

## Latitudinal trends in body size among over-wintering leaf warblers (genus *Phylloscopus*)

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Geographical trends in body size are commonly interpreted in the framework of Bergmann's rule, which states that larger body sizes are found at higher latitudes. Here we demonstrate a negative association of body size with latitude among over-wintering warblers of the genus *Phylloscopus* as well as within a single species (*Phylloscopus trochiloides*) we were able to study in depth. We examine the role of resources in determining body size distributions. In mid-winter in India there are more large prey at southern sites (occupied by large-bodied warblers) than at a northern site (occupied by small-bodied warblers). *Phylloscopus trochiloides* is a relatively large species. The timing of its autumn migration is correlated with the withdrawal of the monsoon through India and its appearance on the breeding grounds in spring is correlated with the appearance of relatively large prey. We suggest that prey size and abundance are the main determinants of the spatial distributions of *Phylloscopus* warblers in winter. Cross-species associations of body size with both time of arrival on the breeding grounds and migration distance may also largely reflect the spatial and temporal distribution of prey. Resources are likely to be more important in determining both the strength and direction of latitudinal associations with body size than is currently appreciated, even in cases where Bergmann's rule is upheld.

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Latitudinal gradients in body size are common both within and between species (Blackburn et al. 1999, Ashton et al. 2000). Climate is correlated with latitude and may directly affect selection pressures on body size, e.g. through heat loss (James 1970, 1991), or indirectly through influences on predators, prey and competitors (McNab 1971). Correlations of body size with latitude are usually interpreted in the framework of Bergmann's rule, which states that among a group of closely related species, the larger species tend to occur at higher latitudes (James 1970, Blackburn et al. 1999). In this paper we show that among over-wintering leaf warblers (genus *Phylloscopus*) the larger species occur further south. This means that hypotheses based on direct

influence of climate devised in the context of Bergmann's rule can be immediately rejected and leaves us with a relatively simple set of hypotheses to account for latitudinal trends.

McNab (1971) emphasized that spatially varying prey size distributions and abundance, mediated by competition, may often lead to spatially varying selection pressures affecting body size. Larger bodied animals are typically able to handle larger prey. Countervailing advantages to small size include both metabolic efficiency and possibly increased handling efficiency of small prey. Under this hypothesis body sizes should track prevailing prey sizes. This has been most clearly demonstrated in Galápagos finches, where finch body

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size across islands closely matches seed size (Schluter and Grant 1984). Among the *Phylloscopus* warblers large species eat larger prey than smaller species (Price 1991, Gross and Price 2000).

Despite their potentially great explanatory power, resources have not been directly measured in the context of latitudinal gradients in body size. Our purposes in this paper are 1) to document associations of latitude with body size in the genus *Phylloscopus* and 2) to demonstrate resource distributions that are consistent with these patterns. We also show that body size is correlated with two life-history variables: time of breeding and migration distance. Both early return to the breeding grounds (Nolan and Ketterson 1990) and migration distance (Blackburn et al. 1999) have been previously proposed to directly influence latitudinal gradients in body size. We argue that in the genus *Phylloscopus* the correlations result from their mediation by spatial and temporal appearance of resources.

## Methods

### Study group

The genus *Phylloscopus* consists mainly of migratory species that breed in the temperate regions of Eurasia and winter in Africa, south Asia and south-east Asia. In this study we consider the non-breeding distributions of 35 migratory taxa from the genus (Table 1). These include some well-marked subspecies as well as species. Five taxa are omitted because their non-breeding season ranges are poorly known. All the omitted taxa are from south-east Asia, and all the main results apply if analysis is restricted to the African and Indian species.

### Ranges and morphology

Non-breeding season ranges were determined from maps and descriptions in Ticehurst (1938), Williamson (1962), Moreau (1972), King et al. (1975), Ali and

Table 1. Characteristics of *Phylloscopus* taxa studied.

Taxon	Abbr.	Range limits (°)				Range area (km <sup>2</sup> × 10 <sup>6</sup> )	PC 1 score
		West	East	North	South		
<i>affinis</i> *§	AF	73	117	29	8	4.66	-0.7
<i>armandii</i>	AR	92	105	17	24	0.85	2.2
<sup>1</sup> <i>bonelli</i> *	BN	-17	25	16	10	6.04	0.8
<sup>1</sup> <i>orientalis</i> *	OR	30	40	20	12		0.6
<i>borealis</i> *	BR	96	130	25	-10	4.56	2.0
<i>tenellipes</i> *	TN	95	109	28	7	0.79	0.9
<sup>2</sup> <i>collybita</i> *	CO	-10	50	50	0	28.08	0.2
<sup>2</sup> <i>tristis</i>	TR	43	93	44	23		0.9
<sup>2</sup> <i>lorenzii</i> *	LR	41	48	42	30		0.6
<sup>2</sup> <i>brehmii</i> *	BH	-10	10	35	13		0.2
<sup>2</sup> <i>sindianus</i> *	SD	63	80	35	27		-0.1
<i>coronatus</i> *	CR	92	120	23	-9	2.89	0.9
<i>ijimae</i> *	IJ	120	122	19	14	0.07	0.9
<i>fuligiventer</i>	FG	85	93	32	30	0.33	0.7
<i>fuscatus</i> *	FU	82	120	30	18	4.79	1.8
<i>griseolus</i> *	GR	70	90	32	14	2.17	1.8
<sup>3</sup> <i>inornatus</i> *	IN	85	120	28	5	9.32	-2.1
<sup>3</sup> <i>humei</i> *§	HU	62	92	34	17.5		-2.1
<i>maculipennis</i> §	MC	77	105	32	18	1.97	-4.7
<i>magnirostris</i> *§	MA	74	82	25	7	0.46	2.8
<i>neglectus</i>	NE	50	73	38	23	1.05	-3.5
<i>occipitalis</i> *§	OC	72	92	30	8	2.69	1.4
<sup>4</sup> <i>proregulus</i> *	PR	92	122	31	16	5.71	-3.6
<sup>4</sup> <i>chloronotus</i> *§	CL	75	92	34	22		-3.9
<i>pulcher</i> *§	PU	74	105	40	18	2.33	-1.0
<i>reguloides</i> *§	RE	78	120	38	12	4.79	-1.0
<i>schwarzi</i>	SW	95	105	28	10	2.03	3.3
<i>sibilatrix</i>	SI	-17	35	15	-13	7.15	2.4
<i>subviridis</i>	SV	70	76	35	30	1.51	-2.3
<sup>5</sup> <i>trochiloides</i> *§	TD	79	97	30	15	6.36	1.0
<sup>5</sup> <i>nitidus</i> *	NI	74	82	15	7		0.3
<sup>5</sup> <i>plumbeitarsus</i> *	PL	94	110	20	8		0.1
<sup>5</sup> <i>viridanus</i> *	VI	74	111	28	10		0.3
<i>trochilus</i> *	TU	-17	42	10	-30	21.06	1.4
<i>tyleri</i> *	TY	73	76	27	16	0.20	-0.8

\* Taxa included on the phylogeny from Price et al. (1997). <sup>1</sup> *bonelli* group; <sup>2</sup> *collybita* group; <sup>3</sup> *inornatus* group; <sup>4</sup> *proregulus* group; <sup>5</sup> *trochiloides* group; § Sympatric taxa breeding in western Himalaya.

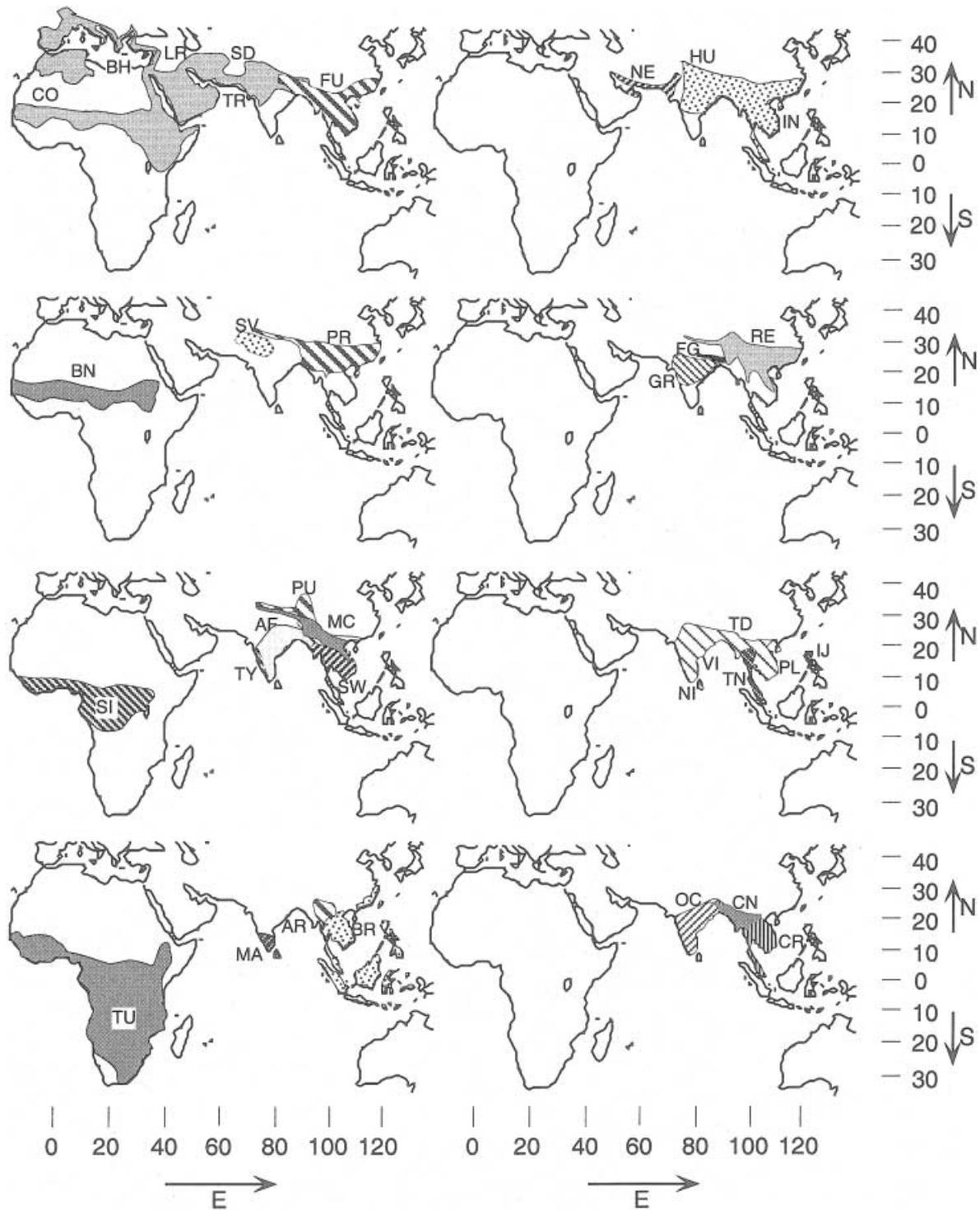


Fig. 1. Non-breeding season distributions of *Phylloscopus* species. Subspecies level boundaries are uncertain for several taxa, and the figure shows the total range of the species with approximate locations of subspecies marked. See Table 1 for key to species abbreviations.

Ripley (1983), Lekagul and Round (1991), Cramp (1992), Baker (1997), and Rasmussen (1998). These ranges were transcribed on to equal area maps and the

area measured using Canvas, v.3.5 for Macintosh (Fig. 1). We also recorded the longitudinal and latitudinal extremes for each species (Table 1).

For breeding distributions and body masses we use data from Price et al. (1997). Other morphological measurements (lengths of wing, tail, tarsus, and beak) were taken from Williamson (1962). For three taxa whose body masses are not available we estimated mass from a multiple regression of mass on the other morphological measurements. We extracted the first principal component (PC1) from the correlation matrix of taxon mean values. Correlations of PC1 scores with the univariate measures varied from 0.69 (tarsus) up to 0.96 (body mass), and we therefore treat PC1 as a measure of body size. Explanations for Bergmann's rule have often been related specifically to body mass. The very high correlation of PC1 with body mass in this dataset indicates that they can be used interchangeably.

Comparative studies have undergone something of a revolution. Because closely related species are demonstrably similar in many traits, it has been argued that they are not statistically independent, resulting in inflated p-values (Felsenstein 1985). This argument depends on the statistical model of evolution employed. In the commonly used model, that of Brownian motion evolution, the use of the species mean values is incorrect, and a correction can be used based on an estimated phylogeny (the method of independent contrasts, Felsenstein 1985). However, an alternative, and we believe more reasonable statistical model is a "niche filling" model (Price 1997, Harvey and Rambaut 2000). If the "niche-filling" model is appropriate, the species values are independent, even though related species are similar (Price 1997, Harvey and Rambaut 2000) but the contrasts are now statistically dependent. We therefore place most stock in results from the species' mean values, but we also present results from the independent contrast comparative method. To do this we used the phylogeny for 30 taxa in Price et al. (1997) and set all branch-lengths equal, which is equivalent to a punctuational model of evolutionary change (Garland et al. 1992). We term correlations between the calculated contrasts "contrast correlations".

We separately analyzed nine *Phylloscopus* species that breed sympatrically in the western Himalaya (Price et al. 1997) and for which we are able to compare time of breeding. We obtained information on breeding date from Baker (1933), who recorded dates of egg collections, and Price and Jamdar (1991a), who presented information on fledging dates for seven of the species.

We also studied geographical variation in body size within a single common, widely, distributed species complex (*Phylloscopus trochiloides*). We measured museum specimens at the Bombay Natural History Society (measurements by MK) and the British Museum (measurements by TP). Results were not affected by who made the measurements, as assessed by including

museum collection as a covariate in the analyses. All specimens were collected in the Indian subcontinent during mid-winter (November–February, N = 107). We measured wing, tail, tarsus, beak length, beak width, and beak depth as in Price (1991). We extracted the first PC1 from the correlation matrix of these measurements. Correlations of PC1 with the univariate measures varied from 0.53 (beak width) to 0.79 (wing length), and we therefore use PC1 as a measure of body size (body mass was unavailable). We recorded the date and location (latitude and longitude) of collection for each specimen. We then conducted regressions of body size vs non-breeding season latitude for the whole *P. trochiloides* complex, and also separately within the two subspecies (*P. t. trochiloides* and *P. t. viridanus*) for which sufficient sample sizes were available. For *P. t. nitidus* which over-winters in south India and Sri Lanka we obtained dates and locations for an additional 74 specimens collected between August–October, in order to map this taxon's autumn migration across south Asia.

## Climate

We used climatological tables published by the India Meteorological Department (Anon. 1967) to obtain monthly temperature and rainfall data (averaged over 30 yr, 1931–1960) for different locations across India.

## Latitudinal comparison of arthropods and foraging

To compare food availability at different latitudes, we worked extensively at two sites in India: Mundanthurai (8°40'N, altitude 200 m) in the southern Western Ghats (see Katti and Price 1996), and Naina Devi (31°N, altitude 300 m) in the Himalayan foothills (see Gross and Price 2000). Both study sites have similar deciduous and semi-evergreen forests (Johnsingh and Joshua 1989, Katti and Price 1996, T. Price, unpubl.). We obtained estimates of mid-winter (January) arthropod abundance at these locations by collecting 50 samples from tree and large shrub species (in which the birds were observed foraging). To obtain a sample, we covered a small branch, up to 4 m high, with a large (ca 200 l) polythene bag, broke off the branch, and dropped in a small piece of cotton soaked with chloroform. All arthropods were carefully sorted a few hours later, and collected in alcohol for measurement and identification in the lab. They were subsequently classified into three size classes based on total body length: small: 0–2 mm, medium: 2–6 mm, large: > 6 mm. Details of size distributions at Mundanthurai were presented in Katti and Price

(1996). Here we focus on the proportion of large items. We estimated arthropod abundance at Mundanthurai during five winters (1993–1997) and at Naina Devi during two winters (1994 and 1998). We also worked more briefly at two other sites near Bombay (ca 18°N), using similar methods, in January 1998 (see Gross and Price 2000). Although the data are somewhat limited, we considered thorough analysis at single sites to be preferable to more widespread, less thorough, investigations across multiple sites.

We include results on the temporal appearance of arthropods in the breeding season based on a study in Kashmir (Price 1991, Price and Jamdar 1991b). In this case arthropods were collected by striking a birch branch with a stick and counting the numbers falling on to a small tray below, and sorting into the three size classes. Collections from 20 branches were made on any one day at any one locality. Collections were made from May–July in 1986 (N = 61 collections) and 1987 (N = 8 collections). Results were very similar in the two years, which are lumped together.

Warblers were observed in January and February of 1994 at Mundanthurai and Naina Devi and their foraging techniques recorded. We followed individual birds and recorded their first successful foraging attempt (Price 1991). Size of prey was classified as large (visible in beak, requiring mandibulation prior to swallowing) or small.

## Results

### Across species patterns

The 35 taxa of *Phylloscopus* that we studied over-winter largely at tropical and sub-tropical latitudes (Fig. 1), with latitudinal extremes of about 50°N (*P. collybita*) and 30°S (*P. trochilus*). Across taxa, midpoint of non-breeding season latitude is negatively correlated with body size (PC1; see Fig. 2a;  $r = -0.41$  for 35 taxa,  $p < 0.05$ ; contrast correlation:  $r = -0.29$ ,  $0.1 > p > 0.05$ ). Larger bodied taxa winter at more southern latitudes than smaller bodied taxa. For comparison we also show the pattern in the breeding season which is in the opposite direction – larger bodied taxa tend to breed at higher latitudes – but the trend is weaker and not statistically significant (Fig. 2b,  $r = 0.32$ ,  $N = 35$  taxa,  $p > 0.1$ ).

The three main wintering areas (Africa, south Asia and south-east Asia) differ greatly in the latitudinal extent of land mass available to migrants. In order to control for these geographical differences, we calculated partial correlations of non-breeding season latitude with both body size (PC1) and midpoint of non-breeding season longitude, holding the other variable fixed. We found no effect of midpoint of non-breeding season longitude on latitudinal position (partial  $r = 0.13$ ,  $p > 0.4$ ), while that for body size remained significant (partial  $r = -0.40$ ,  $p < 0.05$ ). The association of body size

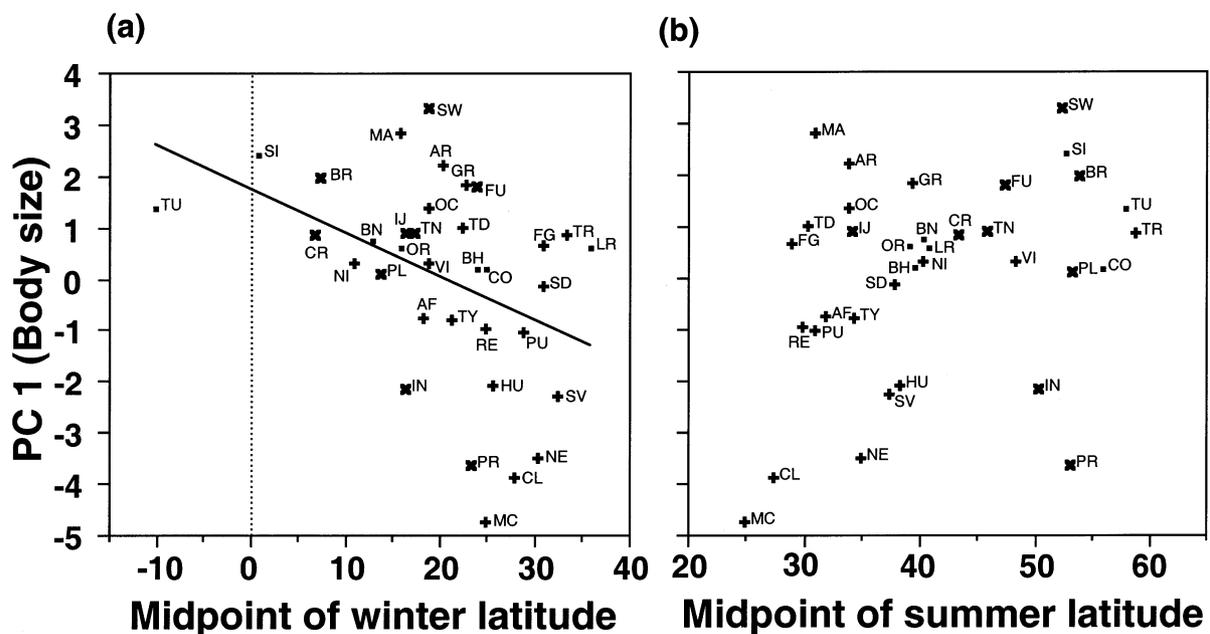


Fig. 2. Correlations of body size (taxon mean values) with (a) non-breeding season latitude, and (b) breeding season latitude (data from Price et al. 1997). The different symbols indicate the three wintering areas: Africa (■), south Asia (+) and south-east Asia (x). See Table 1 for key to species abbreviations.

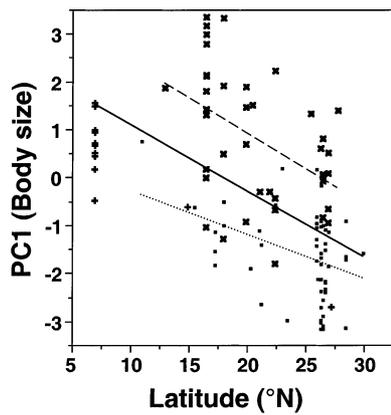


Fig. 3. Correlation of non-breeding season latitude with body size for the *P. trochiloides* complex. The different symbols indicate three different taxa: *nitidus* (+), *trochiloides* (x), and *viridanus* (■).

with latitude thus appears to be independent of the area differences in different geographical regions (Fig. 2).

To compare non-breeding season latitudinal position within a single assemblage of birds all breeding in the same place, we studied the 9 species breeding sympatrically in the western Himalaya (Price et al. 1997), and wintering in India, Myanmar, and Thailand. The negative correlation between body size (PC1) and midpoint of non-breeding season latitude was strong within this group ( $r = -0.72$ ,  $p < 0.05$ ,  $N = 9$ ). The contrast correlation ( $r = -0.43$ ,  $p > 0.1$ ) was not significant. This is an apparent reflection of the fact that large evolutionary changes in body size (and associated latitudinal position) have occurred relatively infrequently in the group (Richman and Price 1992).

### Within species patterns

Among museum specimens of *P. trochiloides* collected in November-February, body size (PC1) was negatively correlated with the latitude at which they were collected. This is true for the whole *P. trochiloides* complex ( $r = -0.54$ ,  $p < 0.001$ ,  $N = 107$ ; see Fig. 3), and within two taxa considered separately: *P. t. trochiloides* ( $r = -0.46$ ,  $p < 0.01$ ,  $N = 40$ ), and *P. t. viridanus* ( $r = -0.38$ ,  $p < 0.01$ ,  $N = 54$ ). Thus, the reversed Bergmann's rule pattern of body size distribution holds within this taxon, as well as across taxa of *Phylloscopus*.

### Resources

We have previously shown a strong correlation between food availability and over-winter persistence of *Phylloscopus trochiloides* at Mundanthurai, southern India, and also that food availability correlates with rainfall (Katti and Price 1996). The common subspecies at this

site, *P. t. nitidus*, arrives relatively late in the winter season, and its passage through the Indian subcontinent is correlated with the withdrawal of the monsoon (Fig. 4). The arrival of *P. trochiloides* on the breeding grounds in Kashmir (early June) is correlated with the appearance of large arthropods, its preferred prey (Price 1991; see Fig. 5). Together these observations suggest a role for resources in determining the presence and abundance *P. trochiloides* at any particular site in India.

We compared two sites in mid-winter (January and February) across multiple years. During this time *P. trochiloides* is the commonest species at Mundanthurai (8°40'N; Katti and Price 1996) but absent from Naina Devi (31°N), where it is replaced by the smaller *P. humei* (Gross and Price 2000). To statistically compare arthropod abundances at Naina Devi and Mundanthurai we used year as the replicate. Although Naina Devi appeared to have fewer arthropods, it did not significantly differ from Mundanthurai (Fig. 6,  $t_5 = 1.33$ ,  $p = 0.24$ ). Use of year as replicate is a highly conservative procedure, especially because fluctuations between years at a single site can be large (Katti and Price 1996). Results using bag as replicate in 1994, when both sites were studied, show that Naina Devi had significantly fewer arthropods than Mundanthurai ( $t_{97} = 3.29$ ,  $p = 0.001$ ). In addition biomass is higher at Mundanthurai (see below).

Naina Devi had far fewer large arthropods ( $> 6$  mm body length, using year as replicate  $t_5 = 2.83$ ,  $p < 0.05$ ) than Mundanthurai. The fraction of all arthropods in the collections which were large was also much lower at Naina Devi than Mundanthurai (arc-sine transformation,  $t_5 = 6.63$ ,  $p < 0.01$ ). *Phylloscopus trochiloides* at Mundanthurai regularly takes large prey (17% of observations on different individual birds,  $N = 75$  observations), whereas *P. humei* at Naina Devi was never seen to capture large prey (0%,  $N = 97$  observations). The distribution of the two species corresponds well with the distribution of large prey. We studied two other sites in 1998, and their resource distributions also predict the presence of large and intermediate species, as are found at those sites (Fig. 6; Gross and Price 2000).

### Alternative explanations

Other associations of body size with behavioral and life-history traits may also affect spatial distributions.

#### Migration distance

Across taxa, midpoint of non-breeding season latitude is negatively correlated with midpoint of breeding latitude ( $r = -0.40$ ,  $p < 0.05$ ,  $N = 35$ ,  $r$  (contrasts) =  $-0.15$ ,  $p > 0.05$ ,  $N = 30$ ). Species which breed farther north tend to winter farther south (Fig 2 and 7). Species wintering in Africa have the greatest range of migration

distances and show this pattern most clearly (Fig. 7). Further, body size is positively correlated with migration distance in this group (Gaston 1974, Marchetti et al. 1995). Larger species may be able to migrate further from their breeding grounds, and hence end up at lower latitudes. Some small species (*P. proregulus*, *P. inornatus*) do migrate very long distances (Gaston 1974), however, so body size is unlikely to be a strong constraint on the evolution of migration distance (see Blackburn et al. 1999). Partial correlations of non-breeding season latitudinal mid-point with body size and breeding season latitudinal mid-point were both close to significance (partial  $r = -0.33$  for body size,

$-0.31$  for breeding latitude,  $p \approx 0.06$  for both). This suggests an independent effect of body size on non-breeding season position even if migration distance is accounted for.

#### Breeding date

In the Himalayan community, there are correlations of body size with breeding date. Smaller species breed earlier than larger species. This is seen both in the data set of Baker (1933);  $r = 0.91$ ,  $p < 0.01$ ,  $N = 8$  species,  $r(\text{contrasts}) = 0.86$ ,  $p < 0.01$ , and Price and Jamdar (1991a);  $r = 0.89$ ,  $p < 0.01$ ,  $N = 7$  species,  $r(\text{contrasts}) = 0.53$ ,  $0.1 > p > 0.05$ . One explanation may be

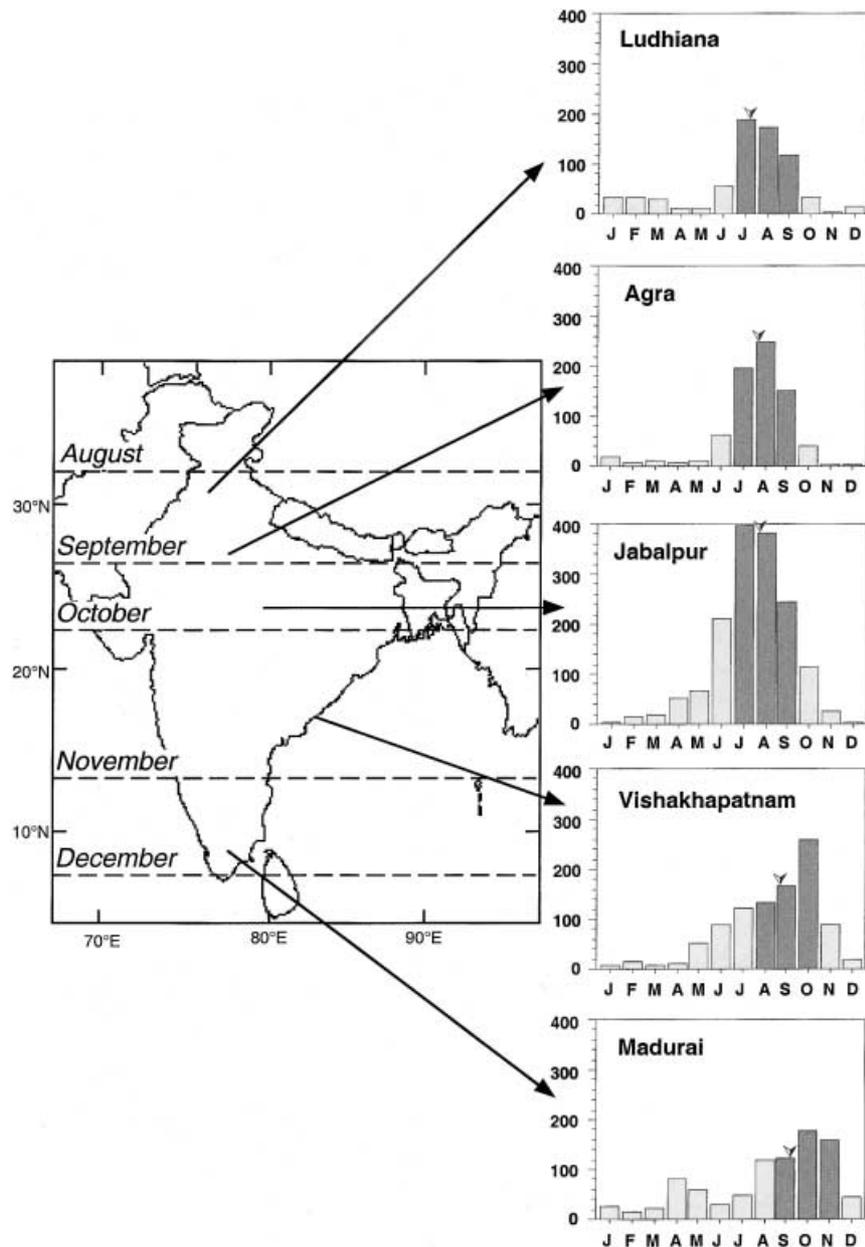


Fig. 4. Median latitude by month for *P. trochiloides nitidus* specimens in the collections of the British Museum and the Bombay Natural History Society (dashed lines). Histograms show rainfall averaged over 30 yr for five cities (Anon. 1967). Arrow marks the date on which 50% of the annual rainfall total was reached at each city. Shaded bars represent the three wettest months.

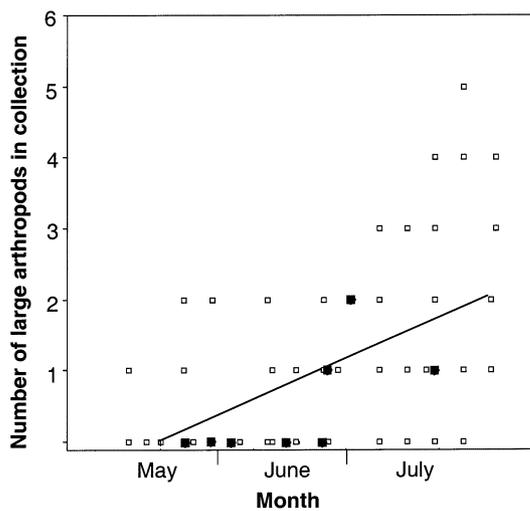


Fig. 5. Association of date in season with number of large arthropods, predominantly caterpillars (> 6 mm and < 20 mm) collected in 20 beats of birch branches made during the breeding season in Kashmir, India. Collections on the same day are made from localities at least 1 km apart. □ 1986 collections, ■ 1987 collections. Line is the least squares linear regression.

that smaller species, by wintering further north are able to more rapidly return to the breeding grounds (see Greenberg 1980, Gauthreaux 1982, Ketterson and Nolan 1983, Nolan and Ketterson 1990). However, large species are commonly found at nearby low elevations in the Himalayas long before they arrive on the breeding grounds (Price and Jamdar 1991a).

In Kashmir the relatively large *P. trochiloides* arrives on the breeding grounds only in June, whereas smaller species are present at the same site throughout May (Price and Jamdar 1991a). On the breeding grounds large arthropods increase in abundance through the

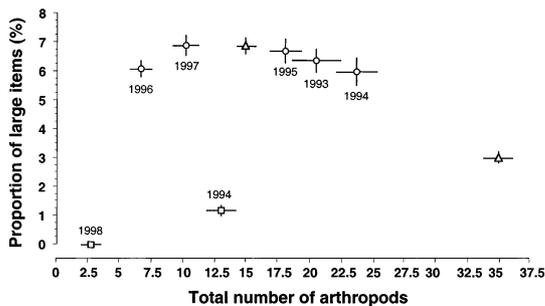


Fig. 6. Comparison of total arthropod abundance, and proportion of large arthropods at Mundanthurai, south India (○) and Naina Devi, north India (□). We also show two sites (△) near Bombay, south-central India, studied in 1998 (Gross and Price 2000). At both these sites a relatively large species *P. trochiloides* outnumbers a relatively small species *P. humei*. At the site with many arthropods, an intermediate sized species, *P. tyleri*, is abundant (Gross and Price 2000). Values are means  $\pm$  1 SE for 50 bags collected. All collections were made in January, except in 1998 at Naina Devi when the collection was in February.

breeding season (Fig. 5; the correlation between time of year and the numbers of large prey is  $r = 0.56$ ,  $N = 69$ ,  $p < 0.001$ ; and the correlation between time of year and the proportion of all arthropods that are large (arc-sine transformed) is  $r = 0.49$ ,  $N = 69$ ,  $p < 0.001$ ). *Phylloscopus trochiloides* appears on the breeding grounds only as large prey become common. These results are consistent with the idea that the temporal appearance of species on their breeding grounds is less restricted by distance from the wintering grounds than by the temporal appearance of suitable prey.

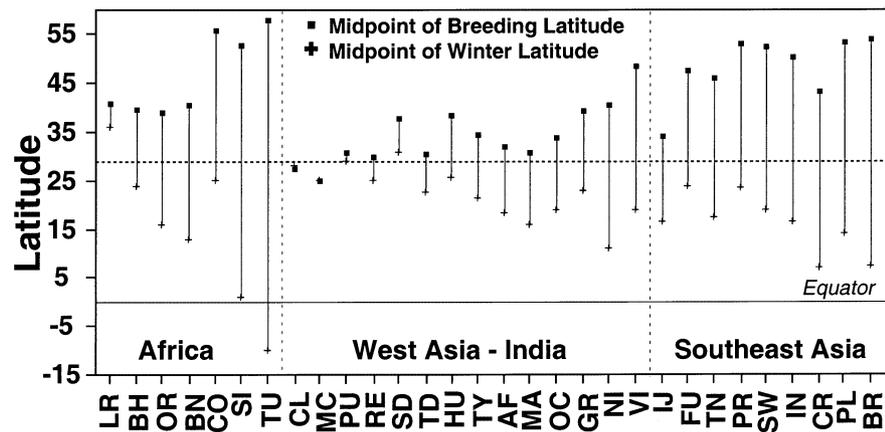
## Discussion

The results in this paper are consistent with the general thesis that the spatial distribution of body sizes is determined by the spatial distribution of resources (McNab 1971). There are two components. First, larger prey occur in the south. Second, the south has a more benign climate (Anon. 1967), a higher abundance of large prey, and a longer day (day-length in mid-winter is 1.5 h longer at the southern site (Mundanthurai) than the northern site (Naina Devi)). This implies that the south generally has more food available to a bird.

The importance of resources in determining species' distributions is suggested by a more detailed study of the *P. trochiloides* species complex. First, across years at Mundanthurai, there is a strong correlation between *P. trochiloides* population size and resource abundance, itself a reflection of rainfall (Katti and Price 1996). Second, the temporal appearance and disappearance of birds in different locations tracks resources: migration through the Indian subcontinent to the winter quarters follows peaks in rainfall, and arrival on the breeding grounds is correlated with appearance of large prey. Rainfall tracking by other migrant species has also been demonstrated in India by Gaston (1976) and in Africa by Moreau (1972) and Pearson and Lack (1992). In Africa (Lack 1986), the New World tropics (Janzen 1993), and the Galápagos (Price 1985), the appearance of caterpillar flushes has been directly related to rainfall; caterpillars form an important large prey item in *P. trochiloides*' diet.

While a lack of large prey in the north may account for the absence of the large species, small prey are present in the south, and climatic conditions appear to be more benign in the south. Therefore the absence of small species from the south cannot be attributed to resources per se. Several observations suggest that competition is likely to be involved, with the larger species excluding the smaller species from the more southerly locales. First, *P. humei* (small) and *P. trochiloides* (large) regularly interact agonistically in the breeding season in Kashmir (Price 1991) and where they co-occur in central India in the non-breeding season (Gross and Price 2000). Second, *P. humei* and *P. trochiloides*

Fig. 7. Latitudinal migration distances for 30 taxa of *Phylloscopus* in the three wintering areas. Figure shows midpoints of breeding and wintering latitudes connected by a line indicating migration distance for each taxon. Taxa are ordered by increasing migration distance within each area. Note that migration distances in south Asia are smaller than in the other two regions. See Table 1 for key to species abbreviations.



are very similar ecologically, and in many areas one or the other is the only small insectivorous species occupying the tree crowns (Gross and Price 2000). Third, within the *P. trochiloides* complex the different subspecies react aggressively towards each other and hold mutually exclusive territories where they co-occur (Katti 1997); the subspecies also sort latitudinally by size, with the smaller body sized taxa occurring at higher latitudes. This suggests a role for direct competition in determining non-breeding season range limits, with the larger species excluding the smaller from more productive areas.

Our observations on resource distributions in the non-breeding season are based on a comparison of just four sites, although two were replicated across years. The pattern we found is consistent with that expected if resource distributions are affecting body size. This is the first attempt we are aware of that relates resources to latitudinal variation in body size, although Schoener (1971) argued that the greater availability of larger insects in the tropics (as found by Schoener and Janzen 1968) supported the larger number of larger-billed insectivorous birds in the tropics. More recent studies have found larger arthropod body sizes in the tropics for select groups (e.g. Lepidoptera in Australia and Africa, Barlow 1994) but there are exceptions for some groups and/or localities (Schoener and Janzen 1968, Hawkins and Lawton 1995). Even if such a general size gradient turns out not to be true year round, our argument requires only that such a gradient exist (as we found) during the non-breeding season.

An alternative explanation for the presence of small species in the north is that small species breed earlier than the larger species, and by wintering farther north they can rapidly return to the breeding grounds. The need to return early to the breeding grounds has been advanced to partially account for the spatial patterns of wintering New World warblers (Greenberg 1980) and body size clines in wintering dark-eyed juncos, *Junco hyemalis* (Nolan and Ketterson 1990). In the *Phyllosco-*

*pus*, however, some early breeding, small species make very long migratory journeys (to northern Siberia from south-east Asia; Gaston 1974), suggesting that wintering far away does not necessarily prevent an early return to breeding grounds. In addition late breeding species are regularly seen in the foothills of the Himalaya long before their breeding season commences (Price and Jamdar 1991a). Our observations on the temporal distribution of resources on the breeding grounds imply that smaller species return to the breeding grounds earlier than the larger ones because their food becomes available sooner. Many of the correlations between breeding and non-breeding season ranges can be explained in terms of responses to different spatial distributions of resources in the non-breeding season and the temporal appearance of resources in the breeding season.

Climatic explanations for body size variation have usually sought to explain Bergmann's rule pattern of larger species further north (James 1970, 1991, Searcy 1980, Murphy 1985). In India climate is colder in the north (Anon. 1967). Near our study areas mean minimum temperatures in January over 30 yr were 1.9°C (Ludhiana, north) and 18.7°C (Madurai, south) (Anon. 1967). Temperature is also more variable in the north. Over 30 yr, extreme temperatures in January differed by 31°C at Ludhiana but only by 18°C at Madurai (Anon. 1967). The usual explanations for latitudinal clines in body size based on climate and climate variability are rejected because climate follows the directions expected from Bergmann's rule models (e.g. Searcy 1980, Murphy 1985, James 1991), but the size of birds does not.

A popular climate-based model for Bergmann's rule is that it arises because larger animals lose less heat per unit body mass than smaller animals (Bergmann in James 1970, Searcy 1980). This explanation has been criticized because larger animals lose absolutely more heat and hence require absolutely more resources (McNab 1971), and because there are other more efficient

ways to deal with heat loss, e.g. by increasing feather density (Ashton et al. 2000). We suggest that spatial variation in prey size and resource density may prove to be a more general mechanism in accounting for body size distributions, even in those cases where Bergmann's rule is upheld. As noted by McNab (1971) resource distributions alone cannot account for all the patterns, and competitive interactions are likely to modify the distribution of resources actually available to individuals, affecting either body size, spatial distributions, or both.

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