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Habitat choice in *Phylloscopus* warblers: the role of morphology, phylogeny and competition

Received: 27 June 2000 / Accepted: 12 February 2001 / Published online: 29 March 2001
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Abstract We studied ecological and evolutionary aspects of habitat choice in a group of closely related bird species to gain insight into factors influencing bird community structure. Seven species of *Phylloscopus* warblers breed sympatrically in the middle taiga subzone of Central Siberia. We examine how the distribution of species among habitats is related to morphology, phylogeny and competition, and we compare our results with an earlier study on the ecomorphology of *Phylloscopus* warblers in Kashmir. We found that in Siberia, large warbler species prefer productive habitats with mostly deciduous vegetation, whereas small species occupy poor coniferous forests. Possible explanations for this finding remain to be tested in the future. Moreover, we found a tendency for species with large feet, small bills and short wings to occupy habitats with an abundance of bush thickets near the ground. In the Kashmir study, competition was considered a major factor in structuring the *Phylloscopus* community, and patterns of habitat choice were not influenced by phylogenetic relationships. In strong contrast, we found that in the Siberian community, closely related species occupy similar habitats. We discuss whether this conservative evolution of habitat preferences in Siberia may be due to low intensity of interspecific competition or to other ecological factors.

Keywords Community ecology · Correspondence analysis · Ecomorphology · Evolution · Phylogenetic lability

Introduction

Several factors have been proposed as being important in habitat choice in birds. Most attention has been paid to food availability (e.g. Ashmole 1968; Schluter 1982; Janes 1994), morphological adaptation to vegetation structure (e.g. Leisler et al. 1989), and interspecific competition (e.g. Lack 1944; Svårdson 1949; Terborgh 1971; MacArthur 1972; Cody 1985; Conner and Bowers 1987). Price and co-workers (Price 1991; Price and Jamdar 1991; Richman and Price 1992) studied the morphology and ecology of eight *Phylloscopus* warbler species breeding along an altitudinal gradient in Kashmir. Their main conclusions concerning habitat selection in this community were as follows:

1. Species with long tarsi and small bills were found at higher elevations where there are fewer coniferous trees.
2. Closely related species occupied very distinct habitats at opposite ends of the altitudinal gradient. It was therefore concluded that habitat choice is not a conservatively evolving species trait.
3. Interspecific competition was suspected of playing a major role in determining habitat distribution of the species in Kashmir.

In contrast to these findings from Kashmir, our study on territorial spacing in a Central Siberian community of seven species of *Phylloscopus* warblers (Bourski and Forstmeier 2000) showed that, at this site, the intensity of actual interspecific competition tends to be low. This might be due to breeding communities at northern latitudes being less saturated, as breeding populations of long-distance migrants are often limited by wintering conditions (e.g. Ricklefs 1983; Greenberg 1986; Peach et al. 1991; Bourski 1993; Bryant and Jones 1995; Szepe

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1995). We ask whether under these ecological conditions habitat choice of species may more closely reflect phylogenetic relationships. Related species may have similar requirements and therefore occupy similar habitats. On the other hand, due to their similarity, they may compete for similar resources (Bourski and Forstmeier 2000) and therefore be forced to separate into different habitats. The present study is designed to investigate the role of these factors (morphological adaptation, phylogenetic similarity and interspecific competition) in structuring the community of seven *Phylloscopus* species in Central Siberia, and to compare the findings with those of the study from Kashmir.

We use differences in the composition of *Phylloscopus* warbler communities between our study plots to identify the main habitat gradients "from a warbler's point of view". Estimating the distinctness of habitats as the distinctness of their communities has the advantage of not involving an anthropocentric measurement. The disadvantage of this method is that interspecific territorialism will result in an overestimation of the distinctness of habitats. As, for the Siberian *Phylloscopus* community, we know which species pairs display territorial avoidance (*P. inornatus* and *P. proregulus*, and to some extent *P. inornatus* and *P. collybita*), we are able to qualitatively allow for this effect. To study the influence of common ancestry on morphology and habitat choice, we use the phylogenetic tree, based on mtDNA sequences, published in Price et al. (1997).

The genus *Phylloscopus* is highly suitable for this kind of study, due to the close relatedness among species (Price et al. 1997), their high ecological and morphological similarity (Gaston 1974; Price 1991) and because of the outstanding species diversity. There is no passerine genus in the temperate or boreal zone of Eurasia with a larger number of species breeding sympatrically. The vast boreal forests of Central Siberia offer excellent opportunities to study habitat choice of birds in a pristine landscape, where only a minute proportion of the huge area has been subjected to any anthropogenic modification. This allows us to study species living in their natural habitats, a point which can be important for ecomorphological studies (Lack 1971).

Materials and methods

Study area

The study area is situated in the middle taiga subzone of Central Siberia at the Yenisei river (62° N, 89° E). Three major habitat types characterise this area (Bourski 1995):

1. Dark coniferous taiga. This consists mainly of mature cedar pines (*Pinus sibirica*), and is a widespread but unproductive forest type.
2. Burned forest. Forests dominated by deciduous trees of varying age, mainly birch (*Betula pubescens*) and aspen (*Populus tremula*), which are derived from coniferous taiga after forest fires. In Central Siberia fires occur naturally and approximately half of the area is affected regularly, i.e. about once per century.

3. Floodplain. Most of this habitat is located along the west side of the Yenisei river. It is much less common than taiga and burned forest habitats, but is extremely productive with regard to primary production of plants, arthropod abundance and bird densities (Bourski 1995). Floodplain is characterised by two main vegetation types: willow (*Salix* sp.) thicket and alder (*Alnus* sp.) forest. Our study plots contain two more habitat types, open bog and human settlement, called Mirnoye. Both of these habitats are rather rare in the middle Yenisei region.

Our 15 study plots, which cover a total area of 450 ha, comprise 131 ha of coniferous taiga forests, 176 ha of burned forest, 101 ha of riparian floodplain, 22 ha of open bog and 20 ha of human settlement. A detailed description of the habitats of the area and their bird communities is given by Bourski (1995).

Territory mapping and habitat analysis

From 1978 to 1996, we mapped the territories of all passerine species for a total of 9–18 years in each plot. We used the mapping census technique described by Pinowski and Williamson (1974) and Tomialojc (1980). We determined territory boundaries by observing movements of singing males and recording them for each species on a separate 1:2,500 map. Each breeding season, we visited plots at least eight times to perform the censuses.

From our 15 study plots we extracted 53 small sample plots that all differ from each other in vegetation features. Each sample plot has an area of 4 ha and is composed of more or less uniform habitat. The census of breeding birds within the small sample plots over many years allows us to reliably estimate the composition of their bird communities despite their small size. Mean breeding densities of bird species on these plots were calculated using all available data from the whole study period. Although plots differ in their sampling periods (from 9 to 18 years), this apparently does not introduce any systematic bias (analysis not shown).

For each plot we estimated the following parameters to describe its vegetation. The amount of plant volume (cubic metres of vegetation per square metre of area) that appears suitable for foraging by *Phylloscopus* warblers (judged from observations) was estimated for each tree or bush species and in each of three vegetation layers separately (ground layer: 0–1 m; middle layer: 1–8 m; tree layer 8–25 m). Plant volume estimates were calculated from three separate estimations: (1) height of respective layer, (2) total cover of that layer, and (3) representation of a given species in that layer. Later in the analysis, several species of tree and bush were lumped into functional groups. These groups either represented a type of vegetation (e.g. coniferous species or dense thickets near the ground) or were typical of a certain habitat type (e.g. typical species of floodplain forest: *Alnus*, *Alnaster*, *Padus* and *Salix*).

In addition, we analysed the condition of the soils on all 4-ha plots, using the method of "Ramensky ecological scales" (Ramensky 1925; Ramensky et al. 1956). This geobotanical method allows the estimation of soil moisture and nutrient richness from the requirements of plant species growing on the ground. The method is comparable to that developed by Ellenberg (1974) for Central European plants. Ramensky et al. (1956) provide specific indicator values for each plant species characterising the condition of soil where the species is typically found. For each 4-ha plot indicator values of all plant species found were averaged. A more detailed description of the method and its application to the habitats of our study area was given by Sheftel (1994).

To analyse food availability we selected four 4-ha plots which, judging from their passerine communities, are representative of the major habitat types, i.e. coniferous taiga, burned forest, alder floodplain and willow floodplain. We sampled arthropods during July 1996 using two methods (similar to Price 1991):

1. On each plot 10 or 15 sticky traps (plates of 10 cm×10 cm with a thick layer of glue on one side) were placed in the vegetation and were exposed for 50 hours.

2. On each plot we took 20 samples by beating branches (of a standardised volume of vegetation) with a stick and collecting arthropods from a tray held below the branch.

The first technique caught mostly Diptera and Hymenoptera, while the second yielded less mobile arthropods (see Price 1991). All arthropods ($n=7,900$) were measured (length, width and height to the nearest 0.1 mm) and a total volume was calculated for each sample (50 sticky trap samples and 80 branch samples).

Defining the main habitat gradients

The method of correspondence analysis, sometimes called reciprocal averaging (e.g. Wiens 1989), is a kind of principal component analysis that involves a double standardisation of count or absence and presence data. In our case, it serves to extract a small number of axes, along which sample plots will be ordered according to their similarities in *Phylloscopus* communities and, at the same time, species will be ordered by their similarities in habitat choice (occupation of sample plots). Short Euclidean distances in this low-dimensional space represent high similarities. Correspondence analysis therefore resembles the multidimensional scaling method, but differs in being designed for producing a good correspondence between two data sets – in this case, sample plots and bird species (SAS Institute Inc. 1989).

We entered abundance data for the seven species on all 53 sample plots and performed the correspondence analysis using SAS statistics package. All axes with inertia values larger than 0.5 were extracted.

Searching for correlations between morphology and habitat choice, we applied a sequential Bonferroni correction (see Rice 1989) as we proceeded from the most to least important dimensions describing variation in habitat choice. As the numbers of correlations performed increased, we increased the threshold for significance from $P<0.05$ for dimension 1 to $P<0.025$ for dimension 2 and to $P<0.017$ for dimension 3. As morphological characters may show meaningful covariation with more than one dimension, we also checked for significant multiple correlations.

Morphological measurements

We obtained morphological measurements from adult birds trapped in the study area and from skins of adult birds collected in Central Siberia:

1. We measured 12 morphological characters of 230 skins at the Zoological Museum of Moscow University: bill length, bill depth, bill width, rictal bristle length, wing length, distance from wing tip to first primary, distance from wing tip to first secondary (primary projection), notch length of the inner web of the second primary, length of alula, graduation of tail and length of hind and middle claw.
2. We took weight, wing length and wing formula of 5,100 adult birds trapped at the Yenisei field station between 1990 and 1997.
3. We measured tail length, tarsus length and footspan with claws of 352 adult birds trapped between 1995 and 1997.

Using the wing formula, we calculated wing pointedness and asymmetry according to Busse (1984), and divided these measures by wing length, a commonly used measure of wing shape. Wing breadth was obtained by subtracting the primary projection from wing length. Footspan without claws was also calculated by subtraction. Illustrations of morphological measurements are shown in Leisler and Winkler (1991). It should be noted that each morphological character was measured consistently, either in the field or from museum specimens, and samples from different sources were never combined.

Statistical approach to morphological data

We corrected morphological data for observer error, sex and fatness of birds (for details see Bourski and Forstmeier 2000). All

measurements (except those of wing shape) were divided by the cubic root of lean body weight and the obtained values were log-transformed to approach a normal distribution. This treatment renders measurements independent of isometric size (Leisler and Winkler 1985) and is preferable to a regression analysis if the number of study species is rather small.

Other studies have used principal component analysis (PCA) to take into account the variation in body size (e.g. Price 1991). It is assumed that the first component will reflect body size and the following components describe the variation in shape. However, when we deal with rather small samples of species, as in our case, much of the variation in shape will be included in the first component and will be lost for the analysis of its function (Somers 1989). This problem is especially serious if we consider functional complexes, such as bill morphology or hind limb morphology, separately.

We assigned the 19 morphological parameters to four functional categories: measurements of flight apparatus (eight wing and two tail measurements), hind limb morphology (five measurements of foot and tarsus), feeding apparatus, (three bill measurements and rictal bristle length) and body size (cubic root of lean body weight). To reduce the number of variables involved in our ecomorphological survey, we extracted one principal component (PC) for each of the first three functional complexes, called “wing”, “foot” and “bill”. These main components primarily reflect the relative size of the flying, climbing and feeding apparatuses (see the high positive factor loadings in Table 1), after correcting for the interspecific differences in body size.

Using PCA to restrict the number of variables analysed reduces the probability of a type 1 error. This is typically high when searching for correlations between large sets of variables. A small number of sample points (seven species) renders a meaningful usage of Bonferroni correction (Rice 1989) difficult. We therefore restricted our analysis to correlations between four morphological parameters and three variables of habitat choice.

Comparison with the Kashmir study

We compared all our results with the findings of a very similar study on *Phylloscopus* warblers in Kashmir (Price 1991). To be able to compare both studies, we analysed the raw morphological data presented by Price (1991) in the same way as our measurements. We calculated body size from body weight. Wing, tarsus and bill measurements were corrected for isometric body size and a principal component of bill morphology was obtained from three bill measures. For measures of habitat choice in the Kashmir study, we used the mean elevation occupied by species along the altitudinal gradient, and the proportion of coniferous trees used for foraging.

Phylogenetic analysis

We implemented the method of independent contrast analysis (Felsenstein 1985; Harvey and Pagel 1991) to control for phylogenetic effects in correlative analyses (for details see Forstmeier and Keßler in press). However, results obtained from contrast correlations were almost identical to those obtained from species correlations, a consequence of the long terminal branches of the phylogenetic tree (Garland et al. 1999; tree shown in Forstmeier and Keßler in press). As incorporation of this method did not add any important result it is not presented here. Using the subdivision of the genus into three main lineages (see Price et al. 1997) appeared a much more informative way to demonstrate the extent to which data points are non-independent of each other. The sister taxa *P. borealis* and *P. trochiloides* form one lineage, *P. inornatus* and *P. proregulus* make up the second, and the remaining three species belong to the third lineage. Indicating these phylogenetic relationships directly in the figures permits a more specific judgement of how consistent correlations are among these lineages.

To address the question of rates of evolutionary change of species characters, we compared the differences in a character between species pairs within the same lineage with the differences observed in species comparisons between the main lineages. The method is similar to that used by Cherry et al. (1982). A total of seven species allowed five species comparisons within lineages and 16 comparisons between lineages. The ratio between the means of these two groups reflects the evolutionary lability of a character. Low ratios, i.e. when the differences within lineages are relatively small, indicate a conservative trait evolution. Ratios larger than one may suggest character displacement between closely related species. The described method is quite acceptable for use in illustrations, but does not allow statistical testing. This was accomplished by ANOVA. We tested whether belonging to one of the three main lineages significantly influenced the characters of species.

Results

Morphology

The three principal components are sufficient to explain most of the variation found within each morphological complex. Only rictal bristle length, notch length and wing breadth are poorly represented. Species scores on the principal components are illustrated in Fig. 1. The relationships between functional complexes are presented in Table 1. There is a significant correlation between foot and bill morphology, indicating that species with a large PC foot have small bills ($R=-0.781$; $P=0.038$). Correlations of PC bill, foot and wing with our measure of body size (cubic root of lean body mass) indicate non-significant deviations from isometry. More detailed information on morphology is given elsewhere (Forstmeier and Keßler, in press).

Habitat choice

We extracted three main axes that describe a total of 81.3% of the observed variation in habitat choice. Dimension 1 separates coniferous taiga plots (occupied by *P. proregulus*) and burned forest plots (occupied by *P. inornatus*) from those of the floodplain habitats (Fig. 2; see also Table 2). The five species that mostly settle in the floodplain are best separated by the second

Table 1 Factor loadings of morphological traits of seven *Phylloscopus* species on three principal components (*top*). Interrelations between four morphological complexes among the seven species (*bottom*). Values in bold are significant at $P<0.05$ without Bonferroni correction

	Factor loadings		
	PC bill	PC foot	PC wing
Bill length	0.906		
Bill breadth	0.898		
Bill depth	0.627		
Rictal bristle length	0.259		
Footspan with claws		0.999	
Tarsus length		0.965	
Hind claw		0.958	
Middle claw		0.938	
Footspan without claws		0.884	
Wing length			0.980
Primary projection			0.950
First primary to wing tip			0.935
Wing asymmetry			0.932
Wing pointedness			0.874
Length of alula			0.630
Graduation of tail			-0.485
Tail length			0.447
Notch length			0.308
Wing breadth			-0.059
Variance explained	0.522	0.902	0.529
	Interrelations		
	PC bill	PC foot	PC wing
Body size	+0.077	+0.421	+0.331
PC bill		-0.781	+0.428
PC foot			-0.494

dimension, which distinguishes the more open willow-dominated habitats of *P. trochilus* and *P. fuscatu*s from the diversely structured alder forest habitats of *P. trochiloides*, with *P. borealis* and *P. collybita* lying between these extremes. The third axis describes the divide between *P. inornatus* (preferring birch undergrowth) and the neighbouring *P. trochilus* and *P. fuscatu*s (preferring willow thickets). Moreover, the species of alder floodplain (*P. borealis* and *P. trochiloides*) are separated from the species of willow floodplain (*P. collybita*, *P. trochilus* and *P. fuscatu*s) by the third axis. Although not shown in

Fig. 1 Scatter plots of functional complexes of species morphology: body size (log cubic root of body mass) and first principal components of feeding apparatus (*PC bill*), hind limb morphology (*PC foot*) and flight apparatus (*PC wing*). Different symbols refer to the three main phylogenetic lineages. For species abbreviations see Table 2

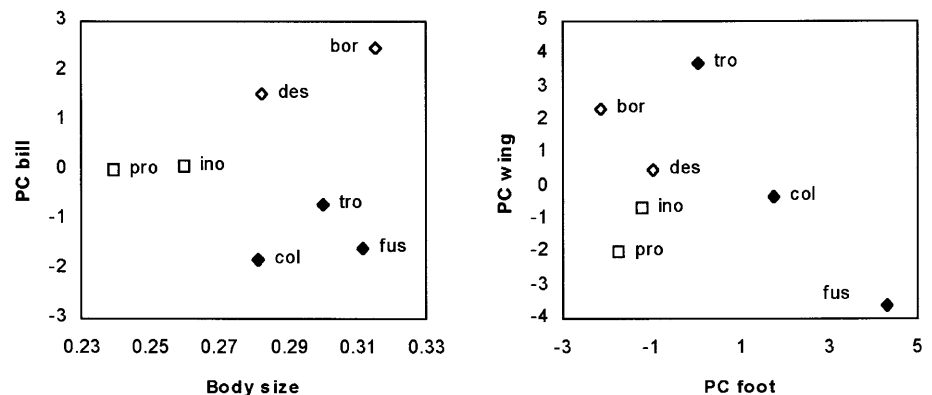


Table 2 Names and abbreviations of the seven study species, number of mapped territories over the whole study period and average breeding density in the study area

Species		Abbreviation	Mapped territories	Territories per km ²
Pallas's warbler	<i>Phylloscopus proregulus</i> (Pallas)	pro	143	2.7
Yellow-browed warbler	<i>P. inornatus</i> (Blyth)	ino	2,049	39.2
Dusky warbler	<i>P. fuscatus</i> (Blyth)	fus	83	1.6
Chiffchaff	<i>P. collybita</i> (ssp. <i>tristis</i>) (Blyth)	col	313	6.0
Willow warbler	<i>P. trochilus</i> (ssp. <i>acredula</i>) (Linnaeus)	tro	21	0.4
Arctic warbler	<i>P. borealis</i> (Blasius)	bor	453	8.7
Greenish warbler	<i>P. trochiloides</i> (ssp. <i>viridanus</i>) (Blyth)	des	86	1.6

Table 3 Correlations between habitat parameters and the first three dimensions of the correspondence analysis describing similarities of *Phylloscopus* communities. The rightmost column gives the coefficient for multiple correlation using all three dimensions as independent variables. Correlations with a value of $r > 0.274$ and multiple correlations with $r > 0.4$ are significant at $P < 0.05$ ($n = 53$ plots)

Habitat parameter	Dimension 1	Dimension 2	Dimension 3	Together
Soil richness	-0.498	-0.570	-0.394	0.802
<i>Pinus sibirica</i> (%)	0.702	0.258	-0.091	0.753
Volume of tree layer (%)	0.717	0.036	-0.031	0.739
Coniferous trees (%)	0.691	0.196	0.011	0.728
Tree species of floodplain (%)	-0.455	-0.523	-0.294	0.716
Total plant volume (all layers)	0.579	-0.181	-0.050	0.659
Volume of ground layer (%)	-0.428	0.086	-0.187	0.618
Canopy height	0.500	0.143	0.231	0.632
<i>Alnus</i> and <i>Alnaster</i> (%)	-0.355	-0.497	-0.205	0.615
Dense thickets near ground (%)	-0.303	0.092	-0.275	0.600
Volume of middle layer (%)	-0.526	-0.092	0.149	0.541
<i>Betula</i> sp. (%)	-0.295	0.386	0.343	0.488
<i>Salix</i> sp. (%)	-0.314	-0.332	-0.211	0.481
Tree species of burned forest (%)	-0.201	0.409	0.340	0.461
<i>Picea</i> and <i>Abies</i> (%)	0.347	-0.219	-0.063	0.450
<i>Pinus sylvestris</i> (%)	0.084	0.237	0.252	0.312
Soil wetness	-0.261	-0.035	-0.054	0.294
<i>Larix</i> (%)	0.110	0.213	0.030	0.252
<i>Populus tremula</i> (%)	0.147	0.192	0.111	0.250

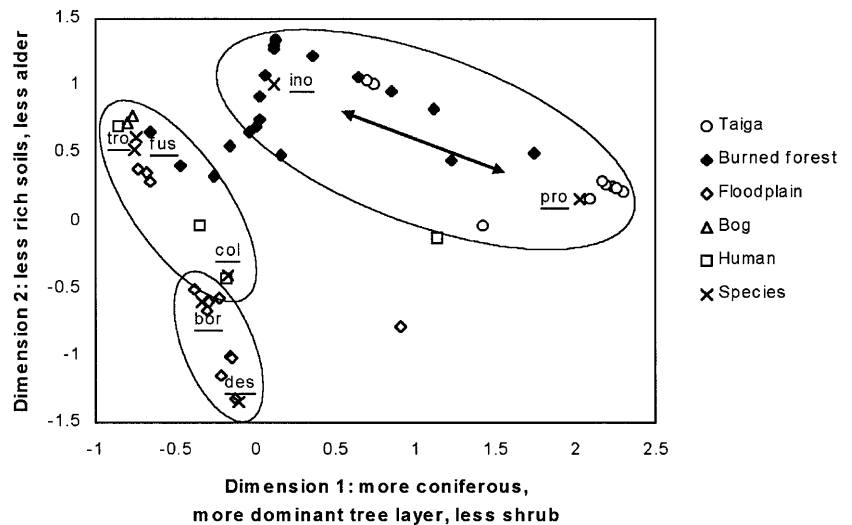
Fig. 2 Ordination of species and sample plots on the first two axes of the correspondence analysis. Distances between species are measures of similarity of their habitat choice and distances between sample plots illustrate the similarity of their *Phylloscopus* species community. The first axis explains 32.7% and the second 24.6% of the total observed variation in *Phylloscopus* warbler communities. Species belonging to the same phylogenetic lineage are encircled. The arrow indicates that the wide separation between *P. inornatus* and *P. proregulus* is a consequence of interspecific territorial avoidance

Fig. 2, the third axis will be taken into account as well for all the following calculations.

Of all the habitat parameters, soil richness best describes the gradients created by the first three dimensions (Table 3). It is strongly correlated with all three dimensions. More coniferous trees and a more dominant tree layer characterise the habitats with high scores on dimension 1. The second axis correlates negatively with soil richness and the abundance of alder bushes.

In a simplified manner, all three dimensions can be summarised by ordering habitat types as shown in Fig. 3. The distribution of species along this habitat gradient reflects phylogenetic relationships. The lineage of *P. borealis* and *P. trochiloides* occupies alder floodplain, the lineage of *P. fuscatus*, *P. trochilus* and *P. collybita* occupies willow floodplain and the lineage of *P. inornatus* and *P. proregulus* occupies the upland habitats outside the floodplain (Fig. 2, Fig. 3).

Fig. 3 Distribution of habitats and *Phylloscopus* warbler species over a typical landscape profile (not to scale). Habitats and species were ordered in such a way as to reflect patterns of similarity of bird communities (accounting for the first three dimensions of the correspondence analysis shown in Fig. 2). The positions of *P. fuscatus* and *P. trochilus* should be regarded as not distinguishable from each other. The phylogenetic relationships between the species are indicated by a simplified tree. For species abbreviations see Table 2

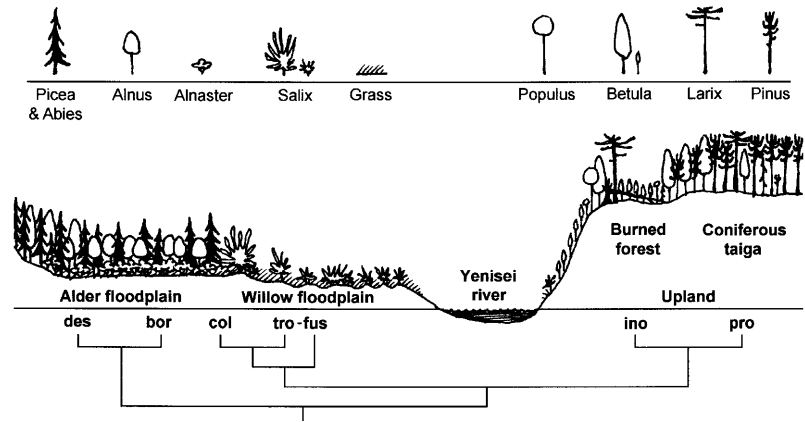


Table 4 Indicators of productivity characterising the four main habitat types: richness of soil nutrients as indicated by plant species according to Ramensky et al. (1956), total passerine density (except Corvidae) and arthropod abundance measured as the total

volume of all arthropods collected per sample or trap. All tests are *t*-tests between adjacent habitat types: $P > 0.05$ (n.s.), $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***)

	Coniferous taiga		Burned forest		Alder floodplain		Willow floodplain
Soil richness: Ramensky scales \pm SE (no. of plant species)	5.53 \pm 0.41 (18)	n.s.	5.81 \pm 0.47 (20)	***	9.29 \pm 0.46 (27)	*	11.2 \pm 0.42 (35)
Passerine density (pairs/ha) \pm SE (years)	1.42 \pm 0.12 (14)	**	2.43 \pm 0.28 (14)	***	5.05 \pm 0.33 (15)	**	6.72 \pm 0.42 (15)
Arthropod volume (mm ³) per branch sample \pm SE (no. of samples)	102 \pm 16 (20)	*	192 \pm 39 (20)	n.s.	260 \pm 24 (20)	n.s.	333 \pm 47 (20)
Arthropod volume (mm ³) per sticky trap \pm SE (no. of traps)	39 \pm 9 (10)	**	106 \pm 15 (10)	**	318 \pm 44 (15)	***	654 \pm 78 (15)

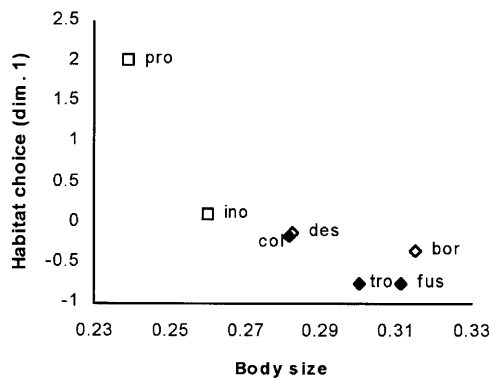


Fig. 4 Scatter plot of *Phylloscopus* body size against species scores on the first dimension of habitat space, obtained by correspondence analysis (see Fig. 2). Different symbols refer to the three main phylogenetic lineages. For species abbreviations see Table 2

Table 4 illustrates the differences in productivity between the four major habitat types. Arthropod abundance and passerine breeding densities increase with soil richness from coniferous taiga to burned forest, to alder floodplain and willow floodplain.

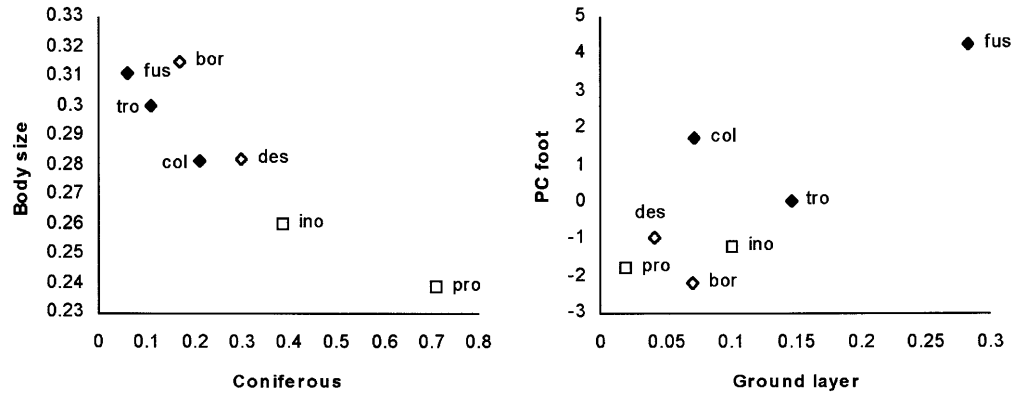
Table 5 Correlations between morphological characters and the first three dimensions of the correspondence analysis, as measurements of habitat choice. Values in bold are significant at $P < 0.05$ using a stepwise Bonferroni correction (see Materials and methods section)

	Habitat dimension 1	Habitat dimension 2	Habitat dimension 3
Body size	-0.866	-0.166	-0.254
PC foot	-0.491	+0.236	-0.441
PC bill	+0.115	-0.520	+0.477
PC wing	-0.354	-0.205	+0.081

Correlation between habitat components and morphology

Only one morphological feature is significantly correlated with habitat choice (Table 5). The main habitat gradient (dimension 1) covaries with body size of *Phylloscopus* species. Sample plots with low scores on habitat dimension 1 (on the left hand side of the scatter plot, Fig. 2), characterised by rich soils, few coniferous trees and low canopies, are preferred by species with larger body size (Fig. 4; $R = -0.866$; $P = 0.012$). Other morphological parameters are only weakly correlated with the habitat gradients that characterise *Phylloscopus* species

Fig. 5 a Scatter plot of the body size of the seven species and the proportion of coniferous vegetation in their habitats; **b** first principal component of hind limb morphology of species and the proportion of vegetation found in the ground layer of their habitats. Different symbols refer to the three main phylogenetic lineages. For species abbreviations see Table 2



communities. Also, the performance of multiple correlations does not yield additional significant results.

In order to interpret these findings, it is necessary to examine vegetation measurements taken from sample plots. Correlating four morphological characters with 19 parameters of vegetation yields a table of 76 correlations (not shown), which is bound to contain many results that appear to be significant by chance alone (Rice 1989). This highlights why we used the techniques of reduction of dimensions. However, the full table largely parallels the results already shown in Table 5, the only major difference being a correlation of PC foot with vegetation in the ground layer ($R=0.818$; $P=0.025$; Fig. 5b). This correlation is caused by the extreme characters of *P. fusca-tus* and is not consistent with the patterns found in other phylogenetic lineages.

The correlation between body size and habitat choice is best described by an increase in body size with decreasing conifer abundance ($R=-0.931$; $P=0.002$; Fig 5a), decreasing canopy cover ($R=-0.884$; $P=0.009$) and increasing soil richness ($R=0.877$; $P=0.01$). The observed patterns of change in body size with the prevalence of coniferous trees and with canopy cover are consistent among all phylogenetic lineages, whereas the occupation of unproductive habitats (low soil richness) involves only the lineage of *P. proregulus* and *P. inornatus*.

Rates of evolutionary change

Phylogenetic constraints on species morphology are obvious (Fig. 1). Body size and bill and hind limb morphology show a high degree of similarity within each of the three phylogenetic lineages. Wing morphology, in contrast, has undergone substantial changes within the group comprising *P. trochilus*, *P. collybita* and *P. fusca-tus*. We tested the significance of this pattern by means of ANOVA. Belonging to either of the three lineages significantly influences bill morphology ($P=0.006$), probably influences body size ($P=0.07$) and hind limb morphology ($P=0.10$), but does not affect morphology of the flight apparatus ($P=0.64$)

The degree to which morphological characters differ between species belonging to the same group, in comparison to differences between groups, is illustrated in

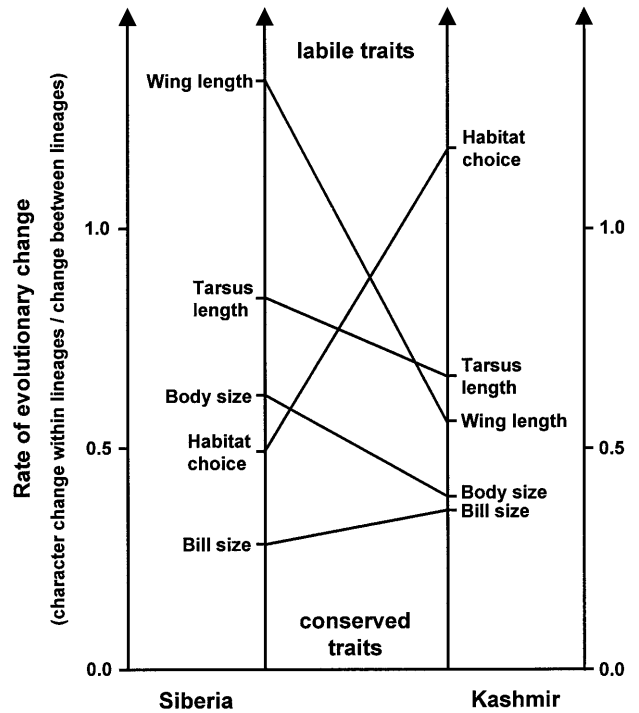


Fig. 6 Evolutionary lability of species traits in two different *Phylloscopus* warbler communities. Species were assigned to one of the three main lineages according to the phylogeny from Price et al. (1997). For both communities we calculated the average character difference between species pairs belonging to the same phylogenetic lineage and divided it by the average character change found between species stemming from different lineages. A ratio below 1 suggests a conservative trait evolution (see text for statistics). Large ratios may indicate character displacement between closely related species. The measure of habitat choice used here reflects the relative amount of coniferous trees in the species' habitats

Fig. 6. In accordance with the results from the Kashmir study, the most conservative morphological character is the feeding apparatus (ANOVA, $P=0.005$ for Kashmir), followed by body size ($P=0.007$ for Kashmir) and tarsus length ($P=0.16$ for Siberia and $P=0.14$ for Kashmir). The main difference between the guilds of Siberia and Kashmir is that wing length shows very high evolutionary lability in the Siberian species (ANOVA, $P=0.70$), whereas in Kashmir it is still influenced by phylogeny

($P=0.035$). This result is independent of whether we use wing length or PC wing to represent the flight apparatus morphology (the same for tarsus length and PC foot), as these variables are highly correlated (see Table 1).

The proportion of coniferous trees in the vegetation is the only habitat parameter available from both study sites. This parameter shows a high correlation with the habitat gradients in Siberia (Table 3) and Kashmir (Price 1991). Comparing the rates of evolutionary change in this parameter of habitat selection between the two sites, we find that habitat choice is conserved in Siberia (ANOVA, $P=0.06$) but not in Kashmir ($P=0.87$; Fig. 6). This result is less significant when using other measures of habitat selection. However, phylogeny probably also affects the position of species on dimension 1 (see Fig. 2; ANOVA, $P=0.15$) and dimension 2 ($P=0.10$) of habitat space in Siberia, but not the distribution of species along the altitudinal gradient in Kashmir (ANOVA, $P=0.58$).

Discussion

We found a strong relationship between the body size of warbler species and the productivity of the habitats they occupy. Large species occupy productive deciduous habitats whereas small species occupy coniferous forests growing on poor soils (Fig. 5a). This interesting phenomenon was previously noted by Gaston (1974), who surveyed a much larger set of 28 *Phylloscopus* species. The adaptive significance of this finding is not yet understood and requires further discussion (see below).

Comparing our results with the earlier study on *Phylloscopus* warblers in Kashmir (Price 1991), we cannot confirm that species with short tarsi and large beaks are associated with coniferous habitats. In contrast, we found that long tarsi were associated with foraging in dense vegetation near to the ground (Fig. 5b), a fact that has been observed repeatedly (e.g. Gaston 1974; Landmann and Winding 1993). The putative mechanism leading to this association will be explained below.

In contrast to the conclusions of Richman and Price (1992) we observed a conservative evolution of habitat choice. In Siberia, closely related species occupied similar habitats (Fig. 3), whereas at the Kashmir site sister taxa were strictly separated by differences in habitat selection. This discrepancy may be caused by several ecological factors that apparently differ between the two study sites, Siberia and Kashmir. This topic will be treated in the last section of the Discussion.

Habitat choice of Siberian *Phylloscopus* species largely reflects their phylogenetic relationships (Fig. 3). This association becomes even more obvious when we take into account the influence of intra- and interspecific competition on habitat choice. As outlined in the Introduction, interspecific territorialism increases the distinctness of warbler communities and, consequently, our esti-

mate of distinctness of habitats. This effect is especially strong in the case of coniferous taiga and burned forest (Fig. 2). Each of these habitats is occupied by only one species (*P. proregulus* and *P. inornatus*, respectively), and these species display strong territorial avoidance (Bourski and Forstmeier 2000). When we estimate the distinctness of habitats by looking at the whole passerine communities (by correspondence analysis using 66 bird species), coniferous taiga and burned forest are clearly separated, but very close to each other as compared to the other habitats (data not shown). This indicates that, "from a passerine's point of view", the two types of upland habitat are much less dissimilar than suggested by Fig. 2. We do not know whether the view of a *Phylloscopus* warbler differs in principle from that of other passerines, but interspecific territorialism between *P. inornatus* and *P. proregulus* (indicated by arrow in Fig. 2) is the most parsimonious explanation.

Intraspecific competition, on the other hand, leads to occupation of a wider range of habitats, including sub-optimal ones, when population sizes are large (shown in: Bourski and Forstmeier 2000). In contrast to upland habitats, floodplains are very limited in space, and two species occupy this habitat at high density (*P. borealis* and *P. collybita*; Table 2). As a consequence, both species settle over the whole range of floodplain habitats, which leads to similar positions in the habitat space shown in Fig. 2. If we consider only the sample plots where *P. collybita* and *P. borealis* reach their highest breeding densities, i.e. their most preferred habitats, we find that these plots are also the favourite breeding sites of their respective sister taxa. *P. collybita*, *P. trochilus* and *P. fuscatu*s all reach their highest breeding densities on the same sample plot, and the three plots most densely populated by *P. borealis* include the two plots which are most favoured by *P. trochiloides*. Moreover, when we use the 19 vegetation parameters (see Table 3) to predict the occurrence of warbler species on the 53 study plots (by linear regression; data not shown), *Salix* sp. gives the highest correlation coefficient for *P. collybita*, while abundance of *P. borealis* is best predicted by *Alnus* and *Alnaster*.

In conclusion, current competition affects our estimates of species' similarity of habitat choice when using the approach presented here (Fig. 2). However, an earlier study (Bourski and Forstmeier 2000) allows us to qualitatively predict these effects beforehand. Interspecific territorial avoidance between *P. inornatus* and *P. proregulus* leads to an overestimation of the dissimilarity of their habitat preferences (indicated by arrow in Fig. 2). Strong intraspecific competition in *P. collybita* and *P. borealis* leads to increased similarity of their distributions among habitats. The fact that species positions on the dimensions in Fig. 2 are only non-significantly influenced by phylogeny ($P=0.10$ and $P=0.15$) is a consequence thereof. The habitat distribution of Siberian *Phylloscopus* warblers largely reflects phylogenetic relationships, but appears to be modified by both intra- and interspecific competition.

What explains the correlation of body size with habitat choice?

In Central Siberia, large *Phylloscopus* warbler species breed in productive habitats, characterised by rich soils and a predominance of deciduous trees and bushes. In contrast, small species settle in unproductive habitats with poor soil conditions and a prevalence of coniferous trees in the vegetation. We propose three hypotheses that could explain these findings.

1. Small species may show a preference for coniferous habitats, because small body size gives them an advantage in foraging on coniferous trees. This hypothesis was originally proposed by Gaston (1974), who found that *Phylloscopus* species of coniferous habitats are significantly smaller than other congeners. His ad hoc explanation that a small body size allows more efficient use of foraging techniques that are advantageous in coniferous vegetation, such as hovering flight and clinging to needles, has not yet been properly tested.
2. Larger species may prefer more productive habitats, if the insects occupying these habitats are larger than average, as Shvarts and Demin (1994) found for ground-dwelling insects. This idea is supported by the finding of Nyström (1990) that deciduous trees hold a higher proportion of large arthropods than coniferous trees. Also, Price (1991) found that larger *Phylloscopus* species prefer larger prey items.
3. More productive habitats offer higher total food abundance (Table 4), and larger warbler species might prefer them due to their higher energetic requirements (Hanski 1994). Smaller species, on the other hand, might profit from lower interspecific competition or lower predation risk when occupying less productive habitats.

Why do we not find morphological adaptations to habitats?

The three functional complexes – flight apparatus, feeding apparatus and hind limb morphology – show no consistent covariation with the main habitat gradients. The only correlation we found was between the extraordinarily large foot and tarsus of *P. fuscatus* and its preference for habitats with bush thickets near the ground. From the literature it is well known that passerine species foraging near the ground tend to have long tarsi (Osterhaus 1962; Grant 1965, 1966; Fretwell 1969; Gaston 1974; Miles and Ricklefs 1984; Landmann and Winding 1993). *Phylloscopus* warblers foraging in vegetation that is too dense to allow effective use of the wings for locomotion have developed large feet, specialised for dextrous climbing and hopping among branches. The negative correlation of PC foot with bill size and wing length suggests that species that forage in more open vegetation, on large flying prey items, have

developed small perching feet, but long and pointed wings and large bills for catching this kind of prey. These relationships are demonstrated by a study on foraging behaviour in this guild (Forstmeier and Keßler in press), and are in accordance with earlier studies (Gaston 1974; Marchetti et al. 1995).

The reason why these morphological aspects, which appear to be adapted to foraging behaviour, do not correlate with habitat choice, is that our study plots (each comprising 4 ha) contain a variety of different microhabitats to which the foraging behaviour of birds is adapted (Forstmeier and Keßler, in press). In the floodplain forest it is common for five species to coexist without displaying interspecific territorialism (Bourski and Forstmeier 2000). Their coexistence is facilitated by differentiation of their foraging niches into separate microhabitats (Forstmeier and Keßler, in press). Therefore, we should expect to find a consistent correlation of *Phylloscopus* morphology with habitat choice only if the habitat-types we defined comprised only one microhabitat. All species coexisting in such habitats would then be constrained by a common selective pressure to be adapted to forage in this microhabitat. Simply structured habitats like reeds promote such general adaptations as were found for *Acrocephalus* warblers by Leisler et al. (1989). In conclusion, in our study, variation in functional morphology reflects microhabitat usage rather than habitat choice.

Rate of evolutionary change of characters

Wing morphology is a much more variable character in the Siberian *Phylloscopus* warblers than in the Kashmir species. The most likely explanation for this is that wing length is strongly influenced by the distance warblers have to travel between breeding grounds and winter quarters (Marchetti et al. 1995). The species breeding in Kashmir spend the winter relatively nearby (Marchetti et al. 1995), whereas Siberian birds have to migrate between 5,000 and 10,000 km to their winter ranges (Glutz von Blotzheim and Bauer 1991). Price et al. (1997) have shown that the latitudinal distribution of *Phylloscopus* species is a trait of high lability due to frequent climatic changes during the Pleistocene period. Selective pressure on the wing lengths of *Phylloscopus* species will therefore have been subject to frequent changes.

One main conclusion of the work of Richman and Price (1992), who were among the first to apply the method of phylogenetic contrasts to ecomorphology, was that closely related species differ primarily along one niche axis – habitat selection. This differentiation was therefore regarded as the possible first step of species divergence. Our findings do not support this hypothesis, as habitat choice appears to be a rather unvarying species trait in Siberia. Therefore, it seems worthwhile to consider why habitat choice is such a conservative trait in Siberia, but not in Kashmir. Although largely speculative, we discuss three, non-

mutually exclusive explanations, which may stimulate future investigations:

1. Habitat choice in Kashmir may have been altered by anthropogenic habitat change. There is little doubt that changes in predator communities can easily result in extinction of species, as demonstrated by the impact of human-mediated invasions of alien predators on island faunas. Price and Jamdar (1991) mention in their work that "much predation was attributable to an unnatural abundance of crows". It might be that only studies from relatively pristine areas like the Siberian taiga allow clear insights into the evolutionary history of habitat choice.
2. Habitats in Siberia may differ from each other more profoundly than do those in Kashmir. Thus, for a bird species, changing between habitats may be less practicable there. Price (1991) found no marked differences in arthropod densities between habitats. In contrast, the gradient of habitat productivity in the Siberian landscape is paralleled by tremendous differences in arthropod densities (Table 4). Therefore, if habitat choice of birds in Siberia is primarily linked to food availability, then changes between habitats may take much longer to evolve than in Kashmir.
3. Interspecific competition may be more intense at the Kashmir site, causing strict habitat exclusion through interspecific aggression. Habitats in Siberia may not be saturated, as population numbers of long-distance migrating passerines are likely to be limited by wintering conditions (Ricklefs 1983; Greenberg 1986; Peach et al. 1991; Bourski 1993; Bryant and Jones 1995; Szep 1995), leading to relaxed competition on breeding grounds (low-competition environment). In Siberia only one species pair, *P. inornatus* and *P. proregulus*, maintains strict habitat separation through territorial avoidance (Bourski and Forstmeier 2000). Interestingly, this is the only Siberian species pair that behaves contrary to the general observation that closely related species occupy similar habitats (Fig. 2). This demonstrates how interspecific competition may promote habitat separation of sister species. It may be speculated that differences in habitat choice evolve slowly in low-competition environments, but rapidly where the intensity of interspecific competition is high.

Acknowledgements We are grateful to the Institute for Problems of Ecology and Evolution of the Russian Academy of Sciences for inviting W. Forstmeier to work at the Yenisei field station. Thanks are due to the Ornithological Department of the Zoological Museum of Moscow University for access to the skin collection. We thank Boris I. Sheftel for providing some of the morphological data. And we also thank Trevor Price, Hans Winkler, Andreas Helbig, Mark Wilson, Yves Van de Peer, Francisco Pulido, Tony Wilson, Tim Coppack and Ann Thorson for comments and suggestions and Karl Eduard Linsenmair for supervision. W. Forstmeier received financial support from the Studienstiftung des Deutschen Volkes.

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