

The Imprint of History on Communities of North American and Asian Warblers

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Submitted October 15, 1999; Accepted May 17, 2000

ABSTRACT: The ecology of the component species of an adaptive radiation is likely to be influenced by the form of the founding ancestor to the radiation, its timing, and rates of speciation and extinction. These historical features complement environmental selection pressures. They imply that, if the history of the species' radiations are very different, ecological communities are unlikely to be completely convergent even when placed in identical environments. We compare the adaptive radiation of the *Dendroica* warblers of North America with that of the *Phylloscopus* warblers of Asia. We consider the ecology of the species in two localities where species' diversity is very high (New Hampshire, U.S.A., and Kashmir, India, respectively) and contrast the history of the two radiations on the basis of a molecular (mitochondrial cytochrome b) phylogeny. By comparison with the *Phylloscopus*, the *Dendroica* are on average larger and morphologically more similar to one another. Although there is some similarity between the *Dendroica* and *Phylloscopus* communities, they differ in foraging behavior and in associations of morphology with ecological variables. The *Dendroica* likely reflect an early Pliocene radiation and are two to four times younger than the *Phylloscopus*. They probably had a colorful sexually dichromatic ancestor, implicating sexual selection in the production of the many ecologically similar species. The *Phylloscopus* are much older and probably had a drab, monomorphic ancestor. Given the difference in ages of the two radiations, it is plausible that the close species' packing of the *Dendroica* warblers is a transient phenomenon. If this is the case, community structure evolves on the timescales of millions of years. Differences in ancestry and timing of the species' radiations can be

related to the different biogeography of the two regions. This implies that the historical imprint on adaptive radiations could be predicted on the basis of the attributes of ancestors and biogeographical context.

Keywords: ancestral reconstruction, community convergence, *Dendroica*, *Phylloscopus*, phylogeny, sexual selection.

Ecological communities in matched habitats across the world are often convergent in such attributes as species' number and niche partitioning (Cody and Mooney 1978; Schluter 1986; Schluter and Ricklefs 1993). Convergence is rarely complete and remaining differences among communities are attributed to so-called historical and regional effects (Ricklefs 1987, 1989; Ricklefs and Schluter 1993). These include the taxonomic affinities of the component species, the time a habitat has been present, rates of speciation in the region in which the local community is embedded, and the ease of dispersal of species into that habitat from other sources (Ricklefs 1987, 1989). Because of the difficulty of reconstructing past events, it has been difficult to evaluate the relative importance of these various causes of differences among communities. In this article, we use phylogenetic relationships among species of two adaptive radiations to compare their histories of diversification. Historical reconstructions have potentially large explanatory power, but the incorporation of effects of history into community ecology lags far behind considerations of local processes, such as competition and predation. Our goal here is to identify historical differences between the species' radiations and then ask how these may have had an impact on the ecological communities of which they are part.

We concentrate on a classic example of fine-scale niche partitioning, that of the *Dendroica* warblers of North America (MacArthur 1958). These are small birds that breed in the woodlands of temperate North America. Most species winter in the Neotropics. The ecological similarity of these coexisting congeners has been a puzzle, originally because it was thought they provide an exception to Gause's principle of competitive exclusion. The puzzle was

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partly solved by MacArthur (1958), who showed there were differences in feeding stations among the species. Nevertheless, Lack (1971, p. 132) pointed out that these warblers “present a more complex case of ecological interdigitation than any found in European passerine species.” The underlying explanation for the coexistence of so many similar species remains obscure.

The effects of history can best be investigated through a comparative approach. In this article, we use the *Phylloscopus* warblers of Asia as a group against which to evaluate ecological patterns in the *Dendroica*. We identify two historical differences between the *Dendroica* and *Phylloscopus* radiations as potential explanations for the ecological differences between them and for the unusual similarity among the *Dendroica* warblers. First, the form of the ancestor is likely to have been different in the two groups: the ancestor to the *Dendroica* was probably bright plumaged and sexually dimorphic, whereas the ancestor to the *Phylloscopus* was probably dull plumaged and sexually monomorphic. Second, the *Dendroica* warblers underwent a burst of speciation perhaps 3–5 million years ago. They are younger than the *Phylloscopus* warblers, which show more dispersed speciation events dating to as much as 12 million years ago. We suggest that the radiation of the *Dendroica* was accompanied by sexual selection, resulting in a small “species flock” of ecologically similar coexisting species that have persisted up to the present day (Lovette and Bermingham 1999).

Methods

The *Dendroica* and *Phylloscopus* warblers are dominant components of their respective forest communities (Sabo and Holmes 1983; Price 1991). Most species are migratory and overwinter in the Tropics (the *Dendroica* in the Americas and the *Phylloscopus* in the Old World). They are small warblers that forage mainly by picking arthropods from arboreal substrates or in flight. The two groups are distantly related to each other. The *Dendroica* are members of the nine-primaried oscines (Raikow 1978), a clade that also includes New World orioles and tanagers, whereas the *Phylloscopus* are allied to Old World babblers and thrushes. According to both traditional systematics (Mayr and Amadon 1951) and recent molecular evidence (Sibley and Ahlquist 1990; Edwards et al. 1991), many ecologically distinct passerines, such as the tits and swallows, form ingroups between the *Dendroica* and *Phylloscopus*. Although we have not conducted a formal reconstruction of ancestral states across distant ancestors, similarities between the *Dendroica* and *Phylloscopus* likely represent considerable convergence to the “warbler” ecotype.

Our goal was to compare ecological communities in habitats matched as far as possible and that are also close

to the centers of species’ diversity for the two groups. Because community structure varies geographically (e.g., Richman 1996), we focused on the locations in each continent where species’ diversity is a maximum and perhaps most likely to represent a coevolved community. We use ecological relationships among the species in these locations as a general indication of the way in which the two adaptive radiations have proceeded. This approach specifically ignores investigations of the rate at which allopatric, ecologically similar species have been formed, and these may form an important component of the complete adaptive radiation of the two groups. Nevertheless, previous phylogenetic analyses based on most of the *Dendroica* and *Phylloscopus* warblers demonstrate that the major phylogenetic patterns that we identify are similar to those based on more complete sampling (Richman 1996; Lovette and Bermingham 1999).

We compare the previously studied breeding community of *Phylloscopus* warblers in Kashmir, India (34°N, 76°E; Price 1991; Richman and Price 1992) with published results on the *Dendroica* warblers of the White Mountains of New Hampshire, U.S.A. (44°N, 72°W; Holmes et al. 1979; Sabo 1980; Sabo and Holmes 1983). We consider patterns of morphology, ecology, and species’ diversity in these communities. Both communities span an altitudinal gradient down from tree line, which is at approximately 3,700 m in Kashmir and 1,450 m in New Hampshire. Not all species occur at each location along the elevational gradient, but we consider the whole gradient to be part of a single community because species’ distributions extensively overlap and the different species interact with each other when they come in contact (e.g., Morse 1976; Price 1991).

In New Hampshire, coniferous trees are at high altitude, up to tree line, and large broadleaf trees occur lower down. The main study sites in New Hampshire are at Mount Moosilake at ~1,100 m, which is mostly in conifer (Sabo 1980; Sabo and Holmes 1983), and Hubbard Brook at ~600 m, which is mostly broadleaf (Holmes et al. 1979; Sabo and Holmes 1983). In Kashmir, birch, rhododendron, and juniper lie in sequence above coniferous woods consisting mostly of fir, pine, and spruce. The high elevation site in Kashmir was in birch and rhododendron (~3,300 m; see Price 1991) and the low elevation site in conifer (~2,400 m). There are eight *Phylloscopus* species in the Kashmir study (Price 1991) and seven *Dendroica* species in the New Hampshire study (Sabo and Holmes 1983). In both localities, there is substantial species turnover along the elevational gradient, and each study site is dominated by one to three species. There are warblers of other genera present in both localities (*Cettia fortipes* in Kashmir; *Vermivora ruficapilla*, *Seiurus aurocapillus*, *Setophaga ruticilla*, and *Wilsonia canadensis* in New Hamp-

shire), as well as ecologically similar vireos (*Vireo* spp., three species in New Hampshire) and kinglets (*Regulus* spp., one species in Kashmir and two species in New Hampshire).

Morphology

Previous studies in Kashmir were based on field measurements of morphology. In order to generate comparable data sets between New Hampshire and Kashmir and also to provide an independent check on the Kashmir results, we measured museum specimens of all species in the current study (10 males per species, collected as close to the study areas as possible; see appendix). We measured beak depth, beak length, beak width, wing length, and tarsus length following the procedures of Price (1991) and also tail length (from the tip to insertion of the longest feather). All measurements were made by T. Price. Body masses were taken from Sabo and Holmes (1983) and Price (1991). We extracted principal components (PCs) from the correlation matrix of ln-transformed species' means of the measurements of the seven *Dendroica* and eight *Phylloscopus* species combined (table 1). Other ecologically similar species were measured in the same way (appendix), and their morphologies were projected on to the principal component space calculated from the 15 focal species. The correlation matrix was employed because the traits are quite disparate, and mass is measured in different units from the other traits. An alternative is to use the covariance matrix (e.g., Warheit et al. 1999). We used the covariance matrix of the ln-transformed structural traits (tarsus length and the three beak measures) as a second means of assessing morphological differences between the groups.

Ecology

There are many ways to classify and to analyze ecological data, and different measurements will imply different levels of convergence between communities. We decided to investigate only those patterns that had previously been observed in the Kashmir community of *Phylloscopus* warblers. In Kashmir, Price (1991) showed that body size correlated with prey size, habitat occupancy with a measure contrasting tarsus and beak size (PC2), and foraging method with a measure of beak shape (PC3). Investigation of these three associations in New Hampshire required some adjustments, as follows. First, prey size data are not available for the White Mountains community. Instead, we obtained stomachs collected by Crawford and Jennings (1989) from five species of *Dendroica*, as well as two other related species (*Vermivora ruficapilla* and *Regulus satrapa*) in a study of spruce-fir woods across the New Hampshire–Maine border. As previously noted by Crawford and

Table 1: Correlations ($\times 100$) of principal component scores

	PC1	PC2	PC3
Wing	92	1	30
Tarsus	59	80	-11
Beak length	93	-20	-24
Beak depth	96	-20	-1
Beak width	97	-14	-13
Tail	95	-5	18
Weight	99	2	2
%variance	83	11	3

Note: Correlations are based on the correlation matrix of ln-transformed original traits; $N = 15$ species.

Jennings (1989), budworms were a large constituent of the diet. We measured right budworm mandibles (up to 10 per stomach) and took the raw average across all stomachs. Second, the correlation between habitat and morphological shape in Kashmir was based on occupancy of pine, spruce, and fir, which are tree species at the bottom of the altitudinal gradient in Kashmir but the top in New Hampshire. We used median elevation of a species as an ecological measure because it was more easily obtained from the New Hampshire data set; consequences for habitat occupancy are considered further in "Discussion." Elevational positions of species in New Hampshire were based on weighting the elevations of three locations by the density of the species at that study location (from Sabo and Holmes 1983). Elevational positions in Kashmir were the estimated midpoint of elevational range.

Foraging observations in New Hampshire were taken from Holmes et al. (1979) and Sabo (1980). If a species was studied by both Holmes et al. (1979) and Sabo (1980), its characteristics were taken to be the simple average. We use the fraction of all foraging movements involving flight as a simple measure directly comparable between the communities. Other information on the ecology of *Dendroica* was taken from Greenberg (1979), Levey and Stiles (1992), and Curson et al. (1994). Some species eat fruit in the nonbreeding season. Frugivorous habit was taken from Levey and Stiles (1992) and recorded on a three-point scale: never recorded, occasional, or regularly incorporated into the diet (appendix). Sexual dichromatism was assessed using Shutler and Weatherhead (1990) and Curson et al. (1994) and was scored as either dimorphic or monomorphic.

Principal components summarizing morphological variation were extracted from the combined New Hampshire–Kashmir data set in this study but from Kashmir only in a previous study (Price 1991). The interpretations of the first two principal components in the two studies are concordant, with the first measuring overall size and

the second a tarsus : beak ratio (table 1; Price 1991). However, the third principal component in the combined data set accounted for little of the variance, and gave loadings difficult to interpret (table 1), whereas in the Kashmir data it was clearly interpretable as a measure of beak shape (Price 1991). As an alternative measure of beak shape in the combined data set, we used ln-transformed beak length minus the average of ln-transformed beak depth and beak width. This measure was moderately correlated with the Kashmir PC3 scores (from Price 1991: $r = 0.56$, $N = 8$, $P > .1$). The beak shape measure was strongly correlated with PC1 across all 15 species (body size, $r = -0.82$) but not PC2 (the tarsus/beak ratio, $r = 0.1$).

Correlations among species' means are presented in all statistical tests. Much has been written on the need to correct P values to account for the statistical nonindependence among species due to differing degrees of relatedness (Harvey and Pagel 1991). Recently, however, an evolutionary model which justifies the significance test derived from the correlation of the raw species' values has been developed (Harvey and Rambaut 2000). This model seems particularly appropriate for species' radiations of the kind we are investigating here (Harvey and Rambaut 2000). We also assigned probability values using the independent contrast method (Felsenstein 1985), based on the phylogeny and branch lengths in figure 1 (*center*). In

all cases, qualitative conclusions were unaltered. This is demonstrated in Richman and Price (1992) for the *Phylloscopus* warblers. The *Dendroica* radiation is starlike (Lovette and Bermingham 1999), which is the situation where the use of species' mean values will be identical to the employment of independent contrasts (Felsenstein 1985; Harvey and Pagel 1991).

Phylogeny

An estimate of phylogeny based on ~1,100 base pairs of the cytochrome b mtDNA sequence is drawn from studies previously described in Lovette and Bermingham (1999) for the *Dendroica* and Price et al. (1997) for the *Phylloscopus* warblers. Lovette and Bermingham (1999) include a much larger sequence base in their analyses of the *Dendroica*, and obtain very similar results in all respects to that based on just the cytochrome b molecule presented here. A previous study comparing the phylogenetic relationships of these two groups (Price et al. 1998) was flawed due to the presence of nuclear homologs in the *Dendroica* sequences ("numts"; see Arctander 1995). Here, we re-analyse the timing of speciation events using the correct sequences, and the methods described in Price et al. (1998).

Phylogenetic relationships were estimated by combining

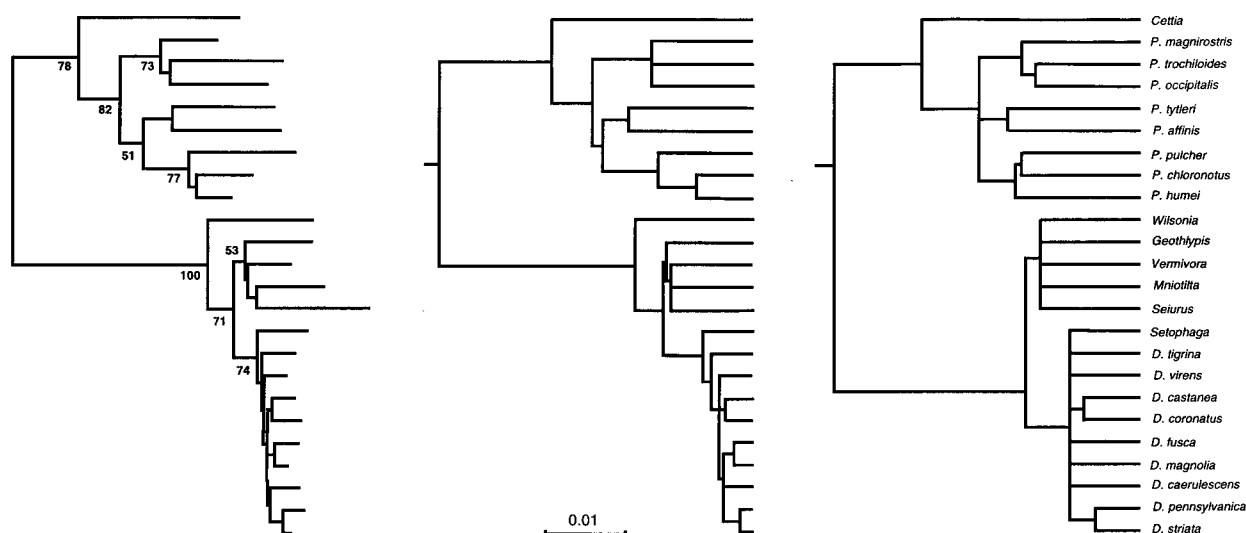


Figure 1: *Left*, neighbor-joining tree for Old and New World warblers produced in LINTRE (Takezaki et al. 1995) and based on mtDNA cytochrome b transversion distances (distance metric of Hasegawa et al. 1985; bootstrap values >50% are indicated). *Center*, linearized version of the same tree; the LINTRE test for deviations from the molecular clock was nonsignificant ($\chi^2 = 29.01$, $df = 23$, $P > .25$). The scale bar corresponds to a 1% transversion difference along a single lineage. *Right*, maximum-likelihood tree using all substitutions and the Hasegawa et al. (1985) substitution metric, assuming across-site variation follows a gamma distribution with parameter $a = 0.2$ and forcing a molecular clock. Both clocklike trees were rooted using the shrike *Lanius ludovicianus* as outgroup. *Phylloscopus* and *Dendroica* are indicated by species names; the other species by genus name (see appendix for full names).

the *Dendroica* and *Phylloscopus* into a single analysis. We also included several other species of warblers (*Cettia fortipes* from Kashmir and two *Dendroica* as well as representatives of six other warbler genera from New Hampshire) that are relevant to understanding the two communities. Because transitions show much evidence of saturation in the *Phylloscopus* (Richman 1996), we used a distance estimate based on transversions only. We used neighbor joining and the distance metric of Hasegawa et al. (1985), assuming that across-site rate variation followed a gamma distribution with shape parameter $a = 1.0$, but results were indistinguishable if raw transversion distances were used instead. The phylogeny was estimated in LINTRE (Takezaki et al. 1995), which also provides a linearized (constant-rate) version of the tree and a test of the molecular clock. For comparison with alternative tree-building methods, we present an additional analysis based on maximum likelihood including both transitions and transversions (using PUZZLE, Version 4.0.2; Strimmer and von Haeseler 1999).

We estimated relative rates of speciation across clades using the program END-EPI (Nee et al. 1996; Rambaut et al. 1997). The method assesses whether a focal lineage at an identified point in time has given rise to disproportionately many present-day descendants (Nee et al. 1996). We estimated relative timing of speciation events within clades using an analysis based on coalescence (Price et al. 1998). This method examines the ratio of terminal branch lengths to internal branch lengths against a simulated null distribution based on the neutral model. Long terminal branch lengths imply that there has been a “slowing down” of speciation events toward the present among the species included in the analysis. Further details of this method, including the simulated distributions against which the statistic can be evaluated, are presented in Price et al. (1998). Both the tests described in this paragraph require clocklike trees.

Ancestral State Reconstruction

We estimated ancestral states for sexual dimorphism in coloration and frugivorous habit at the base of the *Dendroica* and the *Phylloscopus*, using the phylogeny in the center panel of figure 1. In order to place some estimate of confidence in the ancestral reconstructions, we used the approach of Schluter et al. (1997) implemented in Discrete (version 1.01; Pagel 1994, 1997), which assumes a Markov model of evolution. The method involves estimating the likelihood of change between the two states that maximizes the probability of the observed distribution of those states among extant species on the phylogeny. Probabilities of ancestral states at an internal node are based on the contribution of each state at that node to the likelihood. All models of evolution are likely far from correct, but this

model has the desirable property that, if change is estimated to be frequent, the ancestral state should be estimated to be uncertain, whereas if change is thought to occur more rarely, ancestral states are estimated with more confidence. We used the phylogeny and branch lengths in the central panel of figure 1 except that very short branch lengths (<2% of the length of the longest branch, and sometimes 0) were set to the 2% value. We examined the robustness of our conclusions to branch-length manipulations through the use of an alternative (“punctuational”) model where all branch lengths were set to be equal.

A difficulty common to all methods of ancestral reconstruction is that they are sensitive to which groups are included in the analysis. We a priori chose to confine reconstruction based on only those species that occur in each community. We did this for two reasons: because it provides an unambiguous, nonarbitrary choice of species and because these communities may contain many of the important elements of the adaptive radiations of the *Dendroica* and *Phylloscopus*, at least if tropical species are ignored. For example, most other Asian species of *Phylloscopus* are geographical replacements of one or other of the Himalayan species we consider here (Richman 1996).

Results

Morphological Patterns

On the basis of scores derived from a principal components analysis of the two groups combined, the different species of *Dendroica* are less variable than the *Phylloscopus* in both size and shape (fig. 2; table 2). The *Dendroica* also show higher correlations among traits than the *Phylloscopus* (fig. 3; table 2). The higher correlations were quantified by taking the first eigenvalue from a principal components analysis of the three traits in table 2. This eigenvalue accounts for 84% of the variance in the *Dendroica* (jackknifed SD 4.6%) and 56% in the *Phylloscopus* (SD 7.4%). Thus, not only are the *Dendroica* species in New Hampshire quite similar to each other, they show little residual variation in shape once size is removed.

These results were based on the correlation matrix of the original variables. We also used the covariance matrix of (ln-transformed) tarsus and three beak variables and conducted principal components analyses for the two groups separately. The summed eigenvalues provide a measure of overall variability within each group (e.g., Warheit et al. 1999). The sum of the three eigenvalues (0.082) for the *Phylloscopus* is almost four times the sum of the three eigenvalues for the *Dendroica* (0.023). The higher variation within the *Phylloscopus* was confirmed with an additional measure, the mean Euclidean distance between species pairs, which was 1.5 times higher within in the

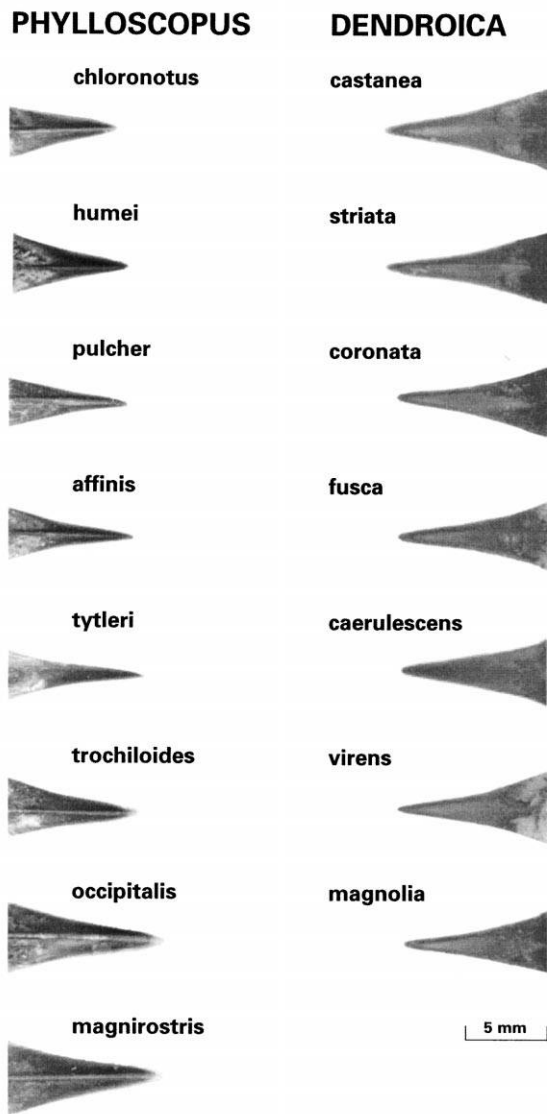


Figure 2: Scanned beaks (from museum specimens) of the eight *Phylloscopus* and seven *Dendroica* warblers being compared in this study.

Phylloscopus (this distance metric was computed as the square root of the sums of squares and calculated for the six ln-transformed mensural traits). The morphological similarity among species of *Dendroica* was previously emphasized by MacArthur (1958).

The *Dendroica* also differ from the *Phylloscopus* in that they are on average larger (e.g., mean body mass is $10.9 \text{ g} \pm 0.6 \text{ SE}$ in the *Dendroica*, but $7.3 \text{ g} \pm 0.6 \text{ SE}$ in the *Phylloscopus*; standard errors are based on species as replicate). There are significant differences in both PC1 and beak shape between the two communities (t -tests, $P <$

.01, using species as the replicate) but not in PC2 ($P > .5$).

Ecological-Morphological Associations

The two communities show some similarities in associations between morphology and ecology. In both the Old World and New World, larger species eat larger prey, and species with longer tarsi and smaller beaks tend to occur at higher elevations (figs. 4, 5). Within the *Dendroica*, neither of these associations is significant, but when species from other New World genera are included, the correlation between body size and prey size is high and significant (fig. 4).

The association of PC2 with elevation in the *Dendroica* is relatively weak. However, the slopes of the regression lines of elevation on PC2 in the *Phylloscopus* and *Dendroica* are close to being “significantly similar,” defined by Schluter (1986) as a P value $>.95$ when species are used as replicates (standardizing elevation within each locality to have mean 0, $SD = 1.0$; ANCOVA, $F = 0.012$, $df = 1, 11$, $P > .91$). Average PC2 scores at each of the study sites (where each species is weighted by its density on the study site) also imply similarity in morphology, with greater similarity across elevations than within regions (fig. 3, left). In contrast to similarity between the two communities in body size—prey size and PC2—elevation associations, the association of beak shape with foraging method is significantly different between the two communities (fig. 6; ANCOVA, $F = 16.9$, $df = 1, 11$, $P < .01$). *Dendroica* species that rarely fly when catching prey have blunt beaks, whereas *Phylloscopus* species that rarely fly have pointed beaks.

In summary, although there are some similarities between the *Dendroica* and *Phylloscopus* communities, there are many differences. The *Dendroica* tend to be larger and more tightly ecologically packed than the *Phylloscopus* and show different associations of foraging method with beak shape. The tight ecological packing in New Hampshire is

Table 2: Correlations between principal component scores extracted from the correlation matrix of 15 species and a beak shape measure ($\times 100$)

	PC1	PC2	Beak shape
PC1	...	−13	−54
PC2	83	...	29
Beak shape	−81	−66	...
Variances:			
<i>Phylloscopus</i>	.761	1.14	.005
<i>Dendroica</i>	.295	.931	.003

Note: Scores are based on the correlation matrix of ln-transformed original traits; $N = 15$ species. *Phylloscopus* is above the diagonal ($N = 8$), *Dendroica* is below the diagonal ($N = 7$).

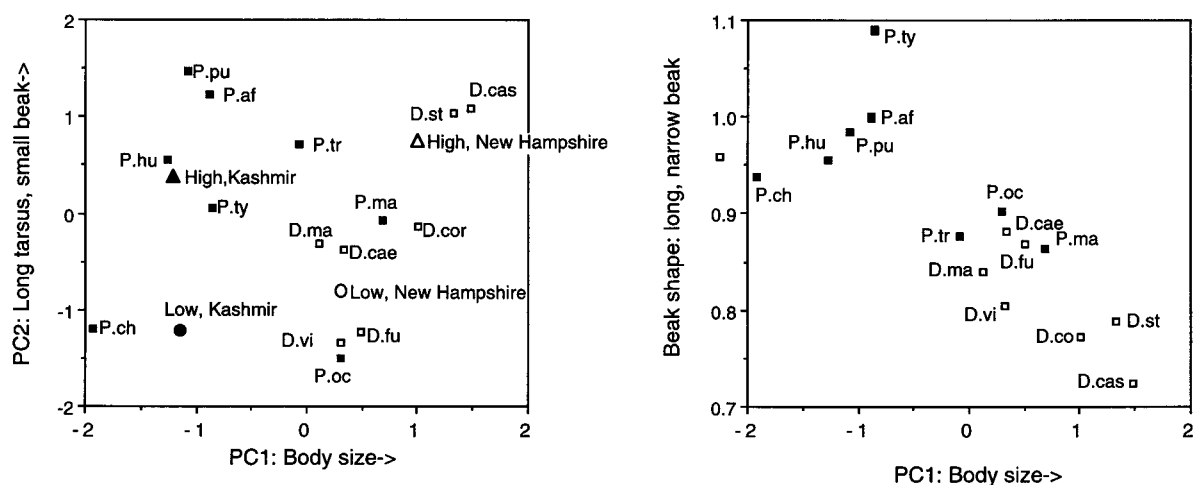


Figure 3: *Left*, plot of principal component scores for the eight *Phylloscopus* (closed squares) and seven *Dendroica* (open squares) species in the study. Also shown are the average scores for two sites in Kashmir (Price 1991) and two sites in New Hampshire (Sabo and Holmes 1983), where the averages were calculated by weighting by densities of each species present on the site. *Right*, plot of a measure of beak shape ($\ln(\text{beaklength}) - 0.5 \times [\ln(\text{beakwidth}) + \ln(\text{beakdepth})]$) against the first principal component score. See figure 1 or the appendix for full species names.

emphasized in figure 7, which shows that other warbler-like species in the New Hampshire community are morphologically quite similar to the *Dendroica*. There are also more of these species in New Hampshire than in Kashmir.

History

The estimate of phylogenetic relationships in figure 1 implies that the *Dendroica* of the New Hampshire community are more recently diverged than the *Phylloscopus*. We confirmed this by applying the methods in Nee et al. (1996) to ask whether the lineage at the root of the *Dendroica* leaves more descendants than expected with respect to other contemporaneous lineages. There are no speciation events inferred to have occurred within the *Phylloscopus* or other New World warblers over the time span of the *Dendroica* radiation, a result highly unlikely to occur by chance ($P < .001$; using the program END-EPI [Rambaut et al. 1997] to compare the seven *Dendroica* in the ecological analysis to either the species in other New World warbler genera or the *Phylloscopus* community in fig. 1).

Absolute Timing. Among the *Dendroica*, raw distances in cytochrome b sequences vary from 4.7% to 7.5% (median 6%), which, using the standard calibration of 2% divergence per million years (e.g., Klicka and Zink 1997), makes them about 3 million years old. This is more recent than the date suggested by Lovette and Bermingham (1999), who used a distance metric that allows for multiple substitutions. The 2% calibration is very uncertain, especially for more ancient radiations (Arbogast and Slowinski

1998). The right-hand panel in figure 1 shows a tree constructed using both transitions and transversions. This tree has the root of the *Phylloscopus* 2.3 times deeper than that of the *Dendroica*, but the likelihood ratio test for a molecular clock fails ($\chi^2 = 43.77$, $df = 23$, $P < .01$). The tree based on transversions only (fig. 1, center) may give a more reliable estimate of relative dates. The transversion distance across the root of the *Dendroica* in this tree is 0.011 and for the *Phylloscopus* is 0.043. If transversions accumulate linearly over the time spans considered here (Moore and deFilippis 1997), this gives a crude estimate of the root of the *Phylloscopus* at >12 million years. This age for the root of the *Phylloscopus* is in rough agreement with the Sibley and Ahlquist (1990) estimate based on DNA:DNA hybridization studies and their calibration of the passerine rate of divergence.

Timing of Speciation Events within Each Group. Lovette and Bermingham (1999) inferred that the *Dendroica* underwent a burst of rapid speciation early in the radiation of the group. We confirmed this to be the case for just the *Dendroica* species on the phylogeny of figure 1, using the coalescent method described in Price et al. (1998). We computed a statistic based on the ratio of terminal branch lengths to internal branch lengths and compared it to the simulated distributions shown in Price et al. (1998); low P values imply overly long terminal branches. Using the phylogeny of figure 1 (center), we obtained probability values of $P < .01$ for the *Dendroica* and $.01 < P < .05$ for the *Phylloscopus*. Although the *Phylloscopus* community shows some evidence of long terminal branches, speciation

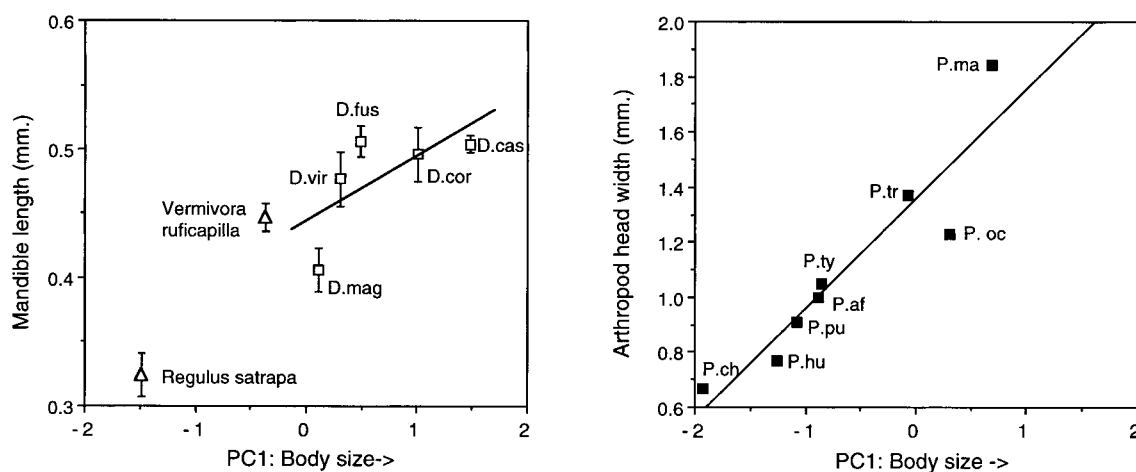


Figure 4: Associations of body size and prey size. *Left*, New England. Standard errors are based on individual budworm mandibles ($N = 21\text{--}58$ per species; from $N = 11\text{--}17$ stomachs per species). Line is least squares regression through *Dendroica* only (open squares, $r = 0.67$, $N = 5$, $P = .2$; the correlation across all species is $r = 0.89$, $N = 7$, $P < .05$). *Right*, Kashmir (from Price 1991; $r = 0.93$, $N = 8$, $P < .05$). See the appendix for full species names.

events are more dispersed through the history of this assemblage than the *Dendroica* assemblage. On the basis of the phylogeny of figure 1, some speciation events in the *Phylloscopus* appear to have occurred millions of years after the initial divergence.

Ancestral States Dimorphism. According to Curson et al. (1994), 24 (89%) of the 27 species of *Dendroica* warblers are sexually dimorphic in coloration (see also Shutler and Weatherhead 1990; Gray 1996). Two of the three monomorphic species are tropical residents. All of the *Dendroica* considered in this study are dimorphic, and the only monomorphic New World warbler on the phylogeny depicted in figure 1 is the ovenbird (*Seiurus aurocapillus*). All of the *Phylloscopus* as well as *Cettia* are monomorphic. We reconstructed the form of the ancestor to the *Dendroica* as $P(\text{dimorphic}) = 1.0$ whether we employed transition rates estimated from this phylogeny or from a much larger sample of passerine birds (Price and Birch 1996) and whether we used the branch lengths in figure 1 (*center*) or a model with all branch lengths set equal to 1.0. The ancestor to the *Phylloscopus* was estimated as monomorphic with probabilities varying from .95 to .99, depending on the model employed.

Frugivory. Some warbler species consume fruit in the non-breeding season (Cramp 1992; Levey and Stiles 1992). Frugivorous habit is uncommon in the *Phylloscopus*, apparently having been rarely recorded only in *Phylloscopus collybita* (Cramp 1992). However, frugivorous habit is scattered throughout the *Dendroica* and even within a single

species of *Dendroica*, the amount of frugivory may vary widely among populations (Levey and Stiles 1992). These observations suggest frugivorous habit in the *Dendroica* may be an evolutionary labile trait partly contingent on prevailing availability of unexploited fruit in the environment. We reconstructed ancestral states based on the phylogeny of the central panel of figure 1 and the frugivory records of Levey and Stiles (1992; species not recorded in Levey and Stiles were excluded; see appendix). Despite the apparent lability of frugivorous habit, which should introduce uncertainty into ancestral reconstruction, we found the ancestor to the *Dendroica* to be frugivorous with high probability ($P = .99$).

The high confidence in the conclusion that the *Dendroica* ancestor was frugivorous is surprising given the ease with which it appears to be gained and/or lost during the course of evolution. The result reflects a maximum likelihood reconstruction where the loss of frugivory is 800 times more likely than its gain. While this may represent the actual evolutionary trajectories, an alternative model where the forward and backward rates are set to be equal may also be reasonable. In this case, as expected, the ancestral state is reconstructed with a high degree of uncertainty ($P(\text{frugivory}) = .46$). A second reason to treat the ancestral reconstruction of frugivory in the *Dendroica* with caution is that bootstrap support for the particular topology used is low. Neighboring topologies based on swapping various *Dendroica* species around gave estimates of frugivory as low as $P = .60$ (with loss about two times more likely than gain). By contrast to the uncertainty surrounding the ancestral state of the *Dendroica* warblers, the

ancestral state to the *Phylloscopus* is estimated to be entirely insectivorous ($P > .9$ in all analyses).

Discussion

The *Dendroica* and *Phylloscopus* warblers are distantly related. This implies substantial convergence from what are likely to have been very different ancestors. Quantifying the extent to which convergence has occurred is fraught with difficulties, stemming from the large number of ecological and morphological measurements that could be compared. In fact, we find little evidence for fine-scale ecomorphological convergence. There is an association of body size and prey size within both communities, but this is a correlation very generally observed across taxa and expected from energetic constraints. In addition, the association is only significant in New Hampshire when other warbler-like species besides the *Dendroica* are included. There appear to be similar associations of morphology with elevation across both communities, but even this correspondence would be scored as a striking failure to converge if coniferous habit was used as an alternative ecological measure (conifers are at lower elevation in Kashmir, higher elevation in New Hampshire). The functional explanation for the association of morphology and elevation is unclear (Price 1991), making any assessment of convergence premature. Finally, associations of beak shape and feeding methods are in opposite directions in the two communities.

In the *Dendroica*, many of the morphology-ecology associations are attributable to variation in body size. Larger species have wider, stubbier beaks (table 2) that use flying movements less often when foraging (fig. 6). The larger

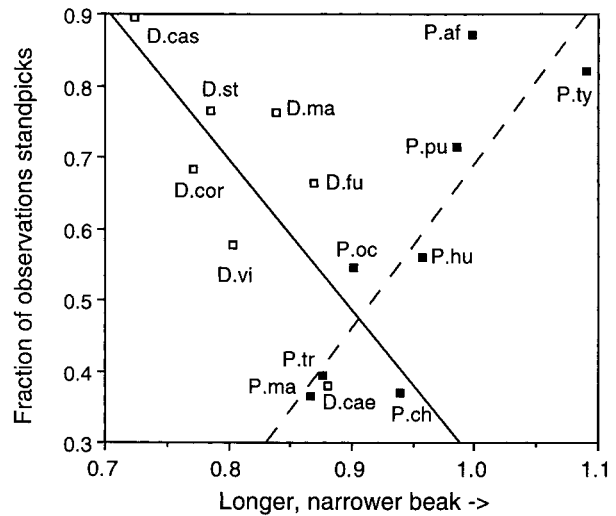


Figure 6: Associations of feeding method and beak shape (see fig. 3). “Standpick” refers to a feeding movement not involving flight. New Hampshire *Dendroica* (filled line, open squares, $r = -0.73$, $N = 7$, $P = .06$) and Kashmir *Phylloscopus* (dashed line, closed squares, $r = 0.84$, $N = 8$). See the appendix for full species names.

species also more often eat fruit (data from the appendix of this article, using PC1 as a measure of body size, $r = 0.8$, $N = 7$, $P < .05$) and occur more often in coniferous woodland (Greenberg 1979). The strong effect of body size on many ecological variables contrasts with patterns among the *Phylloscopus* warblers, where orthogonal size and shape measures are separately associated with different aspects of ecology, at least in the Himalayas (Price 1991). The associations of body size with frugivory and feeding method

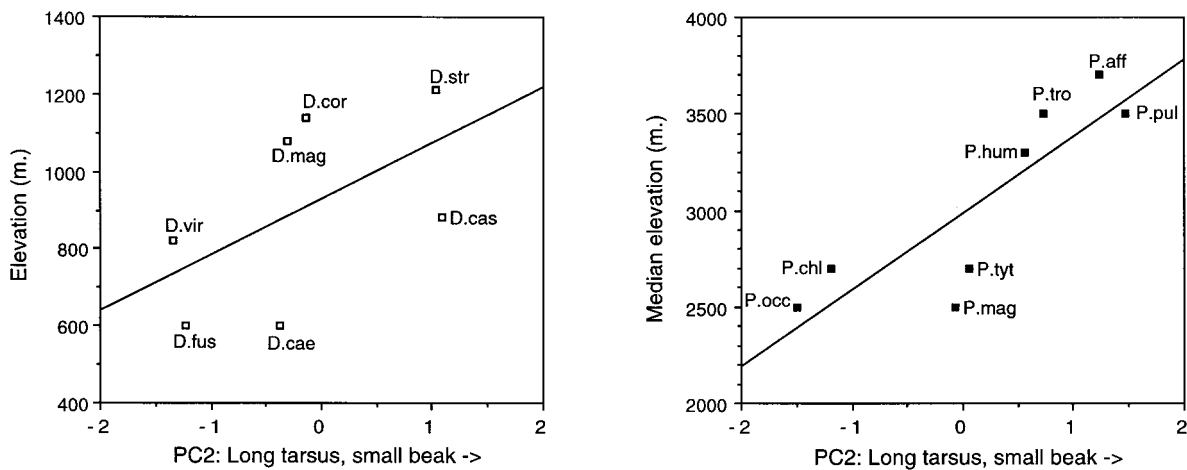


Figure 5: Associations of elevation and morphological shape (PC2 score). *Left*, New Hampshire *Dendroica* ($r = 0.56$, $N = 7$, $P > .5$). *Right*, Kashmir *Phylloscopus* ($r = 0.86$, $N = 8$, $P < .05$). See the appendix for full species names.

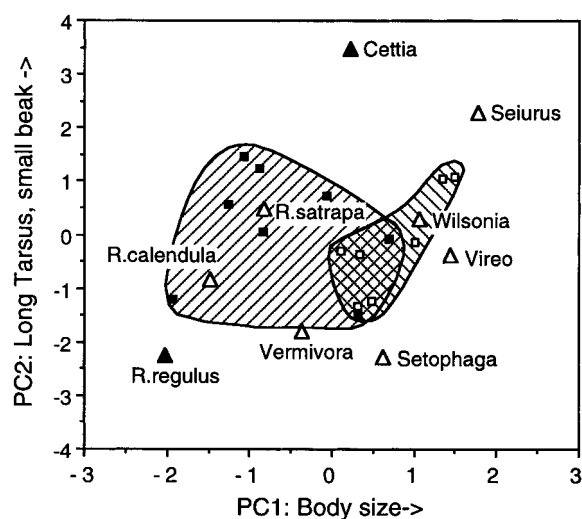


Figure 7: Same plot as the left side of figure 1 but with additional species from each community projected on to the principal component space. Shaded areas encompass the morphologies of the *Phylloscopus* (closed squares) and *Dendroica* (open squares). Closed triangles, Kashmir species; open triangles, New Hampshire species. Species are identified by genus, except for *Regulus* (*R.*), which is represented by three species. See the appendix for full species names.

among the *Dendroica* may partly explain why beak shape shows the opposite relationship with feeding method in the two communities. The flycatching species in both communities are very similar in morphology, but the picking species are very different (fig. 6), and among the New Hampshire *Dendroica*, it is only the picking species that are highly frugivorous.

There are two general explanations for the differences between the *Dendroica* and *Phylloscopus*. The first is that *Dendroica* habitat somehow differs from *Phylloscopus* habitat. This is a so-called local explanation (Ricklefs 1987) and implies that a complete understanding of the communities could in principle be gained by a thorough study of the locality in which they have occurred. The second explanation is historical: even if two localities are identical, their different histories will lead to different communities occupying them (Ricklefs 1987). The different explanations can be contrasted by considering frugivory. We find that the ancestor to the *Phylloscopus* was likely insectivorous, but the ancestor to the *Dendroica* was either frugivorous, with several losses of the habit, or else frugivory has been frequently gained and lost (making ancestral reconstruction uncertain). The “local” explanation is that the differences between the *Dendroica* and *Phylloscopus* warblers reflect differences between North America and Asia in fruit availability. For example, populations of the yellow-rumped warbler *Dendroica coronata* overwinter in

the eastern part of North America by consuming large amounts of bayberry fruits that are readily available (Place and Stiles 1992). The historical explanation is that the *Dendroica* warblers may be more predisposed to evolve frugivorous habit in the right ecological conditions (e.g., the yellow-rumped warbler is especially large and may have had a large ancestor) or that some species have continued to exploit fruit throughout the diversification of the group.

It is rarely possible to eliminate explanations based on unique attributes of different localities (e.g., Cody and Mooney 1978, pp. 315–316). Here we have taken the alternative approach of explicitly considering history. Apart from the uncertain inferences regarding frugivory, we find, first, that the *Dendroica* radiation is younger than the *Phylloscopus* and, second, that the ancestor to the *Dendroica* was likely brightly colored and sexually dichromatic, whereas the ancestor to the *Phylloscopus* was likely dull colored and monochromatic. We consider the possible implications of these two findings on community structure.

The *Dendroica* underwent a burst of speciation probably in the Pliocene, although absolute dating is very uncertain. The first ice ages began at about 2.4 million years ago (Shackleton 1993). Divergence times apparently precede this—during the early to mid-Pliocene, or even late Miocene—when the climate was hot and forests fragmented, at least in North America (Webb et al. 1995) with high potential for vicariant speciation events (Lovette and Bermingham 1999). Divergence may have been aided by sexual selection on plumage patterns and the production of ecologically similar forms that subsequently established sympatry (Lovette and Bermingham 1999). The ancestor to the *Dendroica* was probably sexually dichromatic, and in general surveys of birds, plumage dichromatism has been found to be a correlate of sexual selection (Møller and Birkhead 1994; Owens and Hartley 1998) and speciation rates (Barraclough et al. 1995; Owens et al. 1999).

In birds, sexually dichromatic groups tend to be more species rich than monomorphic groups (Barraclough et al. 1995; Owens et al. 1999). The phenomenon is puzzling because accelerated speciation within dimorphic groups should eventually result in them replacing monomorphic groups, but this has not occurred. If dimorphic groups show high speciation rates at the beginning of species’ radiations, followed by extinctions, then dimorphism can promote speciation, without a net increase in dimorphic species over long periods of time. Thus, it is plausible that the unusually close packing and morphological similarity of the *Dendroica* in New Hampshire is a transient phenomenon, and on even longer timescales (millions of years), some species would disappear from the community and/or evolve such that the communities of New Hampshire and the Himalayas become more similar.

Historical differences should also reflect themselves in

ecomorphological associations. Within the New Hampshire *Dendroica*, body size is correlated with both feeding method and habitat, whereas these correlations are weaker among the Himalayan *Phylloscopus*. Among the *Phylloscopus*, much diversification in body size is inferred to have occurred early in the history of the group (in association with the first two speciation events; Richman and Price 1992). It is notable that the timescale of the whole *Dendroica* radiation is equivalent to the time from the root to just the third speciation event in the *Phylloscopus* (*tyleri/affinis* divergence), according to the phylogeny based on transversion distances. Thus it is possible that much of the ecological variation during the first few million years of the *Phylloscopus* radiation was associated with body size, just as it is with *Dendroica* at the present day.

We conclude that many of the differences between the *Dendroica* and the *Phylloscopus* are attributable to historical differences, by which we mean the form of the ancestor and perhaps the timing of the radiations. Previous emphasis on the importance of history has led to the idea that chance and contingency may have played a large part in community evolution, with accidents of ancestry leaving a large imprint (Gould 1989). In fact, it pushes the chain of causality back one step, to an investigation of why the founding ancestor and timing of radiations should differ. The closest outgroup to the *Phylloscopus* is *Cettia*, a genus of dull insectivorous species that skulk in the undergrowth. Many resident warblers in the Tropics are similar to *Cettia* (Gaston 1974; Levey and Stiles 1992). They are poor fliers, and for this reason are unlikely to initiate a species' radiation in temperate North America, which probably involved a long migration out of the Tropics (Mayr 1946). The proximity of the temperate, seasonal Himalayas to the Tropics would place no similar constraint on dispersal for poor flying species into the temperate regions of the Old World. Finally, frugivory (Levey and Stiles 1992) and/or use of open habitat (Chesser and Levey 1998) have been suggested to be important preadaptations for long-distance

migration out of the Tropics because they are associated with movements within the Tropics. Bright coloration may be a consequence of ancestral frugivory through the presence of carotenoids in the diet (Brush 1978) or through improved color vision (Osorio and Vorobyev 1996). Open habitats may also favor the use of visual communication and bright colors (Crook 1964). It is plausible that the requirements of long-distance migration selected for ancestral characteristics that also favored the development of colorful plumages.

Different biogeographic histories may explain the different timing of the radiations. The *Phylloscopus* appear to have evolved along with the uplift of the Himalayas, which preserved their favored habitats through climatic fluctuations (Price et al. 1998), whereas the *Dendroica* may have diverged as a consequence of habitat fragmentation in the Pliocene (Lovette and Bermingham 1999). Thus, the ultimate determinant of differences in communities may lie in the different biogeography of different regions. These proposals are based on a comparison of just two species' radiations. The comparative study of many radiations (including their timing, ancestral form, and biogeographical context) should eventually lead to the development of a theory of the effect of historical processes on community structure, comparable to that of the effects of local species interactions.

Acknowledgments

We thank K. E. Gibbs for locating the warbler stomachs; the curators of the British Museum, the Royal Ontario Museum and the San Diego Natural History Museum for access to their specimens; D. Irwin, A. Keast, D. Levey, J. Losos, K. Marchetti, D. Miles, D. Schluter, and A. Suarez for comments; K. Marchetti for help in the field; R. Holmes and P. Marra for hospitality in New Hampshire; and M. Pagel for advice on the use of *Discrete*. Supported in part by the National Science Foundation (to T.P.).

APPENDIX

Table A1: Morphology of species in millimeters

Species	Frugivory ^a	Wing length		Tarsus length		Beak length		Beak depth		Beak width		Tail		Weight mean (g) ^b
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
<i>Dendroica castanea</i>	2	72.1	.72	20.5	.28	7.5	.10	3.6	.04	3.6	.10	53.7	.40	13.0
<i>Dendroica striata</i>	...	71.8	.76	20.3	.34	7.4	.10	3.5	.05	3.3	.03	54.8	.98	12.8
<i>Dendroica magnolia</i>	0	57.7	.50	18.8	.23	6.7	.13	2.9	.02	2.9	.06	50.9	.38	9.2
<i>Dendroica virens</i>	0	61.1	.64	18.2	.13	7.0	.06	3.3	.05	3.0	.06	50.9	.69	9.1
<i>Dendroica coronata</i>	2	70.8	.39	19.0	.20	6.8	.07	3.1	.08	3.1	.04	58.2	.98	12.1
<i>Dendroica caerulescens</i>	1	65.3	.60	18.6	.12	6.7	.11	2.8	.06	2.8	.07	52.5	.43	9.9
<i>Dendroica fusca</i> (N = 5)	...	68.0	1.30	18.1	.18	7.1	.23	3.2	.12	2.8	.09	50.2	1.16	10.4
<i>Vermivora ruficapilla</i>	0	60.3	.56	17.4	.13	6.9	.10	2.8	.07	2.5	.05	43.0	.73	9.0
<i>Wilsonia canadensis</i>	0	66.2	.63	19.6	.31	6.7	.09	3.5	.06	3.6	.05	57.6	.58	10.5
<i>Seiurus aurocapillus</i> (N = 5)	0	76.8	.58	22.0	.39	8.5	.21	4.2	.06	3.7	.09	59.2	1.46	19.5
<i>Setophaga ruticilla</i>	0	61.9	.62	17.1	.15	5.9	.06	2.8	.07	3.6	.07	56.5	.60	8.2
<i>Vireo solitarius</i>	2	75.8	.62	19.0	.17	6.7	.14	4.1	.06	3.4	.07	53.7	.59	16.4
<i>Regulus satrapa</i>	0	57.3	.28	17.2	.13	4.7	.08	2.2	.05	1.9	.04	44.8	.52	6.8
<i>Regulus calendula</i>	0	59.2	.27	18.7	.16	5.8	.08	2.1	.05	2.4	.05	43.9	.47	7.0
<i>Regulus regulus</i>	0	55.1	.63	16.3	.33	5.4	.13	2.0	.06	1.8	.05	38.7	.49	5.0
<i>Phylloscopus trochiloides</i>	0	63.6	.49	19.2	.20	6.2	.13	2.5	.06	2.6	.06	48.5	.76	8.3
<i>Phylloscopus chloronotus</i> ^c	0	53.9	.48	17.0	.26	5.0	.09	1.9	.04	2.0	.06	39.9	.68	5.1
<i>Phylloscopus occipitalis</i>	0	65.4	.91	18.0	.12	7.3	.12	2.8	.04	3.1	.07	49.4	.87	8.7
<i>Phylloscopus magnirostris</i>	0	69.9	.82	19.0	.13	7.0	.11	3.0	.05	2.9	.05	53.3	1.03	10.0
<i>Phylloscopus tyleri</i>	0	58.4	.54	18.5	.17	6.4	.07	2.1	.03	2.2	.04	42.0	.52	7.2
<i>Phylloscopus affinis</i>	0	57.8	.88	19.2	.10	5.8	.09	2.1	.04	2.1	.05	45.0	.49	6.7
<i>Phylloscopus humei</i> ^d	0	58.5	.54	18.4	.34	5.3	.09	2.0	.04	2.0	.04	43.9	.57	6.0
<i>Phylloscopus pulcher</i>	0	58.2	.57	19.3	.14	5.5	.08	2.0	.02	2.1	.03	43.0	.70	6.5
<i>Cettia fortipes</i>	0	56.7	.45	21.7	.23	6.1	.07	2.6	.06	2.4	.05	53.7	.88	10.4

Note: Based on 10–12 males per species except where indicated.

^a Frugivory: 0 = no fruit recorded in diet; 1 = some fruit; 2 = much fruit. New World warblers from Levey and Stiles (1992), *Phylloscopus* from Ali and Ripley (1983) and personal observations (T. Price). Four species on figure 1 were not measured. Among these *Geothlypis* is not recorded as eating fruit, whereas *Dendroica pennsylvanica* and *Dendroica rigrina* eat some fruit (Levey and Stiles 1992).

^b From Sabo and Holmes 1983 and Price 1991.

^c Formerly *Phylloscopus proregulus*.

^d Formerly *Phylloscopus inornatus*.

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