MORPHOLOGY AND ECOLOGY OF BREEDING WARBLERS ALONG AN ALTITUDINAL GRADIENT IN KASHMIR, INDIA

BY TREVOR PRICE

Department of Biology, O-116, University of California, San Diego, La Jolla, CA 92093, U.S.A.

SUMMARY

(1) Eight species of *Phylloscopus* warblers, and the closely related goldcrest, *Regulus regulus*, breed along a restricted altitudinal gradient in Kashmir, India. I studied the relationship between morphology, habitat selection, and feeding ecology for these nine species over three breeding seasons 1985–87.

(2) None of the species breed over the entire altitudinal range. Many altitudinal distributions are related to the presence of specific tree species, although most species will readily forage in all trees available on their territory. Arthropod composition was similar among the habitats.

(3) There are striking associations of morphology with ecology. Three orthogonal axes are used to summarize morphological variation among the species. The first principal component (PC1, essentially body size) is correlated with prey size. PC2, a shape measure relating beak size to tarsus length, is correlated with habitat occupied and mean elevation. PC3, a measure of beak width relative to its length, is correlated with feeding method. In total the morphological variation explains 95% of the measured ecological variation.

(4) There are obvious adaptive explanations for the PC1 and PC3 associations, but the adaptive significance of the variation in PC2 is unclear. However, the association of PC2 with elevation is also observed within the one species which is common and widely distributed along the altitudinal gradient.

(5) Differences among species in feeding method, prey size and habitat occupied are largely uncorrelated with one another. I conclude that the breeding season distribution of species among habitats may be partly a result of inherent differences in foraging abilities, but that other factors, probably including current competition, must contribute to limiting distributions.

INTRODUCTION

The adaptive significance of habitat choice in birds is not well understood (Rice, Omhart & Anderson 1983; Cody 1985a; Finch 1989). Most attention has been paid to a possible relationship between foraging efficiency and the habitat occupied. Rosenzweig (1985), for example, considered that 'habitat selection theory is really a branch of optimal foraging theory'. There are other possibilities however, such as thermoregulation (Sabo 1980) or pressures from predation (Ekman 1986; Martin 1988), and different factors may interact (Cody 1985a). Habitat choice may also

have few adaptive consequences, but largely reflect innate preferences (the 'psycho-logical factor' of Lack (1937)). There is abundant evidence that inter-specific compe-tition plays some role in maintaining habitat differences (Cody 1985a; Alatalo, Gustafsson & Lundberg 1986). But competition may have resulted in the species occupying largely different niches, and any role for the current occurrence of compe-tition is largely unassessed.

One way to investigate the significance of habitat choice is to examine associations between morphology and ecology (Miles & Ricklefs 1984; Fitzpatrick 1985). Adaptive significance to habitat occupancy can be ascribed if there is some a priori reason to believe the morphological differences among species to be adaptive, or if good adaptive arguments for the ecological−morphological association can be made. For example, species which forage a great deal on the ground tend to have long tarsi (e.g. Osterhaus 1962; Fitzpatrick 1985). There are several adaptive explanations for the association between ground foraging and tarsus length, mostly based on foraging efficiency (Fitzpatrick 1985). If these explanations are correct then choice of foraging location can be considered adaptive, resulting at least in part from selection pressures on feeding. Clearly this approach will not lead to many insights when applied to very different groups, such as grassland and forest birds. Such groups differ in many ways related to their differential occupancy of habitats, and choice of habitat on this scale is of obvious adaptive significance. The measurement of ecological−morphological associations is potentially most useful when applied within a group of taxonomically and ecologically similar species, where divergence into different habitats has been recent and the reasons for habitat segregation are not easy to understand.

In this study I measured morphological−ecological associations to investigate habitat distributions of a group of warblers. I studied the altitudinal distributions and habitat relationships of eight species of breeding *Phylloscopus* warblers and the closely related goldcrest *Regulus regulus* L. in the Himalayas of Kashmir, India. The species are very similar morphologically and they are all insectivorous, but most have specialized habitat preferences. I set out to determine the extent to which morphology covaries with habitat, diet and feeding behaviour. I found that mor-phology does covary with habitat, but it does so in a way which is uncorrelated with diet or feeding behaviour. It appears that there has been adaptive diversification along each of three niche dimensions − habitat, diet, and foraging behaviour − but that divergence along one dimension is largely uncorrelated with divergence along another.

MATERIALS AND METHODS

I spent May−July 1985, 1986, and 1987 at the Overa Wildlife Sanctuary near Pahalgam, Kashmir, India. Detailed descriptions of the study areas and methods can be found in Price & Jamdar (1990, in press b). I established camps at 2400 m (in the fir *Abies pindrow* Royle forest) and at 3400 m (in the birch *Betula utilis* Don forest), and regularly visited areas at intermediate and higher altitudes.

Study locality

Habitats were assessed by recording tree abundances in five 2−20 ha grids estab-lished along the altitudinal gradient (Table 1). I briefly describe habitat distributions

TABLE 1. Densities of warblers and trees at five altitudes; netting densities in bold type (birds net^{-1} day^{-1} × 100). Adjacent figures are censuses of singing males (numbers ha^{-1} on plots between 2 and 20 ha in size)

Altitude (m)	2430		2800		3340[1]		3550		3725	
P. tyleri	**5**	*	**25**	0·45	**5**	0·5	—	—	—	—
P. affinis	—	—	—	—	—	0·25	—	0·43	**25**	0·75
P. pulcher†	—	—	—	—	**3**	—	**13**	0·68	—	—
P. inornatus†	—	—	—	—	**100**	2·75	**20**	1·25	—	—
P. proregulus	**47**	1·25	**60**	1·55	**8**	0·75	—	—	—	—
P. magnirostris	**3**	0·5	**10**	0·13	—	—	—	—	—	—
P. trochiloides	—	—	—	—	—	—	**11**	0·5	—	—
P. occipitalis	**31**	2·3	**15**	2·4	**8**	0·5	**2**	—	—	—
R. regulus	**1**	*	—	—	**1**	*	—	—	—	—
Totals	**87**	4·35	**110**	4·53	**125**	4·75	**46**	2·86	**25**	0·75
Sample size (**net-days,** census days)	**130**	2	**20**	4	**73**	1	**46**	3	**20**	2
Coniferous trees (numbers ha^{-1})	176		163		20		—		—	
Broad-leaf trees (numbers ha^{-1})	47		18		79		39		—	

* Indicates observed nearby although not recorded on the census plot.
† Census of *Phylloscopus inornatus* at 3340 m by territory mapping (Price & Jamdar, in press b).

here. Additional information on habitat is provided by Price & Jamdar (1990). Measurements of arthropod abundance across habitats are presented in Appendix 1.

From 2200 m up to about 3000 m fir–pine–spruce forests dominate, with a canopy to about 35 m high. Tree densities range up to 200 ha^{-1} (Table 1). In clearings, and along river valleys there are also deciduous trees. The dominant understorey shrub in the coniferous forest is *Viburnum grandiflorum* Wallich. At about 3000 m altitude birch first appears. At 3300 m birch with a canopy at about 12–13 m predominates (approximately 100 trees ha^{-1} with 75% birch), and willow, *Salix denticulata* Andersson, is the common understorey shrub. The willow is ever-green and used extensively by foraging warblers at the beginning of the breeding season when the birch is still leafless. By about 3500 m altitude the birch is thinning, and interspersed with *Rhododendron* spp., growing to 3 m in height and *Juniperus* spp. growing up to 1·5 m. Above the birch-line, which is usually called the tree-line, juniper predominates, although rhododendron stands are found to 3700 m.

Warblers

The *Phylloscopus* species account for *c*. 35% of the passerine birds at the 2400 m site, and *c*. 43% at the 3300 m site (Price & Jamdar, 1990), and form the dominant arboreal leaf-gleaning guild. The goldcrest *Regulus regulus* is included in this study because it is ecologically similar to the *Phylloscopus* warblers (Tiainen *et al.* 1983). Five species of flycatchers (genus *Muscicapa*) occurring predominantly at the low altitude site and five species of tit (genus *Parus*) are the only other species likely to substantially interact with the *Phylloscopus* warblers for food. A species of bush warbler, *Cettia fortipes* Brooks, occurs as a skulker in undergrowth at lower altitudes, and is largely separated from the *Phylloscopus* warblers.

I measured warbler abundance in two principal ways. First, I established regular mist-net positions and trapped birds, particularly in May of each year. Birds trapped per mist-net per morning provided an estimate of relative density. Some species are found at low altitudes early in the season but do not breed there. These were not included in the density estimates obtained from the trapping data. Second, in June, I recorded singing males in the established grids. To do this I walked slowly over the whole grid for at least 2 h on at least two separate occasions. Relative abundances of warblers as estimated from either the mist-netting censuses or the visual censuses are in general agreement (Table 1), and the conclusions of this paper are not altered by use of one over the other. The main discrepancy between the two methods comes from estimates of the abundance of *Phylloscopus occipitalis* Blyth. This species is a loud songster and easily observed, and my estimates of number of singing males from the visual census may overestimate the number of pairs actually breeding on the study plots. For this reason, I use mist-netting censuses throughout. A third census method — the accurate mapping of colour-ringed birds — was used to determine the density of *P. inornatus* Brooks at the 3340 m site (Price & Jamdar, in press b). Limits of a species' altitudinal range were determined by frequent observations throughout the study period over the whole altitudinal gradient.

Morphology

All trapped individuals were measured using methods described in Abbott, Abbott &

TABLE 2. Correlations of morphological variables with principal component scores
(×100)

	PC1	PC2	PC3
Wing length	99	0	1
Weight	98	−10	−1
Tarsus length	68	−73	1
Beak length	87	18	−46
Beak depth	96	26	7
Beak width	90	21	36
% Variance explained	81	12	6

Grant (1977). I measured beak depth and width (at the front of the nares), beak length (from the front of the nares), wing-length, tarsus length, and body weight. Species are substantially sexually dimorphic only in wing-length (Price & Jamdar, in press a). Most individuals could not be sexed so I used simple species averages for each measurement. Means and standard deviations are presented in Appendix 2. To generate uncorrelated morphological axes I extracted principal components from the correlation matrix of ln-transformed species means. The purpose of generating uncorrelated axes was so that any covariation between ecology and morphology along one morphological axis could be interpreted separately from covariation along another axis. The correlation matrix was used because in this particular data set it gave more readily interpretable loadings on PC3 than did the usually preferred covariance matrix. Three axes accounted for 99% of the morphological variation among species (Table 2). The first axis summarizes size variation, the second a ratio between beak size and tarsus length, and the third beak shape (Table 2). Because there is potentially high error in weight measurements (Mosimann & James 1979) and substantial sexual dimorphism in wing-length these characters may be less reliable than the others as measures of species morphology. However, they do not contribute to PC2 or PC3, and hence all analyses can be interpreted in terms of the three beak measurements and tarsus length.

Feeding behaviour and diets

Whenever possible I collected information on feeding behaviour. I watched an individual bird and recorded its first feeding attempt. I did not record more than one feeding observation per bird, or knowingly include the same individual twice in any one day, so the observations are largely independent. There are biases in the data: observations are more easily made at some times than others. For example, a flock of *P. proregulus* feeding in the undergrowth in May is far more easily observed than individual *P. proregulus* feeding at the top of fir trees in June. I used a classification modified from Davies & Green (1976) to describe feeding techniques: a *standpick* is any plucking of resting arthropods not involving flight (termed a glean by Robinson & Holmes (1982)). A *flycatch* is the capture of flying insects by flying, and consists mainly of chasing insects which have been flushed by the foraging bird, but includes a few (< 1%) sallies for insects in the manner of flycatchers. A *flypick* is a capture of resting arthropods which involves flight, if the bird searches for the prey while

hopping or perched. A *hoverpick* is a capture of resting arthropods when the bird searches for the prey while in flight. A flypick and hoverpick were together grouped as hovering by Robinson & Holmes (1982). Less than 0·1% of all feeding observations, such as the leap pick (Davies & Green 1976) did not fall into this classification, and these were excluded from the analysis. I also estimated the height of the bird above the ground, recorded the tree species, and whether the food item was large (i.e. readily visible in the bill before swallowing), and if so whether it was a caterpillar. The sample size is 1235 feeding observations.

I further assessed diets by examining faeces collected from trapped birds and some nestlings. A remarkable feature of the faeces was the large number of beetle heads (Coleoptera) they contained, and few other identifiable items. Feeding observations and examination of a few full stomachs indicate that beetles are not the major component of the diet and I suspect that differential digestion leads to their preponderance in the faeces. Stomachs were provided by A. Richman from a collecting trip to a nearby area in May 1988. Inter-eye widths of arthropod heads in the faeces and stomachs were measured under a dissecting microscope. Inter-eye width was used as a repeatable measure of arthropod size.

Summary ecological axes were obtained using reciprocal averaging, following the methods of Miles & Ricklefs (1984). Reciprocal averaging is similar to principal components analysis in that it generates uncorrelated axes, and collapses many variables into a few. It is a non-parametric method, and hence preferred over principal components for frequency data. However, the main goal of this paper is to interpret univariate ecological variables (for example, the frequency of flycatches), and not complex combinations of the variables. Therefore, I used the species' scores on the axes obtaining from reciprocal averaging to statistically corroborate conclusions from univariate analyses. The results are reported in a separate section in Appendix 3.

RESULTS

Ecological variation

In Fig. 1 I show the dominant vegetation and distributions of each warbler species, and the goldcrest, along the altitudinal gradient. Densities of warblers estimated by two methods at each of several sites are given in Table 1. The *Phylloscopus* assemblage is dominated by two species at the 2200 m site (*P. occipitalis* and *P. proregulus* Gray), and one species (*P. inornatus*) at the 3340 m site, with the other species comparatively rare. Total warbler densities at these two sites are similar, although above 3340 m they decline (Table 1).

Most species show conspicuous habitat associations. I measured such associations by observing singing males, recording foraging locations (Table 3), and noting territory and nest locations (Price & Jamdar, in press a). *P. proregulus* and *R. regulus* only breed in coniferous trees, *P. inornatus* only in the birch woodland, *P. affinis* Tickell only in juniper, *P. pulcher* Blyth only in association with rhododendron, and *P. magnirostris* Blyth only along watercourses. *P. trochiloides* Blyth is found just below the tree-line, while the other two species *P. occipitalis* and *P. tytleri* Brooks are more generalist in their choice of breeding habitat, and have the widest altitudinal distributions (Fig. 1).

Table 3 presents the basic foraging data. There is significant variation among the

TABLE 3. Foraging data

Species	Foraging method (%)				Location (%)						n
	Flycatch	Flypick	Hoverpick	Standpick	Coniferous	Broadleaf bush*	Broadleaf tree	Ground/grass	Juniper	Rhodo-dendron	
P. proregulus	9	39	16	37	50	30	15	3	0	0	350
R. regulus	0	0	8	92	87	0	5	0	5	0	38
P. inornatus	5	35	4	56	11	13	72	1	0	1	414
P. pulcher	2	24	2	71	4	14	47	6	0	29	49
P. affinis	3	6	3	87	6	23	13	16	39	0	31
P. tytleri	4	5	9	82	23	27	41	9	0	0	56
P. trochiloides	12	47	2	39	0	23	68	3	2	5	66
P. occipitalis	12	30	3	55	63	6	29	0	0	0	220
P. magnirostris	0	64	0	36	45	27	18	0	0	0	11

* Includes all foraging observations in broadleaf vegetation where the bird was less than 1 m above the ground.

Ecology of breeding warblers
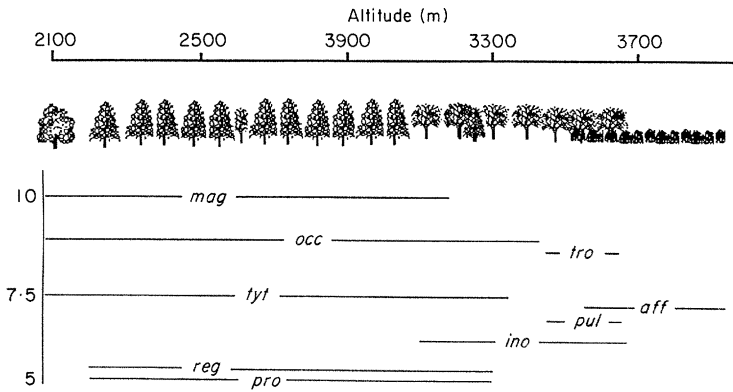
FIG. 1. Altitudinal variation in habitat and warbler distributions. Walnut and other deciduous trees in the villages are replaced by coniferous trees on the mountain-sides, which give way to birch and finally juniper. Species ordered on a body weight (g) axis are: mag, *Phylloscopus magnirostris*; occ, *P. occipitalis*; tro, *P. trochiloides*; tyt, *P. tytleri*; aff, *P. affinis*; pul, *P. pulcher*; ino, *P. inornatus*; reg, *Regulus regulus*; pro, *Phylloscopus proregulus*.
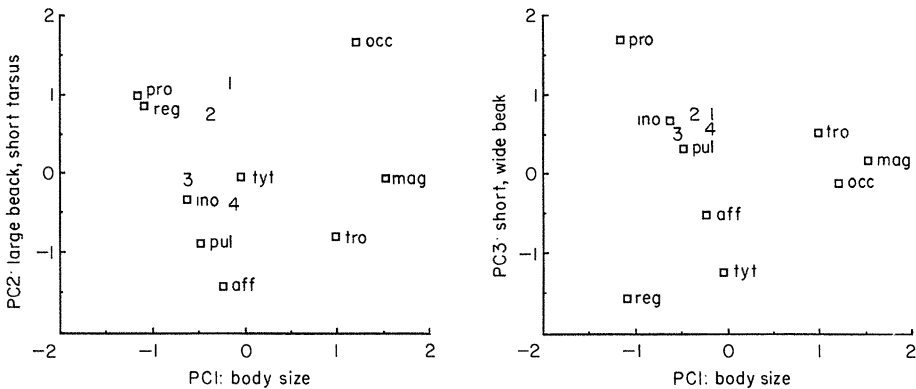

FIG. 2. Scatter plots of principal component scores. The numbers give the average scores at each of the four lower sites of Table 1, based on the mist-netting densities given in Table 1. 1 = 2430 m site, 2 = 2800 m, 3 = 3340 m, 4 = 3550 m.
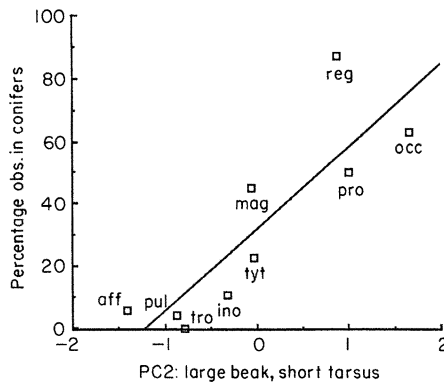
FIG. 3. Scatter of proportion of observations in coniferous habitat against PC2. Line is fit by least squares regression. Sample sizes for the habitat preference data are in Table 3.

Table 4. Correlations between morphological and ecological variables

	Morphological variable		
	PC1	PC2	PC3
Beetle head width in faeces* ($n = 8$)	0·96	−0·06	−0·40
Proportion of feeding observations in conifers[†] ($n = 9$)	−0·13	0·84	−0·31
Proportion of feeding by standpicking[†] ($n = 9$)	−0·47	−0·18	−0·82

* Ln-transformed. No faeces were collected from *R. regulus*.
[†] Arcsine-square root transformed.
Significant correlations ($P < 0.05$) are underlined.
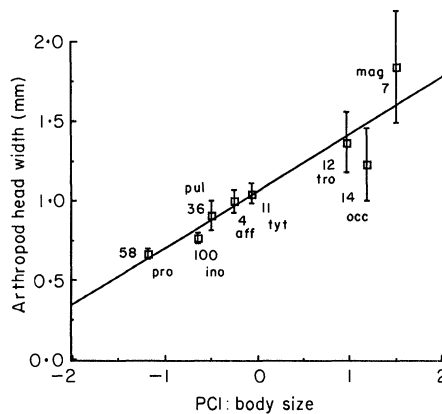
Fig. 4. Scatter of mean arthropod head width against PC1. Figures give numbers of athropods measured for each species (based on from four to more than thirty samples from different birds). The bars are standard errors, based on total arthropods for each species. Line is fit by least squares regression to the (unweighted) species' means.

species in both foraging and habitat choice (*G*-tests, $P < 0.0001$). There are no significant correlations between any measure of foraging and any measure of habitat as presented in Table 3 (assessed using Spearman's rank correlation tests on the relative frequencies).

Morphological and ecological covariation among the species

I show scatter plots of species PC scores in Fig. 2. Also shown in Fig. 2 is the average PC score of all species at each of four sites. These average scores were calculated by weighting each species score by the density of that species, as estimated from the mist-net surveys (see Table 1). At the fifth site above the tree-line there is only one species (*P. affinis*), so the mean score coincides with that species score. There appears to be little variation among habitats in average PC1 score. With the exception of the fifth site average PC3 score is also similar among sites. There is substantial variation among sites in average PC2 score.

Correlations of ecological and morphological variables confirm that habitat differences are associated primarily with variation in PC2 (Table 4, Fig. 3). Neither PC1
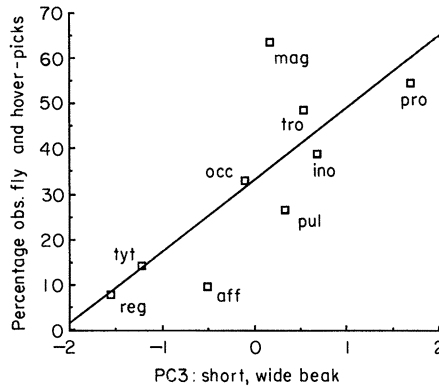
FIG. 5. Scatter of proportion of feeding methods which were either a flypick or a hoverpick against PC3. Line is fit by least squares regression. Sample sizes for the feeding data are in Table 3.

nor PC3 correlate with variation in differential occupancy of habitat, but they do correlate with measures of feeding variation. PC1 correlates with average size of arthropod head widths in the faeces (Table 4, Fig. 4). The proportion of large arthropods in the diet was also estimated from the feeding observations, as the proportion of arthropods easily seen in the bill. The proportion ranged from 0 up to a maximum of 18% for *P. magnirostris* and was correlated with PC1 ($r = 0.85$, $n = 9$, $P < 0.05$).

PC3 is correlated with feeding method (Table 4, Fig. 5). Species with wider, shorter beaks tend to standpick less often (Table 4) and feed by flying manoeuvres, particularly flypicks, more often (Fig. 5). Apart from a negative correlation between frequency of hoverpicking and PC1 ($r = -0.7$, $n = 9$, $P < 0.05$) there are no other significant associations between the ecological measures presented in Table 3 and the morphological axes.

Association of morphological variation with habitat

The three orthogonal axes of morphology are associated differently with ecological variation among the species. PC1, a measure of body size, is associated with prey size, as has been shown in a number of other insectivorous avian genera (Hespenheide 1975). PC3, a measure of bill bluntness, correlates with a greater number of feeding techniques involving flight, and this is expected on the basis of functional considerations, and through inter-generic comparisons (Root 1967; Fitzpatrick 1985).

There are no obvious adaptive explanations for the association of PC2 with habitat. Species with relatively short tarsi for their beaks tend to occupy the coniferous habitat at lower elevations. The ordering of species along the PC2 axis shows a remarkably close association with an ordering of habitat occupancy along the altitudinal gradient, such that species which are primarily ecotonal (*P. magnirostris* and *P. tytleri*) occupy a position on the axis midway between the coniferous and birch species (Fig. 3). The major discrepancy in the ordering comes from *P. occipitalis*, which occupies both deciduous and coniferous habitat, but lies at one end of the PC2 axis. The species is far commoner in the coniferous habitats than birch habitats,

however (Table 1), and it may be primarily adapted to the coniferous woodland at lower elevations. The correlation between mean elevation (Fig. 1) and proportion of observations in conifer (Table 3) is high (Spearman's $r = 0.75$, $P < 0.05$), so explanations based either on habitat structure or a direct response to altitude and associated climatic variables may apply.

Within-species morphological variation among habitats

P. occipitalis occupies both coniferous and birch habitats and the way in which it varies in morphology between the two habitats provides additional support for significance to the PC2–habitat/elevation association. The morphology of eleven *P. occipitalis* breeding in the birch woodlands was compared with fifty-eight breeding in the coniferous woodland. Individuals breeding in the coniferous woodland had significantly shorter tarsi and wider, deeper beaks than did those breeding in the deciduous woodland (Price & Jamdar, in press a). The individual *P. occipitalis* measurements were projected onto the three among-species PC axes and variation compared in the resultant scores among the two habitats. Individuals differed significantly along the PC2 axis ($t = 3.2$, $P < 0.01$) and along the PC3 axis ($t = 2.7$, $P < 0.01$), but not in PC1 ($t = 0.3$, $P > 0.1$). Scores along the three axes are weakly correlated ($r \approx 0.2$), however, and when I contrasted the two habitats using discriminant analysis, PC2 remained strongly significant ($P < 0.01$), while the significance of PC3 was reduced ($P = 0.03$). Mean score on the among-species PC2 axis for
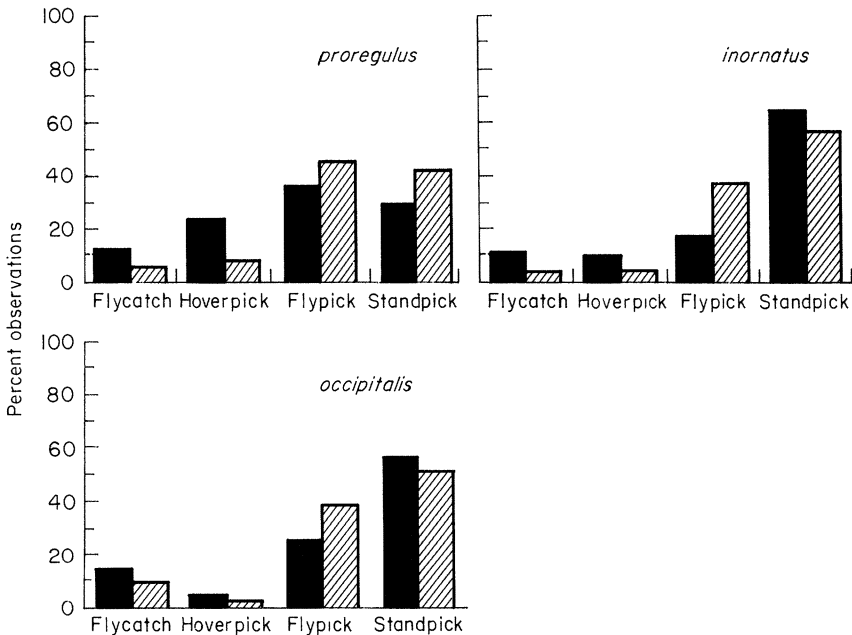

FIG. 6. Utilization of different feeding methods by three species in each of two habitats, coniferous (■) and broad-leaf (▨) trees. Broad-leaf is predominantly understorey for *P. proregulus* and birch for the other species. Sample sizes in each category for each species, with the associated χ^2 test are: *P. occipitalis* 138 coniferous, 78 broad-leaf, $\chi_3^2 = 5.5$, $P > 0.1$, *P. inornatus* 46 coniferous, 354, broad-leaf $\chi_3^2 = 13.2$, $P < 0.01$, and *P. proregulus* 174 coniferous, 158 broad-leaf $\chi_3^2 = 21.5$, $P < 0.0001$.

P. occipitalis in the coniferous was 1·83 ± 0·7 S.D., and for *P. occipitalis* in the birch woodland 1·04 ± 0·7 S.D. Variation within the single species *P. occipitalis* shows a remarkable parallel to that of the among-species variation. While strengthening the argument for a possible adaptive significance of species' morphology with habitat or elevation this does not help with an understanding of what that significance might be.

Within-species variation in feeding across habitats

The significance of the variation in PC2 is unclear. It may be related to climate and the mean elevational range of each species. Alternatively the association may be an adaptive response to habitat structure, reflecting ability to move through the vegetation. If the morphological differences are related to foraging we might expect warblers with similar morphology which forage in different habitats to use different feeding methods. Therefore, we should observe foraging differences when an individual switches between two habitats. In Fig. 6 I contrast the feeding methods of each of the three species for which there are sufficient data, when in coniferous or broad-leaf habitat. *P. inornatus* and *P. proregulus* do show small but significant changes in foraging method with habitat. Observations on *P. proregulus* in the broad-leaf are mainly of birds foraging in the undergrowth beneath the conifers (primarily on *Viburnum*), whereas observations on *P. inornatus* are mainly on trees in their territory. They are both largely a consequence of individuals switching between tree types, whereas the observations on *P. occipitalis*, which does not significantly differ in foraging between habitats (Fig. 6), are mainly on individuals which live in one or the other tree type, and differ to some extent in morphology.

DISCUSSION

Habitat selection

Bird distributions along altitudinal gradients have been widely studied, and in many cases an association of the distribution of a particular species with a particular habitat type has been observed or assumed (Able & Noon 1976; Sabo 1980; Noon 1981; Cody 1985a). However, in the tropical forest there is no such close correlation of altitudinal distribution with habitat (Terborgh 1971; Diamond 1973), and in Galápagos finches Schluter (1982) argued that the main determinant of a species' altitudinal distribution was the distribution of its favoured food, which is only loosely correlated with habitat features. The altitudinal distributions of the leaf warblers studied here are clearly associated with habitat, a feature which appears to be common in temperate assemblages (Able & Noon 1976).

Species confined to specific habitats will inevitably become adapted to them. This may often result in lowered fitness in other habitats. For example, Sabo (1980) argued that cold tolerance of the blackpoll warbler was important in restricting its altitudinal range. The question I address is the extent to which adaptation to a particular habitat has resulted in differential feeding abilities across habitats. The question has been generally asked because competition for food is the most apparent mechanism through which interspecific competition could lead to the maintenance of habitat differences (Cody 1974; Martin 1987).

Members of a single species may occupy different altitudinal distributions and/or

habitats in different parts of the species' geographic range (Diamond 1973; Terborgh & Weske 1975; Noon 1981; Schluter & Grant 1982; Cody 1985b, Alatalo, Gustafsson & Lundberg 1986). Such shifts in habitat correlate with the presence or absence of ecologically similar species and provide evidence that interspecific competition plays a part in determining habitat selection. The extent to which habitat shifts reflect evolution or are immediate responses to current competition is largely unknown, although the few experimental studies on breeding birds have found evidence for current competition (Garcia 1983; Gustafsson 1987).

In this study four results are relevant to understanding the relationship of diet, feeding and competition for food to habitat choice: (i) there is a strong correlation between PC2 and habitat occupied; (ii) the single species which breeds over the most of the altitudinal gradient varies morphologically in a way which parallels the among-species differences; (iii) morphological associations with diet and feeding method are largely uncorrelated with habitat; (iv) species regularly forage in alternative habitats. I consider each of these results in turn. One important assumption I make throughout the discussion is that the morphological differences among species have arisen as an evolutionary response to selection, and that they are not ecophenotypic responses, for example to climate (James 1983). It seems unlikely that the substantial variation among species can be entirely ecophenotypic, but this needs to be tested.

Species with a high beak size : tarsus length ratio tend to occupy coniferous habitats and breed at lower elevations. The correlation suggests an adaptive response to habitat and/or elevation (and associated climatic variables). This could result in maladaptation to non-preferred habitats with respect to the preferred habitat, and would lessen the importance of current competition in maintaining distinct habitat preferences. The argument depends on there being adaptive significance to the correlation, and this significance is unclear.

There have been many comparisons of morphological differences among passerine species occupying coniferous and broad-leaf habitats. Among *Parus* (Partridge 1976) and *Regulus* (Winkler & Leisler 1985), species morphological differences in leg and foot structure can be clearly related to perching on different substrates. Comparisons among warblers have been mostly univariate. Among North American warblers, larger species occupy coniferous woodland (Greenberg 1979). In a breeding population of *Phylloscopus trochilus* in Finland larger individuals occupy the broad-leaf (Tiainen 1982). In one comparison of shape the association of morphology with habitat in two species of North American parulids was opposite to that observed in the leaf warblers (Morrison 1982). One common pattern among groups is for species which are ground-foragers to have longer tarsi than those which are more arboreal (Osterhaus 1962; Miles & Ricklefs 1984). *P. affinis* does forage on the ground substantially, and has the longest relative tarsus length. It is doubtful whether this can be a general explanation, because all the other species are very infrequently seen on the ground. Thus, previous studies on morphology–habitat associations provide no insight to the causal basis of the PC2–habitat/elevation correlation.

An explanation based on adaptation in the non-breeding season seems unlikely to account for the PC2–habitat/elevation correlation because there does not appear to be a good correlation between habitat occupied or climate experienced in the breeding season and that of the non-breeding season (Gaston 1974; Ali & Ripley 1983). Further, the species remain primarily arboreal in the non-breeding season

(Gaston 1974; MacDonald & Henderson 1977; Price 1981), and so the problem of finding a non-breeding season adaptive explanation remains.

Despite the difficulty of determining adaptive significance to the shape − habitat/elevation correlation, the correlation does appear to be real. It is very strong, and the association is observed in comparisons of individuals within the one species which occupies both habitats. This within-species variation presumably requires a similar explanation to that of the between-species variation. Whether the within-species morphology is a phenotypically plastic growth response (James 1983) or not, individuals seem to settle and breed in a habitat for which they are morphologically most suited. This could result from fidelity to natal habitat, or a period of searching prior to breeding.

The three ecological axes − prey size, feeding behaviour, and habitat − are largely orthogonal to one another. In other studies of guilds it has been found that species of different size or in different habitats use different foraging methods, and such associations are readily interpreted (Robinson & Holmes 1982; Sherry 1984). The only such correlation I found was that larger species tend to hoverpick less. The lack of correlation is most strikingly seen in the similarity of mean body size (i.e. prey size) and mean beak shape (i.e. foraging behaviour) across habitats (Fig. 2), despite large differences in the body size and beak shape of the individual species in each habitat. The similarity among habitats in average prey size and foraging behaviours suggests that there are only weak selection pressures associated with efficient exploitation of food as a direct response to the habitat occupied.

This conclusion is supported by several other observations. Arthropod abundances and types do not vary greatly among habitats (Appendix 1). Although morphological differences associated with habitat may affect foraging behaviour there are only small changes in foraging behaviour as individuals move between habitats. Territories always contain trees of preferred habitat but individuals forage freely in other tree species if available on or near territory. *Phylloscopus inornatus* territories, for example, always contain birch, but trees in the territory may be up to 80% coniferous (Price & Jamdar in press b). All species also regularly forage in several tree species prior to establishing territories.

Intrinsic fitness penalties for occupancy of the incorrect habitat appear to be small. Although they may be sufficient to account for differential habitat choice, other explanations, such as non-adaptive preferences, or current competition cannot be ruled out. The most obvious difference among habitats is the distribution of congeners, and current competition accentuating fitness differences among habitats may be the best explanation for the restricted range of habitats actually occupied. Evidence for both interference and exploitative competition among Passerines is accumulating (Alatalo *et al.* 1987; Alatalo & Moreno 1987). While impossible to demonstrate in this system without experiments, species do show inter-specific aggression. I recorded more than fifty aggressive chases between species (none resulted in a fight).

Morphology−ecology associations

In this section I compare the observed associations of morphology and ecology with results from other studies. Although the reason for the covariation of morphology with habitat is not clear, associations of body size with prey size, and beak shape with feeding method, are readily interpretable, although surprisingly strong. Larger

species feed on larger prey, as demonstrated by Hespenheide (1975) for several other insectivorous groups. The association of relative beak width and foraging method has not been specifically demonstrated within a single genus of insectivorous birds, but it is apparent in the data of Eckhardt (1979) studying North American warblers, and the association was also noted in the taxonomically diverse guild of gleaning insectivorous birds studied by Root (1967). It is clearly apparent at the inter-family level: flycatchers have much wider beaks than warblers.

Ecology−morphology associations have been demonstrated in many other studies (Miles & Ricklefs 1984; Winkler & Leisler 1985; Fitzpatrick 1985; Miles, Ricklefs & Travis 1987; Murphy 1989), but the correlations have not been as strong, and have not always been easy to interpret. In an influential paper Wiens & Rotenberry (1980) found ecology−morphology associations among breeding shrub-steppe birds to be weak. The studies have been conducted in different ways, and results will depend on the species included in the analysis, and on the morphological and ecological characters studied. The high correlations I observed must be partly a result of the ecological and morphological variables actually measured, and partly the result of including three ecological dimensions, which appear to be the minimum needed to describe niche space in these foliage gleaning birds.

Methodological differences are unlikely be the entire explanation for the differences in the strength of the morphology−ecology associations found in different studies. Two other factors are likely to be feeding opportunism and lasting phylogenetic effects. Both North American warblers (Greenberg 1979; Robinson & Holmes 1982) and breeding shrub-steppe birds (Wiens & Rotenberry 1980) are quite opportunistic in their feeding, and exploit temporarily abundant prey sources. This will obscure morphology−ecology associations. Such opportunism was not observed in the warblers studied here.

Morphology−ecology correlations will often be weakened by the effect of history (Schluter 1986, 1989; Miles *et al*. 1987). Two species with very different phylogenetic backgrounds (e.g. a finch and a dove, Schluter 1989) are unlikely to ever converge on the same morphology and behaviour, even when exploiting identical resources. In insectivorous birds, morphology−prey size correlations have been shown to be high within genera, with the slope of the association differing across genera (Hespenheide 1975). Lumping genera inevitably reduces the correlation. The group of birds I studied were all very similar, with eight of the species within one genus. Lasting historical effects are likely to be small. In fact, in this group there may be the opposite problem. The strength of the correlations could be artificially inflated by treating the species as independent points, particularly if some species share sufficiently recent ancestry that adaptive diversification is still proceeding (Felsenstein 1985).

Conclusions

The essential conclusion is that there is breeding season adaptation to habitat and foraging pressures in this warbler guild. The result is surprising because of the seemingly intense pressures on foraging ability in the non-breeding season (Price 1981), and it does not seem to be purely a correlated result of those selection pressures. Exactly how the pressures on foraging in the breeding season translate into the different habitat occupancy and other relations among the different species remains unclear.

ACKNOWLEDGMENTS

REFERENCES

Abbot, I., L.K. Abbott & Grant, P.R. (1977). Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecological Monographs*, **47**, 151−184.

Able, K.P. & Noon, B.R. (1976). Avian community structure along elevational gradients in the northeastern United States. *Oecologia*, **26**, 275−294.

Alatalo, R.V., Gustafsson, L. & Lundberg, A. (1986). Interspecific competition and niche shifts in tits *Parus*: evaluation of non-experimental data. *American Naturalist*, **127**, 819−834.

Alatalo, R.V., Eriksson, D., Gustafsson, L. & Larsson, K. (1987). Exploitation competition influences the use of foraging sites by tits: experimental evidence. *Ecology*, **68**, 284−290.

Alatalo, R.V. & Moreno, J. (1987). Body size, interspecific interactions, and use of foraging sites in tits (Paridae). *Ecology*, **68**, 1773−1777.

Ali, S. & Ripley, S.D. (1983). *Handbook of the Birds of India and Pakistan*. Oxford University Press, Delhi.

Cody, M.L. (1974). *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton.

Cody, M.L. (1985a). An introduction to habitat selection in birds. *Habitat Selection in Birds* (Ed. by M.L. Cody), pp. 4−56. Academic Press, London.

Cody, M.L. (1985b). Habitat selection in the Sylviine warblers of western Europe and north Africa. *Habitat Selection in Birds* (Ed. by M.L. Cody), pp. 86−129. Academic Press, London.

Davies, N.B. & Green, R.E. (1976). The development and ecological significance of feeding techniques in the reed warbler (*Acrocephalus scirpaceus*). *Animal Behaviour*, **24**, 213−229.

Diamond, J.M. (1973). Distributional ecology of New Guinea birds. *Science*, **179**, 759−769.

Eckhardt, R.C. (1979). The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecological Monographs*, **49**, 129−149.

Ekman, J. (1986). Tree use and predator vulnerability of wintering passerines. *Ornis Scandinavica*, **17**, 261−267.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, **125**, 1−15.

Finch, D. (1989). Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology*, **70**, 866−880.

Fitzpatrick, J.W. (1985). Form, foraging behaviour and adaptive radiation in the Tyrannidae. *Neotropical Ornithology* (Ed. by P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely & F.G. Buckley), pp. 447−470. Ornithological Monographs 36. American Ornithologists' Union, Washington, D.C.

Garcia, E.F.J. (1983). An experimental test of competition for space between blackcaps *Sylvia atricapilla* and garden warblers *Sylvia borin* in the breeding season. *Journal of Animal Ecology*, **52**, 795−805.

Gaston, A.J. (1974). Adaptation in the genus *Phylloscopus*. *Ibis*, **116**, 432−450.

Greenberg, R. (1979). Body size, breeding habitat, and winter exploitation systems in *Dendroica*. *Auk*, **96**, 756−766.

Gustafsson, L. (1987). Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, **68**, 291−296.

Hespenheide, H.A. (1975). Prey characteristics and predator niche width. *Ecology and Evolution of Communities* (Ed. by M.L. Cody & J. Diamond), pp. 158−180. Belknap Press, Cambridge.

James, F.C. (1983). Environmental component of morphological differentiation in birds. *Science*, **221**, 184−186.

Lack, D. (1937). The psychological factor in bird distributions. *British Birds*, **31**, 130−136.

MacDonald, D.W. & Henderson, D.G. (1977). Aspects of the behaviour and ecology of mixed-species bird flocks in Kashmir. *Ibis*, **119**, 481−493.

Martin, T.E. (1987). Food as a limit on breeding birds: a life-history perspective. *Annual Reviews of Ecology and Systematics*, **18**, 453−487.

Martin, T.E. (1988). Processes organizing open nesting bird assemblages: competition or nest predation? *Evolutionary Ecology*, **2**, 37−50.

Miles, D.B. & Ricklefs, R.E. (1984). The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, **65**, 1629−1640.

Miles, D.B., Ricklefs, R.E. & Travis, J. (1987). Concordance of ecomorphological relationships in three assemblages of Passerine birds. *American Naturalist*, **129**, 347−364.

Morrison, M.L. (1982). The structure of western warbler assemblages: ecomorphological analysis of the black-throated gray and hermit warblers. *Auk*, **99**, 503−513.

Mosimann, J.E. & James, F.C. (1979). New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution*, **33**, 444−459.

Murphy, M.T. (1989). Life-history variability in North American breeding tyrant flycatchers: phylogeny, size, or ecology? *Oikos*, **54**, 3−14.

Noon, B.R. (1981). The distribution of an avian guild along a temperate elevational gradient: the importance and expression of interspecific competition. *Ecological Monographs*, **51**, 105−124.

Osterhaus, M.B. (1962). Adaptive modifications in the leg structure of some North American warblers. (*Dendroica* Parulidae). *American Midland Naturalist*, **68**, 474−486.

Partridge, L. (1976). Some aspects of the morphology of blue tits (*Parus caeruleus*) and coal tits (*P. ater*) in relation to their behaviour. *Journal of Zoology, London*, **179**, 121−133.

Price, T. (1981). The ecology of the Greenish warbler *Phylloscopus trochiloides* in its winter quarters. *Ibis*, **123**, 131−144.

Price, T. & Jamdar, N. (1990). The breeding birds of Overa Wildlife Sanctuary, Kashmir. *Journal of the Bombay Natural History Society*, **87**, 1−15.

Price, T. & Jamdar, N. (in press a). Breeding of eight sympatric species of *Phylloscopus* warblers in Kashmir. *Journal of the Bombay Natural History Society*.

Price, T. & Jamdar, N. (in press b). The breeding biology of the yellow-browed warbler in Kashmir. *Journal of the Bombay Natural History Society*.

Robinson, S.K. & Holmes, R.T. (1982). Foraging behaviour of forest birds: the relationships among search tactics, diet and habitat structure. *Ecology*, **63**, 1918−1931.

Rice, J., Omhart, R.D. & Anderson, B.W. (1983). Habitat selection attributes of an avian community: a discriminant analysis investigation. *Ecological monographs*, **53**, 263−290.

Root, R.B. (1967). The niche exploitation pattern of the blue gray gnatcatcher. *Ecological Monographs*, **37**, 317−350.

Rosenzweig, M.L. (1985). Some theoretical aspects of habitat selection. *Habitat Selection in Birds* (Ed. by M.L. Cody), pp. 517−540. Academic Press, London.

Sabo, S.R. (1980). Niche and habitat relations in subalpine birds of the White Mountains of New Hampshire. *Ecological Monographs*, **50**, 241−259.

Schluter, D. (1982). Distributions of Galápagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology*, **63**, 1504−1517.

Schluter, D. (1986). Tests for similarity and convergence of finch communities. *Ecology*, **67**, 1073−1085.

Schluter, D. (1989). Bridging population and phylogenetic approaches to the evolution of complex traits. *Complex Organismal Functions: Integration and Evolution in Vertebrates* (Ed. by D.B. Wake & G. Roth), pp. 79−95. Wiley, New York.

Schluter, D. & P.R. Grant. (1982). The distribution of *Geospiza difficilis* in relation to *G. fuliginosa* in the Galápagos Islands: tests of three hypotheses. *Evolution*, **36**, 1213−1226.

Sherry, T.W. (1984). Comparative dietary ecology of sympatric, insectivorous neotropical flycatchers (Tyrannidae). *Ecological Monographs*, **54**, 313−338.

Terborgh, J. (1971). Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vicabamba, Peru. *Ecology*, **51**, 23−40.

Terborgh, J. & Weske, J.S. (1975). The role of competition in the distribution of Andean birds. *Ecology*, **56**, 562−576.

Tiainen, J. (1982). Ecological significance of morphometric variation in three sympatric *Phylloscopus* warblers. *Annals Zoologica Fennica*, **19**, 285−295.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. & Virolainen, E. (1983). The habitat and spatial relations of breeding *Phylloscopus* warblers and the goldcrest *Regulus regulus* in southern Finland. *Annals Zoologica Fennica*, **20**, 1−12.

Wiens, J.A. & Rotenberry, J.T. (1980). Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecological Monographs*, **50**, 287−308.

Winkler, H. & Leisler, B. (1985). Morphological aspects of habitat selection in birds. *Habitat Selection in Birds* (Ed. by M.L. Cody), pp. 415−434. Academic Press, London.

Ecology of breeding warblers

APPENDIX 1

Direct measures of arthropod abundance

The conclusion from this paper is that mean prey size in the diet and average foraging method are similar across habitats, although the way in which prey and foraging method are partitioned within each habitat varies. The results predict that prey type does not vary greatly across habitat. I made extensive arthropod collections and can directly assess this prediction.

Arthopod abundance was measured in two ways: (i) branches were beaten with a stick, and arthropods falling on to a tray held below the branch were counted; (ii) white plates containing a water−detergent mix were placed in strategic locations for 1−6 days, and all arthropods which flew or fell into the plates were recorded. All arthropods were recorded by order and size (thorax plus abdomen length to the nearest 2 mm). It is difficult to measure the absolute abundance of arthropods because of micro-habitat heterogeneity and biases in sampling methods. I tried to circumvent these problems by collecting large sample sizes, but with limited success. Nevertheless, the samples can be used to draw conclusions about changes in taxonomic and size-class composition along the gradient, and to make some tentative statements about abundance patterns. I made most collections in 1986, visiting eight localities along a section of the altitudinal gradient (2800−3550 m) every 6 days. These were supplemented with a few preliminary collections in 1985, and an intensive 2-day survey at five localities spaced over the whole altitudinal gradient (2430−3725 m) in 1987.

I present measures of arthropod abundance in Figs A1 and A2. Results of ANOVAs of arthropod abundances classified by size-classes or taxonomic composition generally
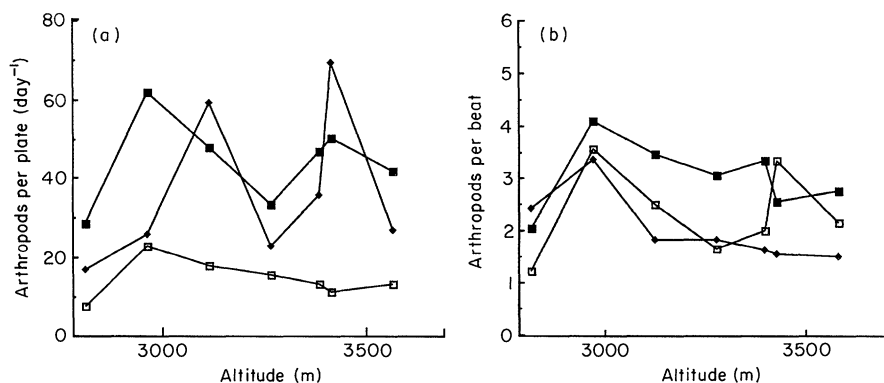

FIG. A1. Patterns in the abundance of arthropods collected in 1986 along a restricted segment of the altitudinal gradient: (a) arthropods collected in water-filled plates (two plates out for 6 days); (b) arthropods collected by beating branches (20 beats per collecting trip). The two lowest altitude sites are in coniferous woodland, the other sites are in the birch. Average number of collecting trips per site: (□) May = 3·4, (◆) June = 6·7, and (■) July = 6·0.
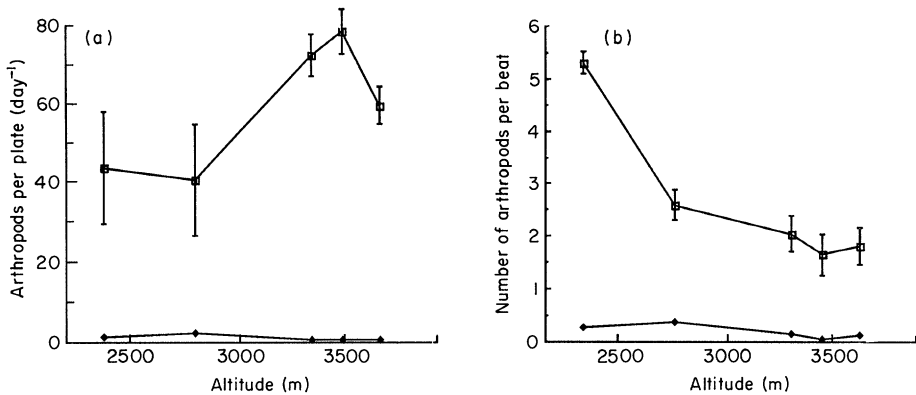
FIG. A2. Patterns of abundance in arthropods collected in (a) water-filled plates, and (b) by beating along the whole altitudinal gradient in June 1987, at the localities given in Table 1 (totals ± S.E.): arthropods (□) and coleoptera (◆) branches. The two sites at the lowest altitude include beats from coniferous trees and broad-leaf undergrowth. The middle site includes collections in the birch and coniferous. The next highest site includes juniper, rhododendron, and also birch, and the top site juniper and rhododendron. Sample sizes are six plates left out for 1 day, and 30 beats per habitat type. Standard errors are based on numbers collected per plate, or per habitat type.

indicated significant variation among locality and month, but not year. Differences among locality, although often highly significant, were not large, and rarely more than two-fold. Habitat type from which the arthropods were collected (coniferous, birch, rhododendron, and juniper) is highly correlated with locality and results were the same if habitat type was substituted for locality. Despite significant variation in arthropod abundance there was often no obvious association of abundance with altitudinal variation (Figs A1 and A2), and at least some of the variation in abundance seems to reflect differences in micro-habitat.

The following trends were identified. First, more resting arthropods were found on the coniferous than birch trees, particularly in 1987 (Fig. A2). Second, more Diptera were collected in the plates in birch woodland than in the coniferous woodland; this may reflect the more open nature of the birch. Third, there were consistently more Arachnida in the conifers and more Homoptera in the birch (ANOVAs, $P < 0.01$, see Fig. A3). Lepidoptera larvae and Coleoptera usually did not vary significantly among locality, and Lepidoptera larvae were generally uncommon (less than 6 per 100 beats even in June). Distributions of arthropods classified by size were similar among localities (Fig. A3).

The overall picture is one of arthropod similarity among localities and habitats. Collections by beating are essentially a density measure and, as coniferous trees are more numerous and larger than the trees in the birch woodlands, the absolute abundance of resting arthropods appears to be greater in the coniferous. In so far as the plate collections measure abundance of flying arthropods, particularly Diptera, these are commoner in the open birch woodland.

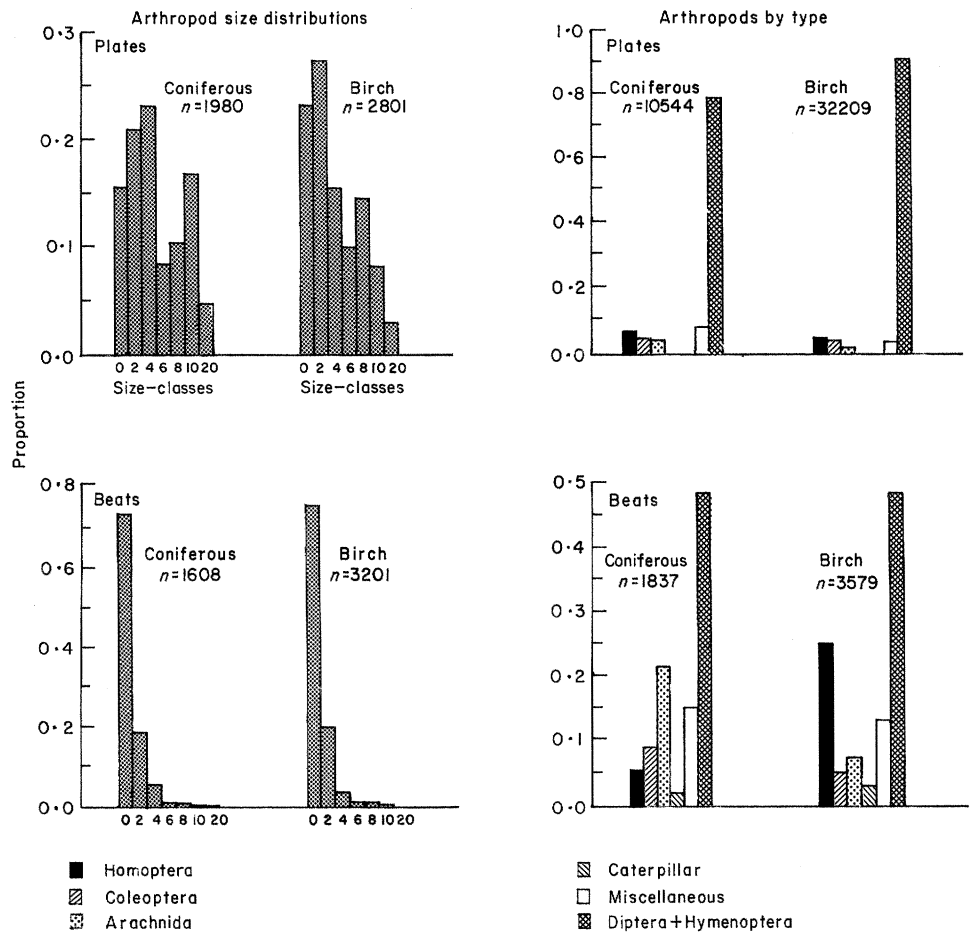*Ecology of breeding warblers*

FIG. A3. Taxonomic and size-class distributions of arthropods in the coniferous and birch woodlands. Based on arthropods collected throughout the study. Diptera and Hymenoptera are combined because the smaller ones were not always distinguished. Some of the rarer arthropod types were not classified by size. Size-class distributions for the plates exclude Diptera and Hymenoptera.

APPENDIX 2

Morphological measurements (mean ± S.E.) for the species studied. The measurements for the eight *Phylloscopus* species are taken from Price and Jamdar (in press a), where more detailed information (e.g. on ranges and sexual dimorphism) is also presented.

Species	Wing length (mm)	Weight (g)	Tarsus (mm)	Beak length (mm)	Beak depth (mm)	Beak width (mm)	Sample size
P. tyleri	56·5 ± 0·40	7·2 ± 0·07	17·7 ± 0·11	6·2 ± 0·07	2·1 ± 0·04	2·2 ± 0·04	30
P. affinis	56·2 ± 0·85	6·7 ± 0·27	18·7 ± 0·36	5·7 ± 0·13	1·9 ± 0·02	2·2 ± 0·04	5
P. pulcher	55·5 ± 0·92	6·4 ± 0·14	18·1 ± 0·28	5·3 ± 0·11	1·9 ± 0·04	2·3 ± 0·04	8
P. inornatus	55·9 ± 0·17	6·0 ± 0·03	17·5 ± 0·04	5·1 ± 0·01	1·9 ± 0·01	2·2 ± 0·01	228
P. proregulus	51·2 ± 0·22	5·1 ± 0·04	16·5 ± 0·05	4·7 ± 0·03	1·9 ± 0·01	2·4 ± 0·02	140
P. magnirostris	67·8 ± 1·17	10·0 ± 0·42	18·7 ± 0·18	6·7 ± 0·21	2·8 ± 0·07	3·0 ± 0·07	8
P. trochiloides	62·5 ± 0·83	8·3 ± 0·18	19·1 ± 0·18	6·3 ± 0·08	2·5 ± 0·03	2·9 ± 0·05	15
P. occipitalis	64·6 ± 0·30	8·7 ± 0·06	17·4 ± 0·06	7·0 ± 0·04	2·8 ± 0·01	3·1 ± 0·02	99
R. regulus	52·6 ± 0·67	5·0 ± 0·15	16·6 ± 0·43	5·8 ± 0·03	1·8 ± 0·08	1·9 ± 0·14	3

APPENDIX 3

Multivariate analysis of the ecological data

Results from univariate analyses of the ecological data are presented in the main body of the text. In this Appendix the results from a multivariate study are outlined. Methods follow those of Miles & Ricklefs (1984). I conducted two separate reciprocal averaging analyses, one for the foraging data, and one for the habitat occupancy data (see Table 3). A single axis summarizes much of the foraging variability among species, and is essentially a flypick : standpick contrast. In reciprocal averaging for habitat I included proportion of observations at each of three foraging heights (< 1 m, 1–10 m, >10 m), in addition to the data on habitat occupancy presented in Table 3. Two orthogonal axes from the habitat data, one contrasting foraging height and the second contrasting deciduous with coniferous substrate summarized most of the variation. Scores on the foraging axis were not significantly correlated with those on either of the habitat axes (for the first habitat axis, $r = 0.18$, $n = 9$, $P > 0.1$, for the second axis $r = 0.39$, $n = 9$, $P > 0.1$). Correlations between the axes obtained by reciprocal averaging of the ecological data and the three morphological axes (PC1, PC2 and PC3) gave results in general agreement with those expected on the basis of the univariate study. The only significant correlations were between the feeding method RA axis and PC3, and between the first RA axis from the habitat data and PC2.

The strength of the association between morphology and ecology can be quantified using the multivariate approach. I calculated canonical correlations between the three morphological axes (PC1, PC2 and PC3), and four ecological axes (the three axes obtained by reciprocal averaging, plus one of average prey size), and determined the proportion of the variation in the ecological data which is explained by the three canonical correlation axes (see Miles & Ricklefs 1984). Data for prey size in *R. regulus* were not obtained, so the analysis is restricted to the eight *Phylloscopus* warblers. The result was that variation in morphology accounted for 94·5% of the variation in ecology, i.e. virtually all of it.