

We suggest that the minimum depth reached by significant volumes of melt along a ridge axis may be influenced by the maximum depth of penetration of major faults (and thus vigorous hydrothermal circulation) and that the consequent cooling constitutes an important mechanism for interaction between the magmatic and tectonic processes occurring on mid-ocean ridges. This relationship would not only lead to variations in crustal structure with spreading rate, but would also control second-order temporal and along-axis variations in the thickness of the volcanic layer. □

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Evolution of ecological differences in the Old World leaf warblers

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SYMPATRIC species that belong to the same ecological guild usually differ in their behaviour and morphology, and these differences are often interpreted as adaptations to having to make use of different resources. Evidence supporting this interpretation comes from association between ecology and morphology among species¹, in which an *a priori* functional relationship is reasonable. But one problem with such comparisons is that members of a guild may be closely related, so the more closely related species can share a greater similarity in their morphology and ecology simply as a result of the lingering legacy of a common ancestor^{2–5}. In principle, the importance of historical legacy can be evaluated from phylogenetic relationships and times since divergence for all species^{2,6}, but this is rarely possible because these data are not available. Here we use a phylogeny for eight sympatric species of warbler in the genus *Phylloscopus*, based on their mitochondrial DNA sequences, to remove the effects of historical legacy. Without these effects, we find strong support for adaptive interpretations of among-species variation in habitat selection, prey-size choice and feeding method. Ecological variation along any of these three niche axes is associated with predictable morphological variation. We also find evidence for historical legacy in that more closely related species are often more similar behaviourally and morphologically. This paradoxical result can be reconciled because the most closely related species tend to differ along only one niche axis, habitat choice. In contrast, the evolution of prey-size choice and feeding method occurred rapidly and early in the diversification of this group. Once a new ecological zone was occupied, subsequent morphological change along these niche axes was limited, accounting for the similarity of closely related species.

We have studied the ecology and breeding of eight species of warblers, which occur in sympatry during the breeding season in the Himalayas of Kashmir, India. The eight warbler species all belong to the same genus (*Phylloscopus*), and together with the goldcrest, *Regulus regulus*, they form the insectivorous leaf-gleaning guild⁷. The species have been shown to differ in habitat choice, size of prey, and feeding method⁸. There are strong correlates of morphology with the ecological differences⁸, as illustrated in Fig. 1a, c and e. Larger species feed on larger prey, species with relatively short tarsi breed in coniferous (versus deciduous) woodlands, and species with wide beaks tend to flycatch more.

We estimated the phylogeny for 19 specific and subspecific taxa within the *Phylloscopus* plus a single species from three other warbler genera, including *Regulus*. The data consist of a contiguous DNA sequence of 910 bases within the mitochondrial cytochrome *b* gene (Fig. 2a). Most observed variation among these closely related species is at third-position sites. The number of observed transitions among species of *Phylloscopus* at third-position sites is similar to that observed for more distant inter-generic comparisons, indicating rapid saturation for transitional changes within the genus, whereas the number of the more slowly accumulating (observed) transversion differences is not similarly affected (Fig. 2b). Similar results have been found in other mitochondrial DNA sequence studies of closely related species^{9–11}. Moreover, a study of cytochrome *b* evolution in mammals found that transversions continue to accumulate approximately linearly for tens of millions of years¹¹. Corrections for multiple substitutions at third-site transversions yield pairwise distances little different from those observed (data not shown). We therefore used the pairwise fraction of observed (untransformed) transversion differences over all sites as a linear measure of species divergence, and estimated the phylogeny using the neighbour-joining algorithm¹² implemented in the program NEIGHBOR in PHYLIP¹³.

The neighbour-joining tree for 22 taxa is shown in Fig. 3. Taxonomic groups identified by the molecular phylogeny are in good agreement with previous suggestions^{14,15} based on characters such as nasal bristles and plumage patterns which were used to distinguish major groups (see Fig. 3). We tested the sensitivity of the tree topology to sampling variation using the bootstrap¹⁶. The frequencies of occurrence of different groups within the eight Indian *Phylloscopus* at our study site in

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Kashmir, and the three outgroup species, were extracted from bootstrap replicates using the larger species set, and are shown in Table 1. The existence of three major clades within this group of *Phylloscopus* is reasonably well supported, with somewhat less support for the order of branching within and among these clades.

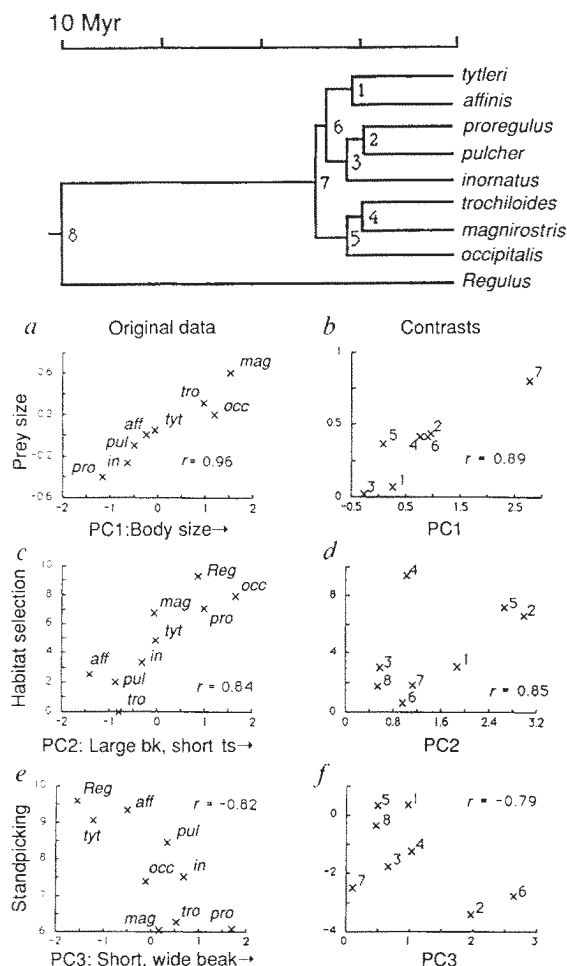


FIG. 1 Top. The phylogeny for eight species of *Phylloscopus*, and *Regulus*, where branch lengths are proportional to time. Branch lengths generated by the program NEIGHBOR do not assume rate constancy, and so are not necessarily proportional to time. Branch lengths were obtained for the topology in Fig. 3 using DNAMLK¹³, a maximum likelihood method which assumes a molecular clock. Only third position sites were used to estimate branch lengths: both transitions and transversions were used, and the (maximum likelihood) ratio of transitions to transversions was specified as 5:1. Numbered tree nodes refer to specific contrasts between taxa. For example, contrast 4 compares {*magnirostris*} to {*trochiloides*}, and contrast 6 compares {*pulcher*, *proregulus*, *inornatus*} to {*affinis*, *tytleri*}. Upper scale represents a calibration of branch length to time, using an estimate of time since divergence between *Phylloscopus* and *Regulus* according to DNA-DNA hybridization data¹⁹. a-f, Original correlations and contrast correlations (using the tree and branch-lengths presented). Morphology is along the abscissa. Principal components were extracted from the correlation matrix of mean values of ln-transformed species⁸. PC1 is a summary measure of body size. PC2 contrasts beak (bk) size to tarsus length (ts) and PC3 is a measure of beak shape. Prey size refers to beetle head widths in faecal analysis: faeces for *Regulus* were not available. Habitat selection is the (transformed) percentage of feeding observations in coniferous vegetation, and is highly negatively correlated with altitude. Stand-picking measures the (transformed) percentage of feeding observations where capture of prey did not involve flight (see ref. 8 for details). Contrast correlations were calculated assuming the average of all contrasts for each character is zero^{4,20}, so correlations for the original data and the corresponding contrast data are not directly comparable. All correlations are significant ($P < 0.05$).

The importance of historical legacy was evaluated using Felsenstein's method of independent contrasts, which requires information on phylogenetic relationships and times since divergence for all species². The method assumes that resemblance between species due to historical legacy decreases with time as the result of the accumulation of many small changes, so that it is adequately described by a Brownian motion model. Large coordinate changes in morphology and ecology are evidence against a purely historical hypothesis. Only pairs of species whose evolutionary histories are independent of all other species in the tree are examined; for example, all sister pairs are considered. These species are then removed from the tree, and their common ancestor is treated as a new species with morphological and ecological character values that are a weighted average of the two descendants². The pruning procedure creates $(n-1)$ independent contrasts (from the n species) in terms of the observed amount of character change between two taxa, scaled by the length of time since their divergence. A correlation between the morphological and the ecological contrasts, which we term a 'contrast correlation', cannot be due to historical legacy and supports an adaptive explanation.

In Fig. 1b, d and f we show scatterplots of morphological and ecological contrasts as constructed using Felsenstein's method² for each of the corresponding morphology/ecology scatterplots (Fig. 1a, c, e, respectively). The contrast analyses confirm the associations between morphology and ecology, once history is removed. This result is surprising in view of the fact that historical legacy is often evident in these data. For example, the effect of phylogeny on body size in Fig. 1a is clear: the three smallest *Phylloscopus* species are most closely related, as are the three largest, and the two intermediate size species. Nevertheless, once this non-independence of morphology and ecology, once history is removed, body size remains correlated with prey size. How is this possible? One reason is that the same trend is repeated within each of the size clades (Fig. 1b, contrasts 1, 2, 4). But the result does not depend on the almost perfect rank correlation in the original data. The largest contrast is between small and large body size clades (Fig. 1b, contrast 7), and this contrast is robust to changes in rank order within clades. Contrast 7 (Fig. 1b) is large not only because it compares (ancestral) taxa of very different size, but because the size shift occurred over a relatively short time, as measured by the short interior branch lengths.

A second result is that different correlations are upheld for different reasons. In the first plot (Fig. 1b), the greatest contrast was between large- and small-bodied clades, but this contrast is fairly small in other correlations. In the second plot (Fig. 1d), internal contrasts of morphology (PC2) between major clades are relatively small (contrasts 6, 7, 8) and large differences in habitat and/or related morphology occur between pairs of species within each of the size clades (contrasts 1, 2, 4, 5). In the third plot (Fig. 1f), there are large contrasts in beak shape and related foraging behaviour both in a pair of sister species (contrast 2) and in an internal contrast (contrast 6).

We found little effect of uncertainty in the reconstruction of phylogeny on the contrast correlations. We repeated the analysis using 100 neighbour-joining trees found from bootstrapped data sets, assuming *Regulus* was the outgroup. Correlations were 0.89 ± 0.02 s.d., 0.86 ± 0.02 s.d. and -0.80 ± 0.03 s.d. for the three sets of contrasts in Fig. 1b, d and f.

Using the results of the contrast analyses in conjunction with the phylogeny, we can reconstruct the temporal sequence of evolution of ecological segregation within the *Phylloscopus*. The first split within the *Phylloscopus* is accompanied by a large change in body size, as indicated by the large value of contrast 7 (Fig. 1b). Subsequent changes in body size within each of these size clades are small compared with the inferred change from the common ancestor to both groups. A secondary splitting is accompanied by a large change in feeding morphology and related behaviour (Fig. 1f, contrast 6). *P. affinis* and *P. tytleri* are mainly standpickers, and have relatively narrow, long beaks

compared with all other species of *Phylloscopus*. Thus, an early ecological innovation seems to have been a change in feeding method. Finally, large differences between more closely related species are observed in habitat choice and/or associated morphology (Fig. 1d, contrasts 1, 2, 4, 5). Thus, early ecological innovations are changes in feeding method and prey size, with habitat selection more recently modified. The inferred sequence of the evolution of ecological differences is reasonably robust to possible errors in the phylogeny, because it depends largely on the monophyly of the three major clades, which occur with high frequency in bootstrap analyses (Table 1).

The approximate timescale in Fig. 1 indicates that all these *Phylloscopus* species may have originated before the beginning of the Pleistocene. Rapid speciation and diversification occurred very early in the history of this group and was not driven by repeated periods of climatic change and subsequent restriction of forest habitats, which are known to have occurred¹⁷. Closely related species mostly differ in habitat and related morphology, yet it appears that these species pairs have been in existence for millions of years. The pattern may be attributed to recent geographic contact¹⁸, due to spread of forests. Alternatively, the present ecological community may be a stable entity which has persisted largely unchanged over long periods of time.

Two results from our study of the evolution of ecological differences among *Phylloscopus* warblers are of general significance. First, the adaptive interpretation of morphological and behavioural variation within this group is upheld, despite

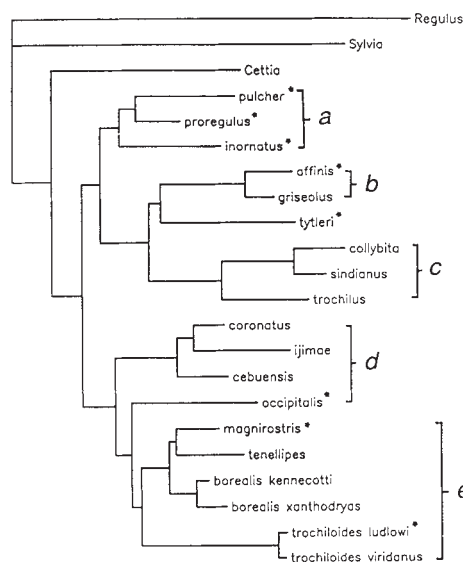


FIG. 3 The neighbour-joining tree for 22 taxa, obtained using the fraction of observed transversion differences over all sites. Asterisks denote the *Phylloscopus* species that occurred at our study site in Kashmir. Lettered brackets to the right indicate taxonomic groups previously recognized on the basis of morphological data^{14,15}. a, Dusky warblers; b, European warblers; c, Asiatic warblers; d, greenish warblers; e, crowned warblers (*cebuensis* was not considered by Williamson¹⁴); f, proposed subgenus *Acanthopneuste*¹⁵. There is a large degree of concordance between the molecular phylogeny and previous classifications (which did not consider relationships within or among groups of more closely related species). The two exceptions are: (1) the crowned warblers (group d) are not monophyletic according to the molecular phylogeny, with the western crowned warbler *P. occipitalis* placed as the outgroup to the greenish warblers (group e), and (2) the position of *tytleri* in the molecular phylogeny is consistent with the classification of Ticehurst¹⁵, but not with that of Williamson¹⁴. Williamson grouped *tytleri* with the greenish warblers (group e). Williamson's classification in this instance is not supported by the bootstrap data, where *tytleri* never occurs with the greenish warblers (Table 1).

TABLE 1 Unrooted groups occurring at least five times in 100 bootstrap replicates*

{ <i>magnirostris</i> , <i>trochiloides</i> , <i>occipitalis</i> }†	88
{ <i>affinis</i> , <i>tytleri</i> }†	86
{ <i>proregulus</i> , <i>pulcher</i> , <i>inornatus</i> }†	71
{ <i>Regulus</i> , <i>Sylvia</i> , <i>Cettia</i> }†	68
{ <i>Regulus</i> , <i>Sylvia</i> }†	63
{ <i>proregulus</i> , <i>pulcher</i> }†	63
{ <i>magnirostris</i> , <i>trochiloides</i> }†	53
{ <i>affinis</i> , <i>tytleri</i> , <i>proregulus</i> , <i>pulcher</i> , <i>inornatus</i> }†	48
{ <i>magnirostris</i> , <i>occipitalis</i> }	39
{ <i>proregulus</i> , <i>inornatus</i> }	34
{ <i>Regulus</i> , <i>Sylvia</i> , <i>Cettia</i> , <i>affinis</i> , <i>tytleri</i> }	30
{ <i>Regulus</i> , <i>Cettia</i> }	20
{ <i>Regulus</i> , <i>Sylvia</i> , <i>affinis</i> , <i>tytleri</i> }	16
{ <i>Cettia</i> , <i>magnirostris</i> , <i>trochiloides</i> , <i>occipitalis</i> }	13
{ <i>Regulus</i> , <i>affinis</i> , <i>tytleri</i> }	10
{ <i>Sylvia</i> , <i>Cettia</i> }	9
{ <i>inornatus</i> , <i>affinis</i> , <i>tytleri</i> }	6
{ <i>Cettia</i> , <i>Sylvia</i> , <i>magnirostris</i> , <i>trochiloides</i> , <i>occipitalis</i> }	6
{ <i>magnirostris</i> , <i>trochiloides</i> , <i>occipitalis</i> , <i>inornatus</i> }	6
{ <i>occipitalis</i> , <i>proregulus</i> , <i>pulcher</i> , <i>inornatus</i> , <i>affinis</i> , <i>tytleri</i> }	5
{ <i>proregulus</i> , <i>pulcher</i> , <i>affinis</i> , <i>tytleri</i> }	5

* Using the neighbour-joining program NEIGHBOR in PHYLIP¹³.

† Indicates that the group is also found on the neighbour-joining tree. In the bootstrap resampling procedure, first and second sites, and third sites alone, were resampled separately and then combined for phylogenetic analysis.

evidence for the importance of phylogeny in causing resemblance among *Phylloscopus* species. The explanation for these apparently contradictory findings is that closely related species tend to differ along a single morphological axis associated with habitat selection, with usually relatively little change along other niche axes. Rather than providing support for the common operating assumption of no phylogenetic constraint, these results underscore the argument² that phylogenies are fundamental to comparative biology. Second, the use of a well supported phylogeny in conjunction with the method of independent contrasts provides insight into the mode and tempo of character change. The sequence of evolution of ecological characters reported, namely that habitat differentiation has changed most recently, and is therefore probably the first step in species divergence, followed by changes in diet, has been shown for other groups using comparisons among genera¹⁸. Thus, it may be a normal mode of species divergence. The contrasts (Fig. 1b, d, f) suggest that there have been long periods of little ecological and morphological change and occasional periods of quite rapid change, usually in just one niche dimension. We believe the observed resemblance between ancestral and descendant taxa within the *Phylloscopus* says little about limitations in the ability of species to respond to selection due to genetic constraints. Instead, it reflects changes in the adaptive topography as the diversity of sympatric species increased over evolutionary time. □

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Travel at low energetic cost by swimming and wave-riding bottlenose dolphins

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OVER the past 50 years there has been much speculation about the energetic cost of swimming and wave-riding by dolphins^{1–11}. When aligned properly in front of the bow of moving ships^{1–3}, in the stern wake of small boats^{4,5}, on wind waves⁶, and even in the wake of larger cetaceans^{7–9}, the animals appear to move effortlessly through the water without the benefit of propulsive strokes by the flukes. Theoretically, body streamlining as well as other anatomical and behavioural adaptations contribute to low transport costs in these animals. The economy of movement permitted by wave-riding has been perceived as an energetic advantage for the swimming dolphin^{2,3,10}, but has been hard to prove in the absence of physiological data for exercising cetaceans. Here we determine the aerobic and anaerobic costs of swimming and wave-riding in bottlenose dolphins and find that the minimum cost of transport for swimming dolphins is $1.29 \pm 0.05 \text{ J kg}^{-1} \text{ m}^{-1}$ at a cruising speed of 2.1 m s^{-1} . Aerobic costs are nearly twice as high for swimming seals and sea lions, and 8–12 times higher for human swimmers¹². Wave-riding by dolphins provides additional benefits in terms of speed. The results indicate that behavioural, physiological and morphological factors make swimming an economical form of high-speed travel for dolphins.

To determine whether there is an energetic saving associated with wave-riding, we trained bottlenose dolphins to follow a moving boat (Fig. 1). Freely swimming dolphins remained at least 1 m below the water surface and were positioned outside the boat's wake. Wave-riding dolphins preferred positions within the stern wake at a depth of $\sim 0.5 \text{ m}$. Heart rate, respiratory rate and post-exercise blood lactate concentration were measured for both positions.

The results show that the physiological responses of swimming dolphins differed from those of wave-riding animals. At swimming speeds up to 2.9 m s^{-1} , the physiological responses of dolphins followed patterns similar to those of other marine mammals^{12,13}: there was a graded, but not necessarily linear, increase in average heart rate, respiration rate and metabolic rate with increased swimming speed (Fig. 2; Table 1). Dolphins swimming at 2.1 m s^{-1} had respiratory rates, heart rates and blood lactate concentrations not significantly different from resting values (two-sample *t*-test¹⁴ at $P < 0.05$). We attribute these results to the relatively low energetic demands of swimming at this speed¹⁵ and to a pre-exercise, anticipatory response that occurred during the resting measurements. All three physio-

TABLE 1 Predicted metabolic rate and aerobic transport costs for swimming and wave-riding bottlenose dolphins

Speed (m s^{-1})	Average heart rate (beat min^{-1})	Metabolic rate ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$)	Transport cost ($\text{J kg}^{-1} \text{ m}^{-1}$)
2.1	76.0 ± 1.0	8.07 ± 0.33	1.29 ± 0.05
2.9	126.3 ± 7.3	24.67 ± 2.41	2.85 ± 0.28
3.8	101.7 ± 6.6	16.55 ± 2.18	1.46 ± 0.19
(wave-ride)			

Only the highest speed was used for wave-riding. Metabolic rates were calculated from average heart rate using equation (1). Transport costs were calculated by dividing metabolic rate by swimming or wave-riding speed¹⁸. For these calculations, metabolic rate ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) was converted to metabolic energy (J^{23} assuming a caloric equivalent of $4.8 \text{ kcal per l O}_2$ and a conversion factor of $4.187 \times 10^3 \text{ J kcal}^{-1}$). Results are presented as the mean value $\pm 1 \text{ s.d.}$; $n = 4$ for each speed.

logical parameters were raised when swimming speed was increased to 2.9 m s^{-1} . For example, at 2.9 m s^{-1} , respiratory rate was 70% higher than resting values, blood lactate was 30% higher, and average heart rate was 62% higher. As the boat speed was increased to 3.8 m s^{-1} , the dolphins preferentially rode the stern wave. During wave-riding at this speed the average heart rate decreased, and respiratory rate and blood lactate concentration were similar to values obtained during swimming at 2.9 m s^{-1} .

By comparing the physiological responses of swimming and wave-riding dolphins travelling at the same speed, we can evaluate the relative effort associated with each mode of travel. At 3.8 m s^{-1} the respiratory rate of wave-riding dolphins was $5.5 (\pm 0.5 \text{ s.d.})$ breaths per min ($n = 3$); this compares with $8.8 (\pm 1.6 \text{ s.d.})$ breaths per min ($n = 5$) for freely swimming dolphins moving at the same speed. Lactate concentration for a swimming dolphin wearing the heart-rate harness was three times higher (103.6 mg dl^{-1} ; 11.6 mM) than the value for wave-riding dolphins moving at a similar speed. Although limitations in the instrumentation prevented the measurement of heart rate during high speed swimming, the results for respiratory rate and blood lactate concentration suggest that the energetic demands of wave-riding are considerably less than those of swimming at comparable speeds.

The aerobic transport costs of swimming and wave-riding dolphins also indicate an energetic advantage associated with wave-riding (Table 1). At 2.1 m s^{-1} , a routine cruising speed for wild bottlenose dolphins⁷, the cost of transport for swimming was $1.29 \pm 0.05 \text{ J kg}^{-1} \text{ m}^{-1}$. Transport costs doubled as swimming speed was increased to 2.9 m s^{-1} . With an increase in boat speed to 3.8 m s^{-1} , the dolphins switched to wave-riding. The resulting transport costs were lower than anticipated, and only 13% higher than for swimming at 2.1 m s^{-1} . Thus, the wave-riding dolphin obtains a significant advantage in speed for little energetic investment.

The hydromechanics that allow this energy savings during wave-riding are difficult to discern. Scholander¹ suggested that propulsion could be gained by simply 'leaning' a streamlined fluke into the forward slope of the bow wave. Others have detailed the theoretical balance between drag and buoyancy of the wave-riding dolphin, and lift forces created by the pressure field in front of a moving ship's bow^{6,9,10}. With sufficient assistance from the wave, propulsive stroking by the dolphin is reduced to the effort required to position the animal. Indeed, the wave-riding dolphin appears motionless once in position, with fluke movements limited to low-amplitude corrective strokes for repositioning. Only brief bursts of inhalation and exhalation at the water surface will interrupt the ride. Such mechanical advantages in the form of assisted propulsion by