

Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds

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The Hawaiian honeycreepers are a dramatic example of adaptive radiation but contrast with the four other songbird lineages that successfully colonized the Hawaiian archipelago and failed to undergo similar diversification. To explore the processes that produced the diversity dichotomy in this insular fauna, we compared clade age and morphological diversity between the speciose honeycreepers and the comparatively depauperate Hawaiian thrushes. Mitochondrial-DNA-based genetic distances between these Hawaiian clades and their continental sister taxa indicate that the ancestral thrush colonized the Hawaiian Islands as early as the common ancestor of the honeycreepers. This similar timing of colonization indicates that the marked difference in diversity between the Hawaiian honeycreeper and thrush clades is unlikely to result from differences in these clades' tenures within the archipelago. If time cannot explain the contrasting diversities of these taxa, then an intrinsic, clade-specific trait may have fostered the honeycreeper radiation. As the honeycreepers have diversified most dramatically in morphological characters related to resource utilization, we used principal components analyses of bill characters to compare the magnitudes of morphological variation in the ancestral clades from which the Hawaiian honeycreeper and thrush lineages are derived, the Carduelini and Turdinae respectively. Although the Carduelini share a more recent common ancestor and have a lower species diversity than the Turdinae, these finch-like relatives of the honeycreepers exhibit significantly greater variation in bill morphology than do the continental relatives of the Hawaiian thrushes. The higher magnitude of morphological variation in the non-Hawaiian Carduelini suggests that the honeycreepers fall within a clade exhibiting a generally high evolutionary flexibility in bill morphology. Accordingly, although the magnitude of bill variation among the honeycreepers is similar to that of the entire passerine radiation, this dramatic morphological radiation represents an extreme manifestation of a general clade-specific ability to evolve novel morphologies.

Keywords: speciation; adaptive radiation; colonization; morphology; Drepaniidae; *Myadestes*

1. INTRODUCTION

The best-known avian adaptive radiations have involved passerine lineages that colonized and then speciated on oceanic archipelagos, most notably the drepanidine honeycreepers of the Hawaiian Islands and the geospizine finches of the Galápagos Islands. Several environmental characteristics of these isolated oceanic archipelagos are thought to have fostered adaptive radiation, including an initial absence of competitors that permitted colonizing lineages to diversify into a variety of otherwise unoccupied ecological niches, and the subsequent possibility of repeated interisland colonizations that permitted allopatric differentiation followed by sympatric reinforcement and ecological divergence (Perkins 1903; Huxley 1942; Lack 1947; Mayr 1963; Grant 1986). Nonetheless, most of the passerine lineages that have successfully colonized these and other archipelagos have failed to undergo dramatic adaptive radiations, suggesting that non-environmental factors are also important in promoting or retarding the adaptive radiation of particular lineages. Important non-environmental influences might include differences among lineages in the timing of colonization, as well as lineage-specific differences in the ability to respond to diversifying

selection. Here, we explore these possibilities by comparing both the timing of colonization and morphological diversity between two Hawaiian passerine bird clades that differ in their realized diversities, the highly speciose Hawaiian honeycreepers and the comparatively depauperate Hawaiian thrushes. These comparisons between two clades occupying a common environmental setting provide an opportunity to explore historical and lineage-specific factors that might promote or hinder adaptive radiation.

The approximately 50 species of Hawaiian honeycreeper, both living and extinct, are the most numerous element of the indigenous Hawaiian songbird fauna. Prior to human colonization of the archipelago, up to 24 honeycreeper species occurred on a single Hawaiian island (James & Olson 1991). Honeycreepers occupied an array of foraging and dietary niches and exhibited a correspondingly high diversity of bill morphology: among the many specialized honeycreepers are seed predators with robust bullfinch-like bills, insectivores with short warbler-like bills, and nectivores with greatly elongated sunbird- or hummingbird-like bills (Amadon 1950; James & Olson 1991). Owing to the high number of honeycreeper species and to the dramatic morphological differences between them, the Hawaiian honeycreepers have become a widely known example of adaptive radiation (e.g. Amadon 1950;

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Mayr 1963; Bock 1970; Freed *et al.* 1987; Futuyuma 1997).

The honeycreeper radiation is dramatic both in numbers of species and in the magnitude of morphological differentiation, but it is anomalous in that four other lineages of passerine birds colonized the Hawaiian archipelago but failed to undergo similarly extreme diversification (James 1991). By comparing groups that differ in taxonomic and morphological diversity, we can explore the processes that promote adaptive radiation. However, most of the low-diversity Hawaiian clades are difficult to study in an historical or phylogenetic context because the historically known Hawaiian taxa are extinct (three *Moho* species and *Chaetoptila angustipluma*) or their closest non-Hawaiian relatives (and hence colonization sources) are not readily identified (*Chasiempis sandwichensis* and *Corvus hawaiiensis*). The sole remaining Hawaiian passerine lineage, the Hawaiian thrushes of the genus *Myadestes*, is amenable for comparative analysis because Hawaiian populations are extant, and because the Hawaiian taxa are clearly allied to congeners in North and South America. The Hawaiian thrushes include five taxa endemic to individual islands, only two of which are sympatric, and these populations lack the dramatic variation in bill morphology, plumage, and other characters that characterize the honeycreeper radiation (Pratt 1982). Four thrush populations are nearly identical in morphology; the largest differences occur between the two sympatric species, which are modestly differentiated in body size (Pratt 1982). Although many honeycreeper taxa are known only from Holocene fossil remains, it is improbable that undocumented extinction has masked a more extensive Hawaiian thrush radiation, as all Hawaiian thrush fossils can be assigned to historically known species (James & Olson 1991). Repeated between-island colonization is often thought to foster adaptive radiations in archipelagos, but the lack of an extensive adaptive radiation of Hawaiian thrushes seems unlikely to have resulted from a lack of dispersal ability. The presence of thrush populations on four Hawaiian islands and the occurrence of two taxa in sympatry demonstrates that the Hawaiian thrushes have undergone at least three successful inter-island colonizations. Other *Myadestes* species are resident on eight West Indian islands, further suggesting that this genus readily crosses substantial water gaps.

Here we use comparisons between the Hawaiian honeycreeper and thrush clades to evaluate two hypotheses about the evolutionary processes that influence adaptive radiations in island systems. We first examine a colonization time-based explanation for the difference in honeycreeper and thrush diversity. If the thrush lineage colonized the islands more recently than the honeycreepers, the lower diversity of the thrush clade could have resulted simply from a lack of time for extensive adaptive radiation. This time-limitation hypothesis can be tested under the assumption of a local mitochondrial clock by determining the magnitude of sequence divergence between Hawaiian and continental representatives of both the honeycreeper and Hawaiian thrush clades. Small genetic distances between the Hawaiian thrushes and their closest mainland congener would suggest that the thrushes have had a short tenure in the archipelago. Alternatively, the time-limitation scenario can be rejected if the ancestor

of the Hawaiian thrushes colonized the archipelago before or contemporaneously with the ancestral honeycreeper.

We also explore a trait-based explanation for the difference in honeycreeper and thrush diversity by examining morphological variation in the two groups. Adaptive radiations in passerine birds frequently involve bill characters that are functionally related to the utilization of food resources. Therefore, passerine lineages that can rapidly evolve novel bill shapes may be predisposed to radiate after colonizing isolated oceanic archipelagos. If the ancestral honeycreeper had an intrinsically high propensity to respond to diversifying selection, then this trait will probably also appear in its close non-Hawaiian relatives. We tested this lability hypothesis by comparing morphological variation in the larger taxa from which the Hawaiian thrushes and honeycreepers are derived. The honeycreepers are cardueline finches (Sibley & Ahlquist 1990) and the Hawaiian thrushes, along with the New World *Myadestes solitaires*, belong to a monophyletic clade within the Turdinae. The clade-specific lability hypothesis predicts that the non-Hawaiian cardueline finches will show a greater variance in bill morphology than will the non-Hawaiian thrushes.

2. MATERIAL AND METHODS

(a) *Sample sources and laboratory techniques*

Myadestes muscle tissues for DNA extraction were either collected by us or obtained from the frozen tissue collections of the following institutions: Academy of Natural Sciences of Philadelphia; Burke Museum of Natural History, University of Washington; Field Museum of Natural History, Chicago; Louisiana State University Museum of Zoology; and the National Museum of Natural History, Washington DC. These DNAs were extracted, amplified and sequenced as described previously (Lovette & Bermingham 1999). Cytochrome *b* sequences generated by R. A. Feldman, L. A. Freed, J. C. Groth and R. L. Cann for the 10 Hawaiian honeycreepers and for the non-Hawaiian cardueline finch *Loxia curvirostra* (accession numbers AF015754–AF015765), and by J. C. Groth for *Loxia leucoptera* and *Carduelis hornemanni* (AF171655 and AF171659), were obtained from GenBank.

(b) *Phylogeny reconstruction and genetic distance comparisons*

All phylogenetic reconstructions and distance estimates presented here are based on the 790 nucleotides of homologous mitochondrial cytochrome *b* sequences available for the thrushes and honeycreepers. However, we confirmed the mitochondrial DNA phylogeny for *Myadestes* using 2849 additional nucleotides of protein-coding sequence from each sample. Phylogenetic relationships and genetic distances were estimated using PAUP* (Swofford 1999). Comparisons of genetic divergence were based upon HKY distances (Hasegawa *et al.* 1985) incorporating nucleotide rate variation ($\gamma = 0.2$). Phylogenetic reconstructions were independently generated for each group via heuristic searches employing a maximum likelihood HKY model with rate variation. We compared these trees to those generated under the assumption of a molecular clock and found no evidence for the heterogeneity of substitution rates within clades, but the large phylogenetic distance between finches and thrushes precluded tests of rate homogeneity between them.

Table 1. Variance ratios in bill measurements and eigenvalues of a principal components analysis of bill measurements comparing Carduelini and Turdinae.

trait	variance or eigenvalue		χ^2 or t	smallest samples that give $p < 0.01^a$
	Carduelini ($n = 110$)	Turdinae ($n = 133$)		
bill length	0.01420 \pm 0.00096	0.01086 \pm 0.00067	$\chi^2 = 2.16$	n.s.
bill depth	0.01794 \pm 0.00121	0.00855 \pm 0.00052	$\chi^2 = 16.4$	50, 50
bill width	0.01844 \pm 0.00124	0.00393 \pm 0.00024	$\chi^2 = 68.2$	13, 13
PCA1	1.0468 \pm 0.0063	0.0209 \pm 0.0026	$t = 6.08$	ca. 30, 30
PCA2	2.0032 \pm 0.0004	0.0017 \pm 0.0002	$t = 4.85$	ca. 40, 40
shape (PCA1/PCA2)	3.83 \pm 0.363	0.51 \pm 0.30	$t = 0.97$	n.s.

^a The large magnitudes of the χ^2 and t statistics would indicate significant differences at a critical value of $p < 0.01$ even if the degrees of freedom were lowered to the values indicated here. This approach provides a conservative test of differences in morphological variation between the clades.

(c) Comparisons of morphological variation

We measured the length, width and depth of the bills of single individuals representing 110 of the 136 species of non-Hawaiian Carduelini and 133 of the 174 species of non-Hawaiian Turdinae (taxonomic designations *sensu* Sibley & Monroe (1990)) in the collection of the Academy of Natural Sciences of Philadelphia. Additional measurements were available (R. E. Ricklefs, unpublished data) for 387 species of New World passerines, including 22 species of Hawaiian honeycreepers and two species of Hawaiian thrushes.

Bill measurements were recorded to the nearest 0.1 mm and were then log-transformed both to remove scaling artefacts associated with body size differences and to achieve a normal distribution of variation (Ricklefs & Travis 1980). All principal components analyses (PCAs) were based on covariance matrices to preserve the relative scaling of distances among points in ordination space. Variances in bill measurements for the Carduelini and Turdinae were compared by Bartlett's test for homogeneity of variances (Sokal & Rohlf 1995); eigenvalues were compared by a t -test with variances for eigenvalues estimated according to Morrison (1976). As data obtained from related species lack independence, the statistics presented in table 1 are accompanied by the smallest sample sizes that would yield $p < 0.01$ for the observed χ^2 or t value.

3. RESULTS

(a) Phylogenetic reconstructions and genetic distances

Figure 1 depicts cytochrome-*b*-based maximum-likelihood reconstructions for the Hawaiian honeycreeper and thrush clades and shows the distribution of pairwise comparisons between Hawaiian and representative mainland taxa. As expected based on previous studies of morphological (Amadon 1950; Raikow 1978) and molecular (Johnson *et al.* 1989; Sibley & Ahlquist 1990; Tarr & Fleischer 1995) characters, the 10 honeycreeper taxa form a monophyletic group with respect to the three mainland taxa. The corresponding reconstruction of phylogenetic relationships among all *Myadestes* species placed the Hawaiian lineage as the close sister taxon to a clade containing the other *Myadestes* species. This basal placement of the Hawaiian thrush lineage is not well supported, however, probably owing to the short internodes that separate most *Myadestes* species-level lineages and to

the very large genetic distance between *Myadestes* and the outgroup taxon *Cichlopsis*. Midpoint-rooted reconstructions (not shown) of the seven *Myadestes* taxa placed the Hawaiian lineage as the sister taxon of *M. townsendi*, a relationship congruent with morphological and behavioural evidence (Pratt 1982). Despite this topological uncertainty, genetic distances between Hawaiian and all New World *Myadestes* species were large, suggesting that the Hawaiian thrush lineage colonized the archipelago before or during the period when the *Myadestes* clade diversified in the New World.

Comparisons of cytochrome *b* distances suggest that the Hawaiian honeycreepers and thrushes have had similar tenures in the Hawaiian archipelago, as indicated by their overlapping distributions of pairwise Hawaii–New World cytochrome *b* divergence (figure 1). Although the smallest Hawaii–mainland distances involved honeycreepers, these comparisons provide only an upper bound on the mitochondrial divergence of the honeycreeper clade because the precise sister taxon of the Hawaiian honeycreepers has not been identified with certainty. If a non-sampled cardueline is more closely allied to the honeycreeper clade than are our representative *Loxia* or *Carduelis* species, our comparisons will overestimate the age of the Hawaiian honeycreeper clade. As the non-Hawaiian relatives of the Hawaiian thrushes are completely represented at the species level, we are able to estimate their magnitude of Hawaiian–continental divergence with greater confidence.

(b) Patterns of morphological variation

Analyses of variation in bill characters indicated that non-Hawaiian carduelines have a greater magnitude of morphological variation than do the non-Hawaiian turdines. In particular, the Carduelini have significantly greater variance in bill depth and width, but not length, than the Turdinae (table 1). PCAs of bill measurements within each clade further indicated that the non-Hawaiian carduelines have diversified significantly more than the non-Hawaiian turdines (figure 2). Factor loadings of the three bill characters (length, depth and width, respectively, with Turdinae to the left of Carduelini) on the three PCA axes were: axis 1, 0.97/0.92, 0.97/0.99, 0.82/0.97; axis 2, -0.21/-0.40, 0.05/0.07, 0.55/0.22; axis 3, 0.13/0.05, -0.24/-0.14, 0.19/0.11. The Carduelini were hence more variable with respect to both the first PCA axis (PCA1),

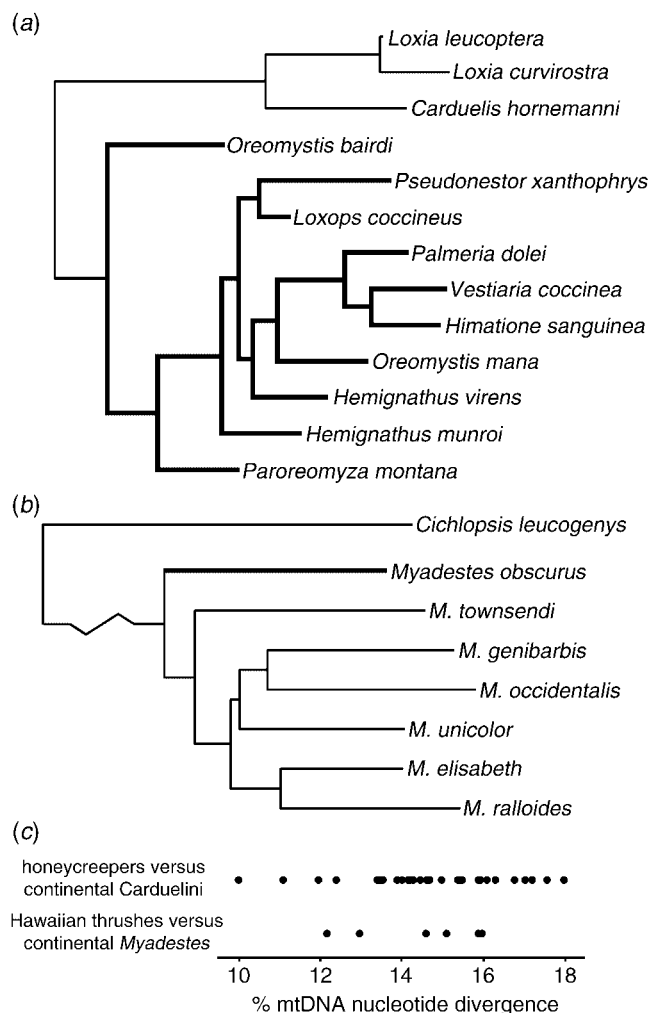


Figure 1. Phylogenetic relationships and genetic divergence of Hawaiian thrushes and honeycreepers based on 790 nucleotides of the cytochrome *b* gene. (a) Phylogenetic relationships among 10 honeycreeper taxa (thick branches) and 3 representative continental cardueline finches. (b) Phylogenetic relationships in the thrush genus *Myadestes* illustrating the early separation of the Hawaiian lineage (thick branch) drawn to the same scale as (a). (c) Range of pairwise cytochrome *b* distances between Hawaiian and mainland *Myadestes* thrushes and between Hawaiian honeycreepers and the two New World cardueline finches.

expressing overall bill size, and the second PCA axis (PCA2), representing bill shape, specifically variation in bill width relative to length and depth (table 1). These differences are consistent with the hypothesis that the honeycreepers are derived from a group that has a high propensity to evolve morphological differences in bill characters associated with resource utilization.

4. DISCUSSION

Considered in concert, the mitochondrial and morphological evidence indicates that time limitation is unlikely to explain the low diversity of the Hawaiian thrushes and suggest that the Hawaiian honeycreepers fall within a clade that exhibits high evolutionary flexibility in bill morphology. We therefore suggest that both the Hawaiian honeycreeper and thrush clades resulted from ancient and possibly nearly contemporaneous colonizations, and that

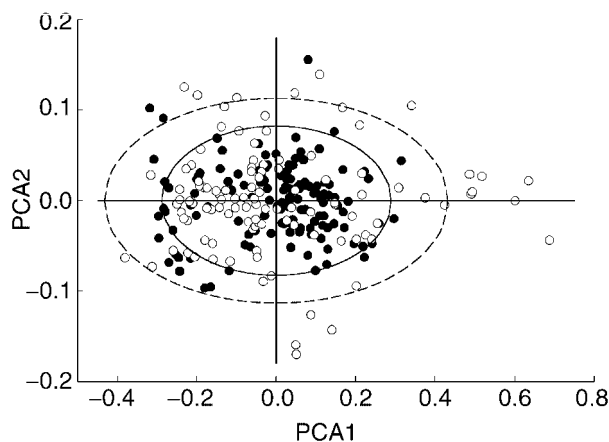


Figure 2. Distribution of species of thrushes and cardueline finches on the first two principal components axes of bill dimensions. PCAs were computed individually for each of the clades. Axis 1 represents an overall size dimension in each clade, whereas Axis 2 expresses a contrast between the length and width of the bill. Ellipses indicate 95% confidence intervals for each clade (dashed lines, Carduelini; solid lines, Turdinae). Black circles, Turdinae; white circles, Carduelini.

the extreme diversification of the honeycreepers has been promoted by a general clade-specific ability to evolve novel morphologies.

The mitochondrial evidence does not support the hypothesis that a more recent colonization by the ancestral Hawaiian thrush is responsible for the lower diversity of the Hawaiian thrush clade. Cytochrome *b* distances between Hawaiian and continental *Myadestes* species exceed the pairwise distances between 10 species representing eight honeycreeper genera and overlap the distances between these 10 honeycreepers and three representative continental cardueline finches (figure 1). The equivalent levels of mitochondrial divergence between the Hawaiian and mainland representatives of these two groups indicate that the Hawaiian honeycreeper and thrush lineages have had similar tenures in the Hawaiian archipelago. This comparison is based on the assumption that the rate of cytochrome *b* substitutions is similar in both clades, but is not dependent on an absolute calibration of that common rate. Avian mitochondrial DNA rate calibrations remain controversial and must be applied with caution, but the widely employed estimate of 2% per million years for avian cytochrome *b* suggests that both the honeycreeper and thrush clades colonized the Hawaiian archipelago during the formation of the oldest of the present-day main islands, as has been previously suggested for the honeycreepers (Tarr & Fleischer 1995; Fleischer *et al.* 1998).

As time does not seem important in explaining differences in the diversity of these groups, we examined clade-specific morphological characteristics that may be associated with rates of diversification (figure 2). These morphological analyses demonstrate that the non-Hawaiian Carduelini exhibit significantly greater variation in bill size and shape among species than the non-Hawaiian Turdinae (table 1). The greater morphometric variation of the carduelines suggests that the ancestor of the honeycreepers may have had an intrinsically higher capacity for mor-

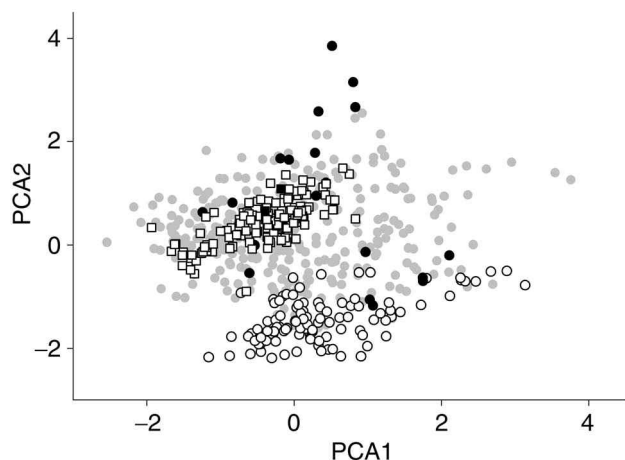


Figure 3. Distribution of Hawaiian and non-Hawaiian Carduelini and Turdinae on the first two principal component axes of bill dimensions calculated over the entire sample of passerine birds. The first axis represents primarily variation in bill width and depth, and the second axis, variation in bill length. Grey circles, all other passerines; white circles, Carduelini; black circles, Hawaiian drepanids; white squares, Turdinae; black squares, Hawaiian thrushes.

phological change than did the ancestor of the Hawaiian thrushes.

We performed a PCA of bill measurements for a combined sample that included both Hawaiian and non-Hawaiian Carduelini and Turdinae, as well as a broad representation of New World passerines. As shown in figure 3, the Hawaiian honeycreepers have diversified well beyond the range exhibited by non-Hawaiian carduelines to fill much of the bill size and shape space occupied by New World passerine birds in general. In this PCA, the first axis primarily reflects bill width and depth, whereas the second axis primarily reflects bill length. The multivariate space occupied by the Hawaiian honeycreepers approaches that of the entire sample, although the non-Hawaiian carduelines, presumably encompassing the ancestor of the honeycreepers, have among the shortest bills of all passerines and cluster at the edge of the passerine morphological space. In contrast to the honeycreepers, the Hawaiian thrushes fall conservatively within the space occupied by the continental thrushes.

The greater morphological diversification of the non-Hawaiian Carduelini compared to the non-Hawaiian Turdinae is especially notable given the greater age of the Turdinae clade. DNA–DNA hybridization distances (Sibley & Ahlquist 1990) place the base of the turdine clade at about 8 °C DTH50 (shift in heteroduplex compared to homoduplex DNA melting temperature) and that of the cardueline clade at about 4.3 °C, a nearly twofold difference in clade age. This large difference in clade origin means that despite the lower absolute species diversity in the carduelines, the more rapid cardueline morphological diversification is paralleled by a higher net rate of diversification (speciation – extinction/time): assuming a constant rate of exponential increase in species number, the species diversity of non-Hawaiian carduelines (137 species, 20 genera) has increased at a rate of 1.14 per °C and that of turdines (174 species, 22 genera) at a rate of 0.64 per °C.

Selection related to diet seems probably to have produced the greater morphological variation of the carduelines and may have simultaneously selected for heightened evolutionary lability in bill morphology. Most thrushes are generalist consumers of insects and soft fruits and act as seed dispersers, whereas most non-Hawaiian cardueline finches are seed predators specializing on hard seeds. A bill trait linked to resource specialization in some Carduelini is their ability to laterally abduct their lower mandible to husk seeds or to force open buds or cones (Nuijens & Zweers 1997). More generally, seed specialization or seed predator/seed prey coevolution could select for bill lability if the Carduelini occupy a region of morphological space with a complicated adaptive landscape, which might foster rapid and frequent adaptive modification as resources change or evolve defences (Schluter & Grant 1984; Price 1987; Benkman 1993, 1999), or if long-term selection on bill characters in the Carduelini has resulted in a high additive genetic variance in these characters (Schluter 1996). Whatever its cause, a propensity for morphological lability then could have promoted the honeycreeper adaptive radiation by allowing the rapid divergence of sister populations in allopatry and by allowing secondarily sympatric taxa to respond more readily to diversifying selection. Consistent with this prediction, the bill morphologies of several honeycreeper species have changed significantly over a few generations in response to changing dietary resources (Conant 1988; Smith *et al.* 1995). Other seed-eating passerines show similar trends: marked morphological variation; associated adaptive diversification; and occasionally rapid morphological change have been documented for such seed-eating passerines as the cardueline crossbills (Benkman & Lindholm 1991) and Hawaiian honeycreepers (Conant 1988; Smith *et al.* 1995) and the non-cardueline Galápagos finches (Grant 1986; Grant & Grant 1995) and estrildid finches (Smith 1987, 1993). The generality of these patterns supports the inference that resource specialization, morphological lability and adaptive potential may be causally related. A high bill-shape lability in the Carduelini and other seed-eating birds might therefore represent a key innovation of morphological versatility (Vermeij 1974) analogous to that proposed for the pharyngeal jaw apparatus in the adaptive radiations of cichlid fish in East African rift valley lakes (Liem 1973; Galis & Metz 1998).

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