

The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator?

MARCEL CARDILLO*

Department of Zoology and Entomology, University of Queensland, Brisbane 4072, Australia

Summary

1. Latitudinal variation among species in life-history traits is often suggested to contribute to high tropical species richness. However, traditional methods of analysing such variation rarely control for phylogeny and latitudinal range overlap between species, potentially giving misleading results.

2. Using a method of pairwise independent contrasts which overcomes these problems, I tested for latitudinal variation among bird species in a number of traits which have been linked, theoretically or empirically, with both latitude and species richness.

3. This method indicates strong support for Rapoport's Rule and decreasing clutch size towards the equator in both hemispheres, but only partial support for decreasing body size and ecological generalism towards the equator.

4. Indirect measures of sexual selection (sexual dichromatism and size dimorphism) show no variation with latitude; an apparent increase in dichromatism towards the equator is shown to be an artefact of phylogeny.

5. Many of the associations between life history and latitude were not detected by traditional cross-species analyses, highlighting the importance of incorporating phylogeny and overlap in studies of geographical life-history variation. Establishing associations between life-history traits and latitude does not prove, but is a necessary prerequisite for, a link between these traits and latitudinal diversity gradients.

Key-words: birds, geographical range, phylogenetically independent contrasts, species richness.

Journal of Animal Ecology (2002) **71**, 79–87

Introduction

Why are there so many species in the tropics? One general explanation is that latitudinal gradients in environmental conditions influence speciation or extinction rates, either directly or by modifying species' life histories. Thus, many explanations for latitudinal diversity gradients are based on the assumption of consistent latitudinal variation in life-history attributes, for example geographical range size or ecological specialization (Fischer 1960; Pianka 1966; Rohde 1992; Rosenzweig 1995; Rohde 1999; Gaston 2000). However, the first step in linking a life-history trait to latitudinal diversity gradients is to demonstrate convincingly that the trait itself is associated with latitude. Unfortunately, the vast majority of cited evidence for latitudinal variation in life-history traits among species comes from studies which suffer from a number of analytical problems.

Often, geographical elements such as gridcells, lines of latitude or latitudinal bands are used as datapoints (e.g. Stevens 1989), but these are non-independent because many species are counted repeatedly. This form of non-independence is overcome by the midpoint method, where each latitudinal band includes only those species whose latitudinal midpoint falls within that band (Rohde, Heap & Heap 1993), or by the cross-species method, which treats each species as an independent datapoint (e.g. Letcher & Harvey 1994; Blackburn & Gaston 1996a, 1996b). However, these approaches still suffer from two additional potential problems.

First, they fail to control for the possible confounding effects of phylogeny (Pagel, May & Collie 1991). This is important because closely related species are likely to be more similar in their biology than more distantly related species due to more recent common ancestry (Harvey & Pagel 1991), and are more likely to inhabit the same geographical region. This means that an apparent latitudinal gradient in a life-history trait may result from changing representation of different phylogenetic groups across latitudes, rather than any

*Present address: School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK. E-mail: mcardillo@sussex.ac.uk

mechanistic association between latitude and life history (Cushman, Lawton & Manly 1993; Blackburn & Gaston 1996a). Hawkins & Lawton (1995), for example, found that geographical body size variation among butterfly species could be attributed mostly to the changing representation of different families at different latitudes. Under traditional methods of analysis, therefore, it is difficult to rule out phylogeny as an explanation for latitudinal variation in life history.

The second problem is that traditional methods fail to consider latitudinal overlap of geographical ranges. The latitudinal position a species occupies is a function not only of the latitudinal midpoint, but also the north–south extent of its geographical range. Two species may differ in their latitudinal midpoints, but the latitudinal range of one species may largely or entirely overlap that of the other (Fig. 1). In such cases, populations of both species will be subject largely to similar latitude-related environmental conditions. Within any given taxon, such cases are probably very common because closely related species will tend to inhabit the same geographical regions. Therefore, analyses using the midpoint or cross-species methods may be prone to unusually high Type 2 statistical error. Ideally, comparisons between species should take into account not only the difference in latitudinal midpoints, but the degree to which the latitudinal ranges of species overlap.

Several previous studies have applied some form of phylogenetic control in measuring latitudinal gradients in life-history traits (Pagel *et al.* 1991; Letcher & Harvey 1994; Taylor & Gotelli 1994; Blackburn & Gaston 1996b; Edwards & Westoby 1996; Gaston & Blackburn 1996; Cowlshaw & Hacker 1997; Blackburn, Gaston & Lawton 1998), but none have addressed explicitly the problem of latitudinal range overlap. In this paper I present an analysis which simultaneously overcomes these two problems. I use pairwise phylogenetically

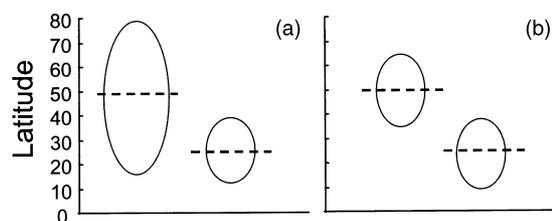


Fig. 1. The problem of latitudinal overlap in selecting latitudinally separated pairs of species. The ovals represent the geographical ranges of hypothetical pairs of closely related species. In (a), the two species are not considered sufficiently latitudinally separated because the latitudinal range of one species lies entirely within that of the other, so populations of the two species are largely subject to the same latitude-related environmental factors. The traditional method of considering only the distance between latitudinal midpoints (dashed lines) may therefore lead to high Type 2 error rates. In (b), there is minimal overlap between the two species, so they can more safely be considered latitudinally separated. In this study, comparisons were only selected if midpoints differed by at least 10° and the two ranges overlapped no more than 25% of the latitudinal extent of either species.

independent contrasts (Felsenstein 1985; Harvey & Pagel 1991) to test for latitudinal variation among bird species in the following traits which have been linked, theoretically or empirically, with both species richness and latitude.

1. Latitudinal extent of geographical ranges. Stevens (1989) suggested that decreasing latitudinal range extent towards the equator (Rapoport's Rule) inflates species richness in the tropics due to spillover of species beyond their usual range limits. Latitudinal range extent may also be a proxy for ecological specificity, which may influence rates of speciation or extinction (see below).

2. Body size. Decrease in body sizes towards the equator associated with Bergmann's Rule (e.g. James 1970; Blackburn & Gaston 1996a; Gaston & Blackburn, 2000) may increase rates of cladogenesis if small body size is associated with higher speciation or lower extinction rates (e.g. Hutchinson & MacArthur 1959; Dial & Marzluff 1988).

3. Clutch size. Reduced clutch size in the tropics (Lack 1954) may result in per-species energy requirements being lower in the tropics, which in turn may lead to higher species richness due to reduced extinction rates or by enabling more species to coexist in a given area (MacArthur 1965).

4. Sexual selection. Moller (1998) predicted that increased parasite impact on host fitness in the tropics should lead to stronger parasite-mediated sexual selection and more extravagant sexual ornamentation at lower latitudes. The theoretical link between sexual selection and speciation is long-standing (Darwin 1871; Lande 1981), and recent empirical tests support this link (Barracough, Vogler & Harvey 1998; Owens, Bennett & Harvey 1999).

5. Ecological specificity. Tropical species have long been assumed to utilize a narrower range of habitat and food types than temperate species (e.g. Dobzhansky 1950; MacArthur 1969; but see Price 1991). Specialization or niche restriction has been suggested to increase species richness by enabling greater coexistence (Hutchinson & MacArthur 1959; Hutchinson 1959; MacArthur 1965) or increasing the likelihood of speciation (see Cracraft 1985).

This is not intended to be a complete list of life-history traits which potentially contribute to high tropical species richness. The traits examined here are those which can be measured relatively accurately and for which data are readily available for a wide range of bird species. Because few southern hemisphere examples exist for some well-known patterns, such as Rapoport's Rule (Rohde 1996; Gaston, Blackburn & Spicer 1998) or the decrease in clutch size towards the equator (Yom-Tov 1994), I examine patterns both worldwide and within each hemisphere. I assume that if life history is not independent of latitude, then pairs of closely related species which differ in the latitudinal positions of their geographical ranges should also differ with respect to life-history traits. The simple question

addressed here is, do life-history traits differ more often than expected by chance, and in predicted directions, among latitudinally separated pairs of bird species?

Materials and methods

SELECTION OF SPECIES PAIRS

From published species-level phylogenies of bird taxa, I identified 69 phylogenetically independent pairs of species (contrasts) in which the two species differed in the latitudinal position of their breeding ranges (see Appendix I for a list of the species pairs and references for the phylogenies used). Species were chosen so as to maximize the number of contrasts from each phylogeny which were suitable for inclusion in this analysis, and for which data on the relevant life-history traits were obtainable for both species. Contrasts were chosen before life-history data were collected, minimizing the possibility of bias in choosing contrasts which varied with latitude in the traits of interest.

To ensure a sufficient degree of latitudinal separation between the two species in each contrast, two criteria were applied: (1) the latitudinal midpoints of the geographical ranges of the two species must be separated by at least 10° of latitude, regardless of hemisphere, and (2) the amount of latitudinal overlap between the two ranges must be no more than 25% of the latitudinal extent of either species. In most cases I was able to find contrasts in which there was very little or no latitudinal overlap between the two species' ranges.

LIFE-HISTORY VARIABLES

For each species I recorded latitudinal range extent, mean female mass, mean clutch size, two indirect measures of sexual selection (sexual size dimorphism and sexual plumage dichromatism), habitat specificity and food specificity, using a wide range of published sources (data set and references are available on request). Where differing values were given by different sources, or a range of values given by one source, I used mean values. Sexual size dimorphism was measured as $1 - [\text{weight of smaller sex} / \text{weight of larger sex}]$. Latitudinal range extent was measured in two ways. The first way was to measure the range of latitudes covered by the species, regardless of hemisphere; thus if a species' range extends from 35° north to 10° south, its latitudinal extent would be 35°. The second way was to measure the entire latitudinal distance between the northern and southern extremes of the species' range; the same species would therefore have a latitudinal extent of 45°. These two measures differ only in species whose ranges cross the equator. Sexual dichromatism was also measured in two ways. First, a species was classed as dichromatic simply if it was represented by separate male and female illustrations in guidebooks, and monochromatic if only one illustration was provided. Secondly, species were subjectively classed as 0 (monochromatic),

0.5 (slightly dichromatic) or 1 (strongly dichromatic). This was carried out with the list of species randomized to lessen the possibility of bias in assigning the level of dichromatism. The number of breeding habitats and food types used by each species were determined using categories modified from Owens *et al.* (1999). The habitat categories used were (1) saltwater, (2) freshwater lakes and wetlands, (3) running water, (4) forest, (5) woodland and scrub and (6) open habitats. The food type categories were (1) vertebrate carrion, (2) vertebrate prey, (3) invertebrate prey, (4) nectar and pollen, (5) fruit and seeds and (6) leaves, stems and roots.

CALCULATION AND ANALYSIS OF CONTRASTS

Contrasts in latitudinal range, dichromatism and habitat and food specificity were calculated additively, as $V_H - V_L$, where V_H and V_L are the values for the higher-latitude species and lower-latitude species, respectively. For female mass, size dimorphism and clutch size, it was inappropriate to calculate contrasts additively because the magnitude of trait values influences the size of the contrast (e.g. the contrast between 80 and 100 is 10 times the size of the contrast between 8 and 10). For these traits, contrasts were calculated as $1 - [V_S / V_G]$, where V_S and V_G are the smaller and the greater of the two values. Contrasts in which the lower-latitude species had the higher trait value were arbitrarily given a negative sign. Under the null hypothesis that life-history traits are independent of latitude, the number of positive and negative contrasts, and their magnitudes, should be approximately equal. I used non-parametric Wilcoxon signed-ranks tests to test for significant departures from this expectation.

To examine whether latitudinal variation in life-history traits occurs both north and south of the equator, I carried out additional tests on northern and southern hemisphere contrasts separately. Northern hemisphere contrasts were defined as those in which both species' geographical ranges lie entirely north of 10° south, and southern hemisphere contrasts were those where both species' ranges lie entirely south of 10° north.

I also compared the results obtained using phylogenetically independent contrasts with those obtained by traditional cross-species analyses. I analysed relationships between trait values and latitudinal midpoint using least-squares regression (logistic regression for sexual dichromatism), treating all species in the dataset as independent observations without controlling for phylogeny. Log-transformation of the continuous variables before analysis gave acceptably normal error distributions and stable variances.

RANDOMIZATION TESTS FOR SAMPLING BIAS

Applying the minimal-overlap criterion for selecting species pairs imposes restrictions on the types of pairs that can be selected, principally that it will be difficult

for two species with large latitudinal ranges to be selected as a pair. Despite this, there ought to be no possibility of sampling bias towards or against a latitudinal effect on latitudinal range generated by this restriction. This is because if there is no real association between latitude and latitudinal range, it should be no more likely for a high-latitude species with large range to be paired with a low-latitude species of small range than for a high-latitude species of small range to be paired with a low-latitude species of large range, or for two species of small range to be paired. To test this formally I carried out a simple randomization test, in which I reshuffled the values for latitudinal midpoint and latitudinal range among the species included in the analyses. I selected randomly, without replacement, one species from the reshuffled list. I then selected further species at random until one was able to be paired with the first species under both of the imposed criteria (described above). Pairs were thus selected until the list

was exhausted. For each pair I calculated the contrasts in latitudinal range and tested for an effect of latitudinal midpoint on latitudinal range, using the same statistical methods as in the main analysis. A significant effect would indicate an artefactual latitudinal trend in latitudinal range caused by the method of choosing species pairs.

Results

Results of Wilcoxon signed-ranks tests for all contrasts (Table 1a) show that the two measures of latitudinal range extent, clutch size, habitat specificity and food specificity show significant positive associations with latitude. In other words, bird species inhabiting higher latitudes are likely to occupy a greater range of latitudes, have a greater north–south geographical distribution, larger clutches and broader ecological niches than their lower-latitude close relatives. Female mass,

Table 1. Associations between latitude and life-history traits among birds (a) worldwide, (b) in the northern hemisphere only, and (c) in the southern hemisphere only. Results are shown for analyses on pairwise phylogenetically independent contrasts (Wilcoxon signed-ranks tests) and for non-phylogenetic cross-species analyses (ordinary least-squares regression, logistic regression for the two measures of dichromatism). Direction of the relationship is shown where $P < 0.1$. All P -values are one-tailed because all hypotheses tested were for unidirectional associations (see Introduction). Latitudinal range 1 is the range of latitudes covered by a species; latitudinal range 2 is the entire north–south extent of a species' range. Dichromatisms 1 and 2 are objective and subjective measures, respectively. Further details are given in the text

Trait	Method of analysis					
	Independent contrasts			Cross-species		
	<i>N</i>	Direction	<i>P</i>	<i>N</i>	Direction	<i>P</i>
(a) Worldwide						
Latitudinal range 1	69	+	0.0004	149	+	0.0004
Latitudinal range 2	69	+	0.03	148	+	0.07
Female mass	35		0.11	88		0.94
Size dimorphism	29		0.15	80		0.22
Clutch size	40	+	< 0.0001	121	+	0.0001
Dichromatism 1	17		0.42	143	–	< 0.0001
Dichromatism 2	26		0.16	143	–	< 0.0001
Habitat specificity	37	+	0.02	147	+	0.04
Food specificity	19	+	0.05	121		0.23
(b) Northern hemisphere						
Latitudinal range 1	28	+	< 0.0001	74	+	0.0001
Latitudinal range 2	29	+	0.0009	74	+	0.0003
Female mass	15		0.15	45		0.98
Size dimorphism	15	+	0.08	42		0.77
Clutch size	13	+	0.007	59	+	0.03
Dichromatism 1	6		0.5	73	–	0.004
Dichromatism 2	8		0.5	71	–	0.003
Habitat specificity	17	+	0.002	57		0.2
Food specificity	6		0.5	45		0.27
(c) Southern hemisphere						
Latitudinal range 1	23	+	0.002	53		0.83
Latitudinal range 2	22	+	0.01	53		0.9
Female mass	22	+	0.02	30		0.35
Size dimorphism	8		0.34	28		0.73
Clutch size	15	+	0.001	44	+	0.006
Dichromatism 1	6		0.17	54		0.45
Dichromatism 2	9	–	0.07	53		0.99
Habitat specificity	10		0.6	50		0.9
Food specificity	8		0.1	42		0.99

sexual size dimorphism and the two measures of sexual dichromatism show no significant variation with latitude. Results of cross-species regressions in which phylogeny is not controlled for are not wholly consistent with the independent contrast results (Table 1a).

In the northern hemisphere (Table 1b), the two measures of latitudinal range extent, clutch size and habitat specificity show highly significant positive associations with latitude. Other traits show no significant associations. In the southern hemisphere (Table 1c), latitudinal range extent and clutch size are also positively associated with latitude. Additionally, female mass becomes significantly positively associated with latitude in the southern hemisphere. Cross-species regressions fail to detect many of the significant associations indicated by the independent contrasts analysis.

Results of the randomization tests for sampling bias in the analyses of latitudinal range are non-significant under Wilcoxon signed-ranks tests, for both measures of latitudinal range ($n = 65$ pairs, $P = 0.11$ and $n = 61$ pairs, $P = 0.45$, respectively). This indicates that the association between latitudinal midpoint and latitudinal range extent is not subject to sampling bias resulting from the method of choosing independent contrasts.

Discussion

This study confirms a number of long-held assumptions of latitudinal variation in life-history traits among bird species (see Introduction), although it does not support the more recent prediction of latitudinal variation in the degree of sexual selection (Moller 1998). Latitudinal variation in life history among species may arise in three ways: (1) natural selection imposed by environmental conditions; (2) selective extinction of species from high-latitude assemblages; and (3) selective recolonization of high latitudes following periods of climate change. This study cannot distinguish between these mechanisms, but the explicit inclusion of phylogeny and latitudinal range overlap in the analyses, and the testing of patterns in both hemispheres, means that it can reject the possibility that patterns have arisen simply through phylogenetic or geographical bias. It appears therefore that latitude does influence many aspects of avian life history which potentially determine rates of speciation or extinction.

There has been little previous evidence for Rapoport's Rule (decreasing latitudinal range extent towards the equator) in the southern hemisphere, most tests having shown equivocal results (Gaston *et al.* 1998; Gaston 1999). This has led to doubts about the generality of Rapoport's Rule and suggestions it may be a relatively local pattern, existing primarily in the northern hemisphere at latitudes above approximately 30–40° (Rohde *et al.* 1993; Rohde 1996; Gaston *et al.* 1998; Gaston 1999). My results, however, suggest that in birds there is indeed a strong Rapoport effect in the southern hemisphere, and that the pattern may in fact

be more general than is currently recognized. The pattern is nevertheless not as strong in the southern compared to the northern hemisphere, most probably because smaller continental land masses result in a more moderate increase in climatic seasonality with latitude (Gaston 1999). This probably explains why the Rapoport effect in the southern hemisphere has been difficult to detect in the past: more sensitive analytical methods which are less prone to Type 2 statistical error are needed to detect the pattern. My results for the southern hemisphere (Table 1c) appear to bear this out: the effect of latitude on latitudinal range is significant when independent contrasts are used, but nonsignificant when cross-species analyses are used.

The results are also strongly supportive of the traditional view that clutch size among bird species increases away from the equator (Lack 1954). As with Rapoport's Rule, however, there have been very few tests for this pattern within the southern hemisphere, and these have indicated either a weak or non-existent effect of latitude on clutch size (Moreau 1944; Yom-Tov 1987, 1994). Again, one possible explanation for this is that none of the previous tests used phylogenetically explicit methods for analysing clutch size variation with respect to latitude, so may have lacked the power to detect patterns. However, my analysis indicates strong latitudinal effects on clutch size in both northern and southern hemispheres, regardless of whether or not phylogenetically independent contrasts are used (although patterns are much stronger when independent contrasts are used, despite greatly reduced sample sizes). Clutch size variation with latitude may therefore be another pattern which is more general than it currently appears. Further studies using appropriate analytical methods are needed to confirm this.

Other results only partly support predicted patterns of latitudinal variation. Female mass increased with latitude in the southern hemisphere, supporting the predictions of Bergmann's Rule (James 1970), but showed no latitudinal effect in the northern hemisphere. Moller (1998) also used independent contrasts to examine bird body size differences across latitudes, and found no body size variation with latitude. Both mine and Moller's results contrast with a large-scale analysis by Blackburn & Gaston (1996a) which showed a strong interspecific decrease towards the equator in mean body size of birds in the New World, in both hemispheres. It is difficult to explain why these results differ, but one possibility is that Blackburn & Gaston's analyses used a different method of controlling for the effect of phylogeny. They did not apply phylogenetically independent contrasts using the method of Felsenstein (1985), but rather they found that the pattern of smaller body size towards the equator was repeated within taxa more often than expected by chance. This minimizes the likelihood that the pattern results entirely from phylogenetic artefact, although Blackburn & Gaston conclude that the lack of a strong association within taxa suggests that there may be

some truth in explanations for latitudinal variation in body size among species based on phylogenetic history.

The predicted patterns of increasing ecological specificity towards the equator were supported in the northern hemisphere, but not the southern hemisphere. If it is assumed that more seasonal or variable climates promote ecological generalism (see Letcher & Harvey 1994), then there are several reasons to expect stronger latitudinal variation in ecological specificity in the northern hemisphere. Land extends to higher latitudes in the northern hemisphere, so bird species are distributed across a wider range of climatic zones. Seasonality is enhanced further by the vast continental land masses of the northern hemisphere: much of the land area of Eurasia and North America is far from the moderating influence of the ocean. Glaciation during the Pleistocene was more extensive and severe in high northern compared to high southern latitudes (Markgraf & Hope 1995), which may have led to selective extinction of species which were more specialized, and hence less tolerant of climatic fluctuation. Finally, high northern latitudes may have been selectively recolonized by ecological generalists following glacial retreat at the end of the Pleistocene (Price, Helbig & Richman 1997). An alternative explanation for the observed increase in ecological specificity towards the equator is that it results not from a real pattern but from sampling bias. Measures of niche breadth often increase with a species' abundance because less abundant species are more likely to be recorded from fewer sites than they actually occupy (Gaston 1994). If tropical species are less abundant than those at higher latitudes, this could create a bias in the number of recorded habitats or food types for any given species. However, this would not explain the lack of an observed latitudinal gradient in niche breadth in the southern hemisphere, unless patterns of latitudinal variation in abundance differed between hemispheres.

The analyses of the two indirect measures of sexual selection (size dimorphism and dichromatism) do not support predicted patterns of latitudinal variation. When cross-species analyses are used, sexual dichromatism increases significantly towards the equator. At first, this does appear to support the prediction of Moller (1998) that increased parasite impact on host fitness in the tropics should lead to stronger parasite-mediated sexual selection and more extravagant sexual ornamentation. However, when phylogeny is controlled for, these relationships disappear, suggesting that the apparent latitudinal variation in dichromatism is due to phylogenetic bias and not to selection for greater dichromatism at lower latitudes. The phylogenetic bias probably stems from the high representation of taxa in my dataset which are largely dichromatic and tend to inhabit low latitudes, particularly the families Bucerotidae (hornbills), Pittidae (pittas) and Maluridae (fairy-wrens).

Overall, the discrepancies between results from independent contrasts and traditional cross-species

analyses indicate the susceptibility of traditional analyses to both Types 1 and 2 statistical error, emphasizing the importance of controlling for phylogeny and range overlap in the analysis of geographical patterns of life history. The results do not prove that the life-history traits associated with latitude contribute to high species richness in the tropics. However, establishing a convincing link between life history and latitude is a necessary prerequisite to any claim that life history underlies latitudinal diversity gradients. It seems clear that the latitude at which a species lives does influence numerous aspects of its life history, which in turn may determine its likelihood of speciating or of going extinct.

Acknowledgements

Many thanks to Ian Owens and Klaus Rohde for comments. I am supported by a University of Queensland Graduate School Award.

References

- Avice, J.C. & Zink, R.M. (1988) Molecular genetic divergence between avian sibling species: king and clapper rails, long-billed and short-billed dowitchers, boat-tailed and great-tailed grackles, and tufted and black-crested titmice. *Auk*, **105**, 516–528.
- Badyaev, A.V. (1997) Altitudinal variation in sexual dichromatism: a new pattern and alternative hypotheses. *Behavioral Ecology*, **8**, 675–690.
- Barracough, T.G., Vogler, A.P. & Harvey, P.H. (1998) Revealing the factors that promote speciation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **353**, 241–249.
- Blackburn, T.M. & Gaston, K.J. (1996a) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.
- Blackburn, T.M. & Gaston, K.J. (1996b) Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **351**, 897–912.
- Blackburn, T.M., Gaston, K.J. & Lawton, J.H. (1998) Patterns in the geographic ranges of the world's woodpeckers. *Ibis*, **140**, 626–638.
- Blondel, J., Catzeflis, F. & Perret, P. (1996) Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *Journal of Evolutionary Biology*, **9**, 871–891.
- Brown, D.M. & Toft, C.A. (1999) Molecular systematics and biogeography of the cockatoos (Psittaciformes: Cacatuidae). *Auk*, **116**, 141–157.
- Christidis, L. & Schodde, R. (1992) Relationships among the birds-of-paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae): protein evidence. *Australian Journal of Zoology*, **40**, 343–353.
- Christidis, L. & Schodde, R. (1997) Relationships within the Australo-Papuan fairy-wrens (Aves: Malurinae): an evaluation of the utility of allozyme data. *Australian Journal of Zoology*, **45**, 113–129.
- Cowlishaw, G. & Hacker, J.E. (1997) Distribution, diversity, and latitude in African primates. *American Naturalist*, **150**, 505–512.
- Cracraft, J. (1985) Biological diversification and its causes. *Annals of the Missouri Botanical Gardens*, **72**, 794–822.
- Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.

- Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- Dial, K.P. & Marzluff, J.M. (1988) Are the smallest organisms the most diverse? *Ecology*, **69**, 1620–1624.
- Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.
- Edwards, W. & Westoby, M. (1996) Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. *Journal of Biogeography*, **23**, 329–338.
- Erritzoe, J. & Erritzoe, H.B. (1998) *Pittas of the World*. Butterworth Press, Cambridge.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- Fischer, A.G. (1960) Latitudinal variation in organic diversity. *Evolution*, **14**, 64–81.
- Friesen, V.L. & Anderson, D.J. (1997) Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative models of speciation. *Molecular Phylogenetics and Evolution*, **7**, 252–260.
- Friesen, V.L., Baker, A.J. & Piatt, J.F. (1996) Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Molecular Biology and Evolution*, **13**, 359–367.
- García-Moreno, J., Arctander, P. & Fjeldsa, J. (1999a) A case of rapid diversification in the Neotropics: phylogenetic relationships among *Cranioleuca* spintails (Aves, Furnariidae). *Molecular Phylogenetics and Evolution*, **12**, 273–281.
- García-Moreno, J., Arctander, P. & Fjeldsa, J. (1999b) Strong diversification at the treeline among *Metallura* hummingbirds. *Auk*, **116**, 702–711.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Gaston, K.J. (1999) Why Rapoport's Rule does not generalise. *Oikos*, **84**, 309–312.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gaston, K.J. & Blackburn, T.M. (1996) Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology*, **65**, 701–714.
- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Scientific, Oxford.
- Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's Rule: time for an epitaph? *Trends in Ecology and Evolution*, **13**, 70–74.
- Gerwin, J.A. & Zink, R.M. (1989) Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymic perspective. *Wilson Bulletin*, **101**, 525–705.
- Hackett, S.J. (1995) Molecular systematics and zoogeography of flowerpiercers in the *Diglossa baritula* complex. *Auk*, **112**, 156–170.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, **102**, 31–36.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.
- Hutchinson, G.E. & MacArthur, R.H. (1959) A theoretical ecological model of size distribution among species of animals. *American Naturalist*, **93**, 117–125.
- James, F.C. (1970) Geographic size variation and its relationship to climate. *Ecology*, **51**, 365–390.
- Johnson, K.P. & Lanyon, S.M. (1999) Molecular systematics of the Grackles and allies, and the effect of additional sequence (cyt b and ND2). *Auk*, **116**, 759–768.
- Johnson, K.P. & Sorenson, M.D. (1999) Phylogeny and biogeography of Dabbling Ducks (Genus: *Anas*): a comparison of molecular and morphological evidence. *Auk*, **116**, 792–805.
- Joseph, L. & Moritz, C. (1993) Phylogeny and historical aspects of the ecology of eastern Australian scrubwrens *Sericornis* spp.—evidence from mitochondrial DNA. *Molecular Ecology*, **2**, 161–170.
- Kemp, A. (1995) *The Hornbills*. Oxford University Press, Oxford.
- Krajewski, C. & Fetzner, J.W. (1994) Phylogeny of cranes (Gruiformes: Gruidae) based on cytochrome-B DNA sequences. *Auk*, **111**, 351–365.
- Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic characters. *Proceedings of the National Academy of Sciences, USA*, **78**, 3721–3725.
- Letcher, A.J. & Harvey, P.H. (1994) Variation in geographical range size among mammals of the Palearctic. *American Naturalist*, **144**, 30–42.
- MacArthur, R.H. (1965) Patterns of species diversity. *Biological Reviews*, **40**, 510–533.
- MacArthur, R.H. (1969) Patterns of communities in the tropics. *Biological Journal of the Linnean Society*, **1**, 19–30.
- Markgraf, V.M.M. & Hope, G. (1995) Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems – a southern temperate perspective. *Trends in Ecology and Evolution*, **10**, 143–147.
- Moller, A.P. (1998) Evidence of larger impact of parasites on hosts in the tropics: investment in immune function within and outside the tropics. *Oikos*, **82**, 265–270.
- Moreau, R.E. (1944) Clutch size: a comparative study, with special reference to African birds. *Ibis*, **86**, 286–347.
- Owens, I.P.F., Bennett, P.M. & Harvey, P.H. (1999) Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society of London Series B, Biological Sciences*, **266**, 933–939.
- Pagel, M.D., May, R.M. & Collie, A.R. (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *American Naturalist*, **137**, 791–815.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, **100**, 33–46.
- Price, P.W. (1991) Patterns in communities along latitudinal gradients. *Plant–Animal Interactions: evolutionary ecology in tropical and temperate regions* (eds P.W. Price, T.M. Lewisohn, G.W. Fernandes & W.W. Benson), pp. 51–69. John Wiley & Sons, New York.
- Price, T.D., Helbig, A.J. & Richman, A.D. (1997) Evolution of breeding distributions in the old world leaf warblers (genus *Phylloscopus*). *Evolution*, **51**, 552–561.
- Rohde, K. (1992) Latitudinal gradients in species-diversity – the search for the primary cause. *Oikos*, **65**, 514–527.
- Rohde, K. (1996) Rapoport's Rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters*, **3**, 10–13.
- Rohde, K. (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography*, **22**, 593–613.
- Rohde, K., Heap, M. & Heap, D. (1993) Rapoport's Rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist*, **142**, 1–16.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rowley, I. & Russell, E. (1997) *Fairy-Wrens and Grasswrens*. Oxford University Press, Oxford.
- Seibold, I., Helbig, A.J. & Wink, M. (1993) Molecular systematics of Falcons (family Falconidae). *Naturwissenschaften*, **80**, 87–90.
- Sheldon, F.H., Whittingham, L.A. & Winkler, D.W. (1999) A comparison of cytochrom b and DNA hybridization data bearing on the phylogeny of swallows (Aves: Hirundinidae). *Molecular Phylogenetics and Evolution*, **11**, 320–331.

- Slikas, B. (1997) Phylogeny of the avian family Ciconiidae (Storks) based on cytochrome b sequences and DNA-DNA hybridization distances. *Molecular Phylogenetics and Evolution*, **8**, 275–300.
- Stevens, G.C. (1989) The latitudinal gradient in geographic range – how so many species coexist in the tropics. *American Naturalist*, **133**, 240–256.
- Taylor, C.M. & Gotelli, N.J. (1994) The macroecology of Cyprinella: correlates of phylogeny, body size, and geographic range. *American Naturalist*, **144**, 549–569.
- Yom-Tov, Y. (1987) The reproductive rate of Australian passerines. *Australian Wildlife Research*, **14**, 319–330.
- Yom-Tov, Y. (1994) Clutch size in passerines of southern South America. *Condor*, **96**, 170–177.
- Zink, R.M. & Avise, J.C. (1990) Patterns of mitochondrial DNA and allozyme evolution in the avian genus *Ammodramus*. *Systematic Zoology*, **39**, 148–161.
- Zink, R.M. & Blackwell, R.C. (1998) Molecular systematics and biogeography of aridland Gnatcatchers (genus *Poliophtila*) and evidence supporting species status of the California Gnatcatcher (*Poliophtila californica*). *Molecular Phylogenetics and Evolution*, **9**, 26–32.
- Zink, R.M. & Dittmann, D.L. (1993) Population structure and gene flow in the Chipping Sparrow and a hypothesis for evolution in the genus *Spizella*. *Wilson Bulletin*, **105**, 399–413.
- Zink, R.M., Dittmann, D.L., Klicka, J. & Blackwell-Rago, R.C. (1999) Evolutionary patterns of morphometrics, allozymes, and mitochondrial DNA in Thrashers (Genus *Toxostoma*). *Auk*, **116**, 1021–1038.
- Zink, R.M., Dittmann, D.L. & Rootes, W.L. (1991) Mitochondrial DNA variation and the phylogeny of *Zonotrichia*. *Auk*, **108**, 578–584.
- Zink, R.M., Weller, S.J. & Blackwell, R.C. (1998) Molecular phylogenetics of the avian genus *Pipilo* and a biogeographic argument for taxonomic uncertainty. *Molecular Phylogenetics and Evolution*, **10**, 191–201.

Received 12 March 2001; revision received 20 September 2001

Appendix I

List of phylogenetically independent pairs of bird species used in the analysis

Family	Lower-latitude species	Higher-latitude species	Phylogeny reference
Alcidae	<i>Synthliboramphus antiquus</i>	<i>Synthliboramphus wumizusumi</i>	Friesen <i>et al.</i> 1996
Anatidae	<i>Anas aucklandica</i>	<i>Anas chlorotis</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas versicolor</i>	<i>Anas puna</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas acuta</i>	<i>Anas bahamensis</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas rubripes</i>	<i>Anas fulvigula</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas castanea</i>	<i>Anas bernieri</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas penelope</i>	<i>Anas sibilatrix</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas querquedula</i>	<i>Anas hottentottus</i>	Johnson & Sorenson 1999
Anatidae	<i>Anas clypeata</i>	<i>Anas smithii</i>	Johnson & Sorenson 1999
Anatidae	<i>Speculanas specularis</i>	<i>Amazonetta brasiliensis</i>	Johnson & Sorenson 1999
Bucerotidae	<i>Tockus leucomelas</i>	<i>Tockus deckeni</i>	Kemp 1995
Bucerotidae	<i>Tockus bradfieldii</i>	<i>Tockus fasciatus</i>	Kemp 1995
Bucerotidae	<i>Tockus monteiri</i>	<i>Tockus alboeristatus</i>	Kemp 1995
Bucerotidae	<i>Ocyrceros birostris</i>	<i>Ocyrceros gingalensis</i>	Kemp 1995
Bucerotidae	<i>Buceros hydrocorax</i>	<i>Buceros rhinoceros</i>	Kemp 1995
Bucerotidae	<i>Anorrhinus austeni</i>	<i>Anorrhinus galeritus</i>	Kemp 1995
Bucerotidae	<i>Penelopides manillae</i>	<i>Penelopides exarhatus</i>	Kemp 1995
Cacatuidae	<i>Callocephalon fimbriatum</i>	<i>Probosciger aterrimus</i>	Brown & Toft 1999
Cacatuidae	<i>Cacatua sanguinea</i>	<i>Cacatua alba</i>	Brown & Toft 1999
Certhiidae	<i>Poliophtila californica</i>	<i>Poliophtila albiloris</i>	Zink & Blackwell 1998
Ciconiidae	<i>Mycteria leucocephala</i>	<i>Mycteria cinerea</i>	Slikas 1997
Corvidae	<i>Chlamydera maculata</i>	<i>Chlamydera nuchalis</i>	Christidis & Schodde 1992
Corvidae	<i>Ptiloris paradiseus</i>	<i>Ptiloris magnificus</i>	Christidis & Schodde 1992
Falconidae	<i>Falco naumanni</i>	<i>Falco punctatus</i>	Seibold, Helbig & Wink 1993
Falconidae	<i>Falco rusticolus</i>	<i>Falco cherrug</i>	Seibold <i>et al.</i> 1993
Fringillidae	<i>Serinus scotops</i>	<i>Serinus capistratus</i>	Badyaev 1997
Fringillidae	<i>Serinus alaria</i>	<i>Serinus nigriceps</i>	Badyaev 1997
Fringillidae	<i>Serinus flaviventris</i>	<i>Serinus donaldsoni</i>	Badyaev 1997
Fringillidae	<i>Serinus citrinella</i>	<i>Serinus canicollis</i>	Badyaev 1997
Fringillidae	<i>Serinus leucopterus</i>	<i>Serinus burtoni</i>	Badyaev 1997
Fringillidae	<i>Serinus totta</i>	<i>Linurgus olivaceus</i>	Badyaev 1997
Fringillidae	<i>Serinus citrinipectus</i>	<i>Serinus dorsostratus</i>	Badyaev 1997
Fringillidae	<i>Carduelis barbata</i>	<i>Carduelis spinescens</i>	Badyaev 1997
Fringillidae	<i>Agelaius thilius</i>	<i>Agelaius xanthophthalmus</i>	Johnson & Lanyon 1999
Fringillidae	<i>Pseudoleistes virescens</i>	<i>Agelaius icterocephalus</i>	Johnson & Lanyon 1999
Fringillidae	<i>Agelaius tricolor</i>	<i>Agelaius humeralis</i>	Johnson & Lanyon 1999
Fringillidae	<i>Quiscalus major</i>	<i>Quiscalus lugubris</i>	Johnson & Lanyon 1999
Fringillidae	<i>Molothrus ater</i>	<i>Scaphidura oryziphora</i>	Johnson & Lanyon 1999
Fringillidae	<i>Spizella arborea</i>	<i>Spizella atrogularis</i>	Zink & Dittmann 1993
Fringillidae	<i>Pipilo chlororus</i>	<i>Pipilo ocai</i>	Zink, Weller & Blackwell 1998
Fringillidae	<i>Pipilo crissalis</i>	<i>Pipilo albicollis</i>	Zink <i>et al.</i> 1998
Fringillidae	<i>Zonotrichia querula</i>	<i>Zonotrichia capensis</i>	Zink, Dittmann & Rootes 1991
Fringillidae	<i>Ammodramus bairdii</i>	<i>Ammodramus aurifrons</i>	Zink & Avise 1990
Fringillidae	<i>Diglossa carbonaria</i>	<i>Diglossa humeralis</i>	Hackett 1995

Family	Lower-latitude species	Higher-latitude species	Phylogeny reference
Furnariidae	<i>Cranioleuca obsoleta</i>	<i>Cranioleuca vulpina</i>	Garcia-Moreno, Arctander & Fjeldsa 1999a
Gruidae	<i>Grus monachus</i>	<i>Grus nigricollis</i>	Krajewski & Fetzner 1994
Gruidae	<i>Grus vipio</i>	<i>Grus rubicunda</i>	Krajewski & Fetzner 1994
Gruidae	<i>Anthropoides virgo</i>	<i>Anthropoides paradisea</i>	Krajewski & Fetzner 1994
Hirundinidae	<i>Riparia riparia</i>	<i>Riparia cincta</i>	Sheldon, Whittingham & Winkler 1999
Maluridae	<i>Malurus pulcherrimus</i>	<i>Malurus amabilis</i>	Christidis & Schodde 1997
Maluridae	<i>Malurus cyaneus</i>	<i>Malurus coronatus</i>	Christidis & Schodde 1997
Maluridae	<i>Malurus melanocephalus</i>	<i>Malurus alboscapulatus</i>	Rowley & Russell 1997
Maluridae	<i>Stipiturus mallee</i>	<i>Stipiturus ruficeps</i>	Christidis & Schodde 1997
Maluridae	<i>Stipiturus malachurus</i>	<i>Clytomyias insignis</i>	Rowley & Russell 1997
Pardalotidae	<i>Sericornis magnirostris</i>	<i>Sericornis beccari</i>	Joseph & Moritz 1993
Pittidae	<i>Pitta sordida</i>	<i>Pitta steerii</i>	Erritzoe & Erritzoe 1998
Pittidae	<i>Pitta nympha</i>	<i>Pitta megarhyncha</i>	Erritzoe & Erritzoe 1998
Pittidae	<i>Pitta versicolor</i>	<i>Pitta elegans</i>	Erritzoe & Erritzoe 1998
Scolopacidae	<i>Limnodromus scolopaceus</i>	<i>Limnodromus griseus</i>	Awise & Zink 1988
Sturnidae	<i>Toxostoma redivium</i>	<i>Toxostoma ocellatum</i>	Zink <i>et al.</i> 1999
Sulidae	<i>Morus bassanus</i>	<i>Papasula abbotti</i>	Friesen & Anderson 1997
Sylviidae	<i>Sylvia curruca</i>	<i>Sylvia leucomelaena</i>	Blondel, Catzeflis & Perret 1996
Sylviidae	<i>Phylloscopus schwarzii</i>	<i>Phylloscopus affinis</i>	Price <i>et al.</i> 1997
Sylviidae	<i>Phylloscopus trochilus</i>	<i>Phylloscopus lorenzii</i>	Price <i>et al.</i> 1997
Sylviidae	<i>Phylloscopus proregulus</i>	<i>Phylloscopus chloronotus</i>	Price <i>et al.</i> 1997
Sylviidae	<i>Phylloscopus borealis</i>	<i>Phylloscopus magnirostris</i>	Price <i>et al.</i> 1997
Sylviidae	<i>Phylloscopus plumbeitarsus</i>	<i>Phylloscopus trochiloides</i>	Price <i>et al.</i> 1997
Trochilidae	<i>Heliodoxa branickii</i>	<i>Heliodoxa gularis</i>	Gerwin & Zink 1989
Trochilidae	<i>Metallura aeneocauda</i>	<i>Metallura williami</i>	Garcia-Moreno, Arctander & Fjeldsa 1999b