results), I also performed the analyses described above with the root of each tree fixed a priori as a generalist and fixed as a specialist (branch lengths set to one).

RESULTS

When each group of insects was considered separately and uniform branch lengths were used, a model of evolution where the transition rate from generalization to specialization (forward rate) and the transition rate from specialization to generalization (backward rate) were free to vary was significantly better than a model where transition rates were forced to be equal in only two cases (Table 2). In these two instances, the forward transition rate was greater in one case (*Enchenopa* treehoppers), whereas the backward transition rate was greater in the other (*Dendroctonus* bark beetles). Using Grafen branch lengths, a model of evolution where the forward and the backward transition rate were free to vary was signifi-

TABLE 2. Results of maximum-likelihood analyses estimating the evolutionary transition rate toward specialization (spec) and the rate toward generalization (gen) within 15 different groups of phytophagous insects. Reported in the table is the ratio of the transition rate toward specialization to the rate toward generalization (Rate spec/rate gen). Also shown is the change in $-2 \log LR$ between a model where transition rates toward specialization and toward generalization were free to vary and a model where these two rates were forced to be equal. A significant result implies directional evolution toward specialization or generalization (if the ratio of rates is greater than or less than one, respectively). Results are shown from analyses using uniform branch lengths (polytomies resolved using infinitesimal branch lengths, also shown in brackets is the range of ratios when polytomies were resolved arbitrarily in all possible topological combinations) and from analyses using Grafen branch lengths (Grafen 1989; for fully resolved phylogenetic trees only).

Taxon	Branch lengths uniform			Grafen branch lengths		
	Rate spec/ rate gen	Directional evolution ($-2 \log LR$)	P (df = 1)	Rate spec/ rate gen	Directional evolution ($-2 \log LR$)	P (df = 1)
<i>Timema</i> walking sticks	1.83	2.70	0.09	1.83	1.49	0.22
<i>Nymphalini</i> butterflies	0.29	3.00	0.08	0.43	2.72	0.09
<i>Uroleucon</i> aphids	1.25	0.64	0.42	1.25	0.64	0.42
<i>Oreina</i> leaf beetles	1.08	0.02	0.89	1.09	0.02	0.89
<i>Papilio</i> butterflies	1.00	0.02	0.89	1.01	0.01	0.92
<i>Ophraella</i> leaf beetles	1.44	0.72	0.40	1.41	0.69	0.41
Elachistidae	0.08	0.26	0.61	4.00	3.98	0.046
<i>Chrysolina</i> leaf beetles	2.33	3.24	0.07	2.10	3.78	0.05
<i>Timarcha</i> leaf beetles	1.31	0.76	0.38	1.36	0.82	0.37
<i>Dendroctonus</i> bark beetles	0.46	5.28	0.02	0.46	5.28	0.02
<i>Gonioctean</i> leaf beetles	1.99 (1.98–2.00)	3.20	0.07	—	—	—
<i>Graphium</i> butterflies	1.96	2.26	0.13	1.86	1.53	0.22
<i>Enchenopa</i> treehoppers	3.50	5.26	0.02	3.25	4.00	0.045
<i>Drosophila</i> flies	2.58	2.20	0.14	2.88	8.94	0.003
Heliothinae butterflies	0.90 (0.88–0.90)	0.06	0.80	—	—	—

cantly better than a model where transition rates were forced to be equal in four cases. Among these, the forward transition rate toward specialization was greater in three instances (*Enchenopa*, *Drosophila*, and Elachistidae), whereas the backward transition rate toward generalization was greater in one case (*Dendroctonus* bark beetles).

When the root state was allowed to be indeterminate, the transition rate from generalization to specialization tended to be slightly higher than the transition rate from specialization to generalization (mean ratio of forward rate/backward rate = 1.47, SD = 0.92, $t_{14} = 1.98$, $P < 0.05$, one-sample t -test against a null value of one; root of each tree estimated, uniform branch lengths, Table 2). I obtained similar results when the κ scaling parameter was applied to the two phylogenetic trees with polytomies (mean ratio = 1.47, SD = 0.92, $t_{14} = 1.97$, $P < 0.05$; ratio = 1.98 for *Gonioctean* beetles and 0.89 for Heliothinae), when I excluded the two trees with polytomies (mean ratio = 1.47, SD = 0.97, $t_{12} = 1.77$, $P = 0.05$) and when Grafen branch lengths were used instead of uniform branch lengths (mean ratio = 1.76, SD = 1.06, $t_{12} = 2.58$, $P < 0.05$; for cases where a fully resolved tree was available). Furthermore, the transition rate toward specialization was higher than the transition rate toward generalization when the root of each phylogenetic tree was fixed as a generalist (mean ratio of forward rate/backward rate = 1.79, SD = 0.96, $t_{14} = 3.20$, $P < 0.01$; Table 3) and nearly so when the root was fixed as a specialist (mean ratio = 1.38, SD = 0.86, $t_{14} = 1.70$, $P = 0.056$).

DISCUSSION

The evolution of diet breadth or niche width has been a central topic in the evolutionary and ecological literature for several decades, and the factors thought to promote and constrain specialized versus generalized patterns of resource use

have been well outlined (for reviews see Futuyma and Moreno 1988; Jaenike 1990). Transitions from both generalization to specialization and from specialization to generalization have been reported in a wide range of taxa (e.g., toward specialization; butterflies, Courtney 1986; lizards, Losos et al. 1994; toward generalization, birds, Lanyon 1992; bees, Muller 1996; Armbruster and Baldwin 1998). However, differences in transition rates between these two states have not been well established; thus, whether specialization evolves at a faster rate than generalization remains unclear. Among the 15 groups of insects examined in this study, the evolutionary transition rate from generalization to specialization tended to be slightly higher than the transition rate from specialization to generalization. This result was not dependent on how polytomies were resolved, how branch lengths were assigned, or the state of the root. These data suggest that there may be a general, yet weak, tendency for phytophagous insects to exhibit directional evolution toward increased specialization.

Constraints in the ability to shift between unrelated or otherwise dissimilar host plants (Miller 1987; Futuyma and Moreno 1988; Farrell et al. 1992; Farrell and Mitter 1994; Futuyma et al. 1995; Crespi and Sandoval 2000; Janz et al. 2001) and the high incidence of specialist species in nature has led to the suggestion that ecological specialization represents an evolutionary dead-end that limits further evolution (Simpson 1953; Moran 1988; Kelley and Farrell 1998). For example, in *Dendroctonus* beetles the number of hosts used is correlated with number of hosts encountered in generalists but not specialists (Kelley and Farrell 1998). However, host-plant shifts have been documented between unrelated and chemically or structurally dissimilar host plant species (Dobler et al. 1996; Crespi and Sandoval 2000) and often also depend on the geographical distribution of hosts and thus

TABLE 3. Results of maximum-likelihood analyses estimating the evolutionary transition rate toward specialization and the rate toward generalization when the root of each phylogenetic tree was fixed as a generalist (gen) and when the root was fixed as a specialist (spec). Reported in the table is ratio of the transition rate toward specialization to the rate toward generalization (Rate spec/rate gen) for each analysis. Also shown is the change in $-2 \log LR$ between a model where transition rates toward specialization and toward generalization were free to vary and a model where these two rates were forced to be equal (roots fixed as noted above).

Taxon	Rate spec/ rate gen. (root = gen)	($-2 \log LR$)	<i>P</i>	Rate spec/ rate gen. (root = spec)	($-2 \log LR$)	<i>P</i>
<i>Timema</i> walking sticks	2.04	2.96	0.08	1.83	3.00	0.08
<i>Nymphalini</i> butterflies	0.43	1.98	0.16	0.14	9.06	0.002
<i>Uroleucon</i> aphids	1.25	0.20	0.65	1.25	0.14	0.71
<i>Oreina</i> leaf beetles	1.16	0.10	0.75	1.00	0.32	0.57
<i>Papilio</i> butterflies	1.10	0.06	0.81	0.88	0.14	0.71
<i>Ophraella</i> leaf beetles	1.51	0.90	0.34	1.42	0.20	0.65
Elachistidae	2.50	0.26	0.61	0.09	0.32	0.57
<i>Chrysolina</i> leaf beetles	2.75	5.34	0.02	1.86	1.46	0.23
<i>Timarcha</i> leaf beetles	1.36	0.06	0.81	1.33	0.52	0.42
<i>Dendroctonus</i> bark beetles	0.46	5.10	0.02	0.46	5.06	0.02
<i>Gonioctean</i> leaf beetles	2.00	3.38	0.06	1.93	1.82	0.18
<i>Graphium</i> butterflies	2.68	2.76	0.01	1.98	2.10	0.15
<i>Enchenopa</i> treehoppers	3.50	5.90	0.02	3.25	3.26	0.07
<i>Drosophila</i> flies	3.23	9.20	0.002	2.37	1.50	0.22
Heliethinae butterflies	0.98	0.00	1.00	0.85	0.16	0.69

availability of plants (i.e., ecological opportunity; Mardulyn et al. 1997; Gómez-Zurita et al. 2000). The results of the current study also suggest that specialization does not always limit further host range evolution; higher transitions rates both toward and away from specialization, as well as equal transition rates, were inferred. This dynamic view of the evolution of specialization is supported by the lack of evidence for directional evolution toward increased specialization within many groups of phytophagous insects (e.g., Wood 1993; Gómez-Zurita et al. 2000; Janz et al. 2001) and by the observation that, although host plant gains may be more likely in generalists, they are by no means restricted to generalists. For example, in *Timarcha* beetles, widening of the trophic niche appears to represent a derived state (Gómez-Zurita et al. 2000) and among largely monophagous species of butterflies, host-plant switching has often occurred (Holloway and Hebert 1979). Differences among groups in the tendency to evolve specialized patterns of resource are likely mediated by interactions between fitness trade-offs in the use of different habitats favoring specialization and risk-spreading and ecological opportunity favoring generalization (for review see Jaenike 1990).

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