

Extrapair paternity, migration, and breeding synchrony in birds

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To understand interspecific patterns in the strength of sexual selection, variation in the costs and benefits of exercising mate choice needs to be evaluated. One manifestation of sexual selection in birds is the occurrence of greatly variable levels of extrapair paternity (EPP). A proposed general explanation for this variation is that the benefits to females in seeking extrapair copulations vary in a predictable manner according to the degree of breeding synchrony because females are better able to assess potential extrapair partners when males are simultaneously in breeding condition. This hypothesis predicts a latitudinal trend in EPP because birds tend to breed more synchronously away from the equator. Expanding on previous geographically and taxonomically restricted tropical/temperate comparisons, we used phylogenetically independent standardized linear contrasts to show that this positive relationship persists when all bird species for which EPP estimates currently exist are considered. However, if a third factor covaries with latitude in the same way as breeding synchrony and EPP, this relationship need not be causal. Migration could also account for latitudinal variation in the benefits to females of pursuing EPP, if migration is associated with (1) hasty or (2) inaccurate mate choice, (3) facilitated assessment of male quality through the condition-dependence of arrival time, or (4) increased genetic variance in male quality. We show that migration distance is positively related to the proportion of EPP and that migration can statistically explain the latitudinal trend in EPP, even when confounding factors are simultaneously controlled. Hence, alternative explanations for latitudinal variation in EPP may be feasible, and careful intraspecific tests are needed to assess their relative importance and their implications for geographical variation in life-history evolution. *Key words:* breeding synchrony, comparative analysis, extrapair paternity, migration, sexual selection. [*Behav Ecol* 15:41–57 (2004)]

Females of many socially monogamous bird species pursue extrapair copulations (EPCs), apparently to obtain superior or more compatible genes for their offspring (e.g., Johnsen et al., 2000; Kempenaers et al., 1992). The extreme variation discovered in extrapair paternity (EPP), both within and among species, has attracted a large body of research attempting to identify its benefits and constraints (reviews in Birkhead and Møller, 1992; Petrie and Kempenaers, 1998; Slagsvold and Lifjeld, 1997; Westneat et al., 1990), yet its ecological correlates remain surprisingly poorly known (Birkhead and Møller, 1996; Petrie and Kempenaers, 1998).

One proposed general explanation for variation in EPP in birds is that different levels of breeding synchrony alter the opportunities to males or benefits to females of pursuing EPCs (Birkhead and Møller, 1992; Emlen and Oring, 1977; Stutchbury and Morton, 1995). This relationship has been argued to be both negative and positive. A negative relationship could result if high breeding synchrony constrains EPP if mate guarding or paternal care restricts male pursuit of EPCs (Birkhead and Biggins, 1987; Ims, 1990; Westneat et al., 1990). In contrast, a positive relationship could result if (1) synchrony results in reduced male–male competition and hence fewer constraints to males in pursuing EPCs, or (2) deriving from the realization that female control of EPP is commonplace (reviewed by, e.g., Cunningham and Birkhead, 1997; Gowaty, 1996; Kempenaers et al., 1992), synchrony promotes EPP by facilitating female assessment of the quality of potential extrapair mates by the synchronized display of most males in the population (Slagsvold and Lifjeld, 1997;

Stutchbury, 1998a,b; Stutchbury and Morton, 1995). Asynchronously breeding females are suggested to experience fewer potential benefits from EPP, owing to an inability to accurately compare the relative quality of potential extrapair mates (Stutchbury and Morton, 1995, 2001). There is no reason to suppose that similar mechanisms do not also act in other socially monogamous taxa where female choice is prevalent.

Interspecific studies across a selection of passerine species have tended to support a positive relationship between EPP and breeding synchrony. First, pairwise comparisons showed that tropical species, which generally breed less synchronously than temperate species, had smaller testes (an index of the strength of sexual selection; Møller, 1991) than their temperate counterparts (Stutchbury and Morton, 1995). Second, in eight species pairs, the counterpart with a higher breeding synchrony index (Kempenaers, 1993) always experienced higher EPP (Stutchbury, 1998a). Third, a phylogenetically controlled, positive correlation was shown between synchrony index and EPP across 34 largely temperate species (Stutchbury, 1998a,b; but see Westneat and Sherman, 1997). However, there has been a call for more convincing comparative evidence (Weatherhead and Yezerinac, 1998), particularly in the light of the highly inconsistent outcomes of intraspecific tests: while some studies have shown that more synchronous populations do indeed experience elevated levels of EPP (e.g., Stutchbury et al., 1997), others have detected the opposite trend (e.g., Saino et al., 1999; Thusius et al., 2001) or found no unequivocal relationship (e.g., Dunn et al., 1994; Kempenaers, 1997; Perreault et al., 1997; Yezerinac and Weatherhead, 1997).

A previous meta-analysis of the 12 studies examining the effect of synchrony revealed a significant negative relationship of small magnitude ($r = -.086$) between breeding synchrony and extrapair paternity within species (Møller and Ninni,

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1998). The inclusion of five subsequent studies on breeding synchrony does not alter this conclusion (see Appendix A). Hence, there is a weak, consistent intraspecific relationship opposite to that expected for the breeding synchrony hypothesis. However, contrasting intra- and interspecific predictions are not uncommon in evolutionary ecology, where the intraspecific prediction often involves a mechanism, and the interspecific one involves an evolutionary outcome (e.g., Martin et al., 2001). In this study, we investigated primarily the latter, but also discuss possible mechanisms.

The breeding synchrony hypothesis draws heavily on life-history differences between tropical and temperate regions. Tropical species living in stable, saturated environments tend to breed throughout the year (Baker, 1938) and also usually experience less EPP than do generally synchronous, temperate or high-latitude species (reviewed by Stutchbury and Morton, 2001). However, there are other important ecological factors that vary with latitude and synchrony, suggesting that the interspecific relationship between EPP and breeding synchrony needs to be carefully examined to distinguish causality from correlation (Weatherhead and Yezerinac, 1998). If a third variable is associated with both EPP and synchrony, it is possible that a different process could account for this relationship.

Most striking, migratory behavior is associated with generally more synchronous breeding, due to strong selection on arrival time in most migratory species. Two classes of alternative hypotheses could provide mechanisms that link migration and selection on arrival time to variation in the costs and benefits to females of pursuing EPCs. First, Weatherhead and Yezerinac (1998) hypothesized that patterns of male and female territory settlement in synchronously breeding (and hence usually migratory) species may lead to enhanced benefits to females in pursuing EPCs. Two mechanisms may apply. First, if territory establishment is simultaneous in synchronously breeding species, territory quality could be a less reliable indicator of male quality in such species, leading to females having more to gain from EPCs (Weatherhead and Yezerinac, 1998). Second, if females are obliged to settle quickly on territories due to an ecological need to start breeding immediately, choice of genetic mate could occur only after choice of social mate, as reflected by higher EPP (Weatherhead and Yezerinac, 1998; Westneat et al., 1990). These two mechanisms are suggested to lead to a greater proportion of high-quality females being socially mated to low-quality males than in less synchronously breeding species and hence to lead to the benefits of EPCs being greater and constraints diminished for a larger proportion of females.

A second class of hypotheses proposes that migration (and hence apparent breeding synchrony) could be associated with increased variance in male quality, and therefore that in migratory species females may stand to gain greater benefits from pursuing EPCs. First, elevated EPP could be associated with migration because the costs of migration may enable females to better assess potential extrapair mates. Given that migration generates considerable additive genetic variance in male arrival time (Møller, 2001a) and that such arrival time is related to male quality (Møller, 1994), females of migratory species may be able to more accurately judge potential extrapair mates on the basis of this easily assessed trait and hence obtain greater benefits from pursuing EPCs. Second, migration itself may generate genetic variance by one of the pathways hypothesized by Fitzpatrick (1994). If so, migratory species could be expected to experience higher EPP because increased variance in male genetic quality is associated with higher returns from female choice (Petrie and Lipsitch, 1994; Petrie et al., 1998).

The foregoing hypotheses propose two processes leading to variation in the benefits to females of pursuing EPCs: compensation for inaccurate or hasty choice of social mate and enhanced incentive to pursue or opportunity to assess extrapair mates. These hypotheses are difficult to distinguish comparatively because they make similar predictions about the correlates of synchrony and EPP. In this study, we tested for correlational evidence for these alternative pathways. First, we assessed the taxonomical and geographical generality of the controversial interspecific relationship between synchrony and EPP by examining all species for which EPP data are available while controlling for similarity due to common descent. Latitude was used as an index of synchrony, given that life-history studies suggest that breeding synchrony increases with latitude (we also tested this assumption). Second, before investigating migration behavior as an alternative explanation, we tested the assumptions that synchronous breeding and occurrence at high latitudes are also associated with migration. Third, we used interspecific evidence to test the hypothesis that EPP is associated with migratory behavior. Fourth, by statistically controlling for migration distance and restricting the analysis to sedentary species, we tested whether the latitudinal trend is dependent on migratory behavior and hence whether migration-related hypotheses can potentially provide a general explanation for latitudinal variation in EPP.

METHODS

Data sets

Estimates of the proportion of extrapair paternity in 186 species were compiled from published and unpublished studies; all data and sources are reported in Appendix B. All studies available up to January 2002 were included, except, given the geographical emphasis of this study, three species with important introduced populations that may not accurately reflect long-term selective pressures (viz. *Phasianus colchicus*, *Columba livia*, and *Passer domesticus*). Where studies involved experimental manipulations (e.g., Ellegren et al., 1995), only EPP in control broods was included. We defined EPP as the percentage of offspring sired by males other than the attending male; hence, for species with cooperative breeding systems, EPP was defined as the percentage of offspring sired by males other than the attending males. Where estimates of EPP were available from more than one study, we used a mean weighted by sample size. EPP estimates have previously been shown to be highly repeatable among independent studies (Petrie et al., 1998).

A breeding synchrony index (SI, the percentage of females fertile on any given day during the breeding season; Kempenaers, 1993) was obtained for 34 species from published comparative studies (Stutchbury, 1998a; Stutchbury and Morton, 1995, 2001) and for a further 3 species from recent intraspecific studies (Dunn et al., 1999; Thusius et al., 2001). Given the much longer breeding seasons of birds in the tropics, SI and latitude are expected to be highly correlated, though we also tested this assumption. We used latitude as a continuous variable, in contrast to past studies that have considered only the categorical temperate/tropical comparison (Stutchbury, 1998b; Stutchbury and Morton, 1995). Latitudinal information was obtained from distribution maps published in standard ornithological handbooks (e.g., Cramp, 1977–1994; Marchant and Higgins, 1990–2001; Poole and Gill, 1992–2000; Ridgely and Tudor, 1989–1994), supplemented where necessary by regional field guides. Mean latitude was taken as the midpoint of the northernmost and southernmost limits of each species' geographical breeding

range, which has previously been shown to be a biologically meaningful measure (Gaston and Blackburn, 1996). We scored a subjective measure of mean migration distance, to the nearest 1000 km, from information or distribution maps published in the handbooks cited above, as well as from Sibley and Monroe (1990).

There are several confounding variables that could affect this study. (1) Sexual dichromatism is correlated with extrapair paternity (Møller and Birkhead, 1994) and with migration ability (Fitzpatrick, 1994, 1998) in birds. Hence, we tested for any latitudinal trend in sexual dichromatism that could confound the analyses and attempted controlling for sexual dichromatism in all tests. Sexual dichromatism was taken as the difference in plumage brightness scores of males and females of each species, as assigned by independent scorers (Møller and Birkhead, 1994). (2) We also entered summed sample sizes for the paternity studies and entered these into multivariate analyses to test for any bias caused by variation in the number of individuals sampled. For both sexual dichromatism and sample size, significant relationships did exist with several of the variables under test. However, when entered simultaneously into multivariate analyses, results did not qualitatively differ from those reported below, suggesting that they reflect largely independent components of the variance in EPP. We do not report all tests in this multivariate fashion due to the possibility that sexual dichromatism evolves in response to female choice in the ecological conditions discussed here, under the same selective pressures that are hypothesized to shape EPP, and a reduction in the number of possible contrasts due to incomplete data on sample size (available for 152 of 186 species).

A further possible source of bias in the data set could be island species, because these are expected to exhibit low EPP for reasons that are independent of their latitudinal position (Griffith, 2000; Møller, 2001b). Furthermore, most of the terrestrial island endemics in the present data set were tropical or subtropical (*Acrocephalus sechellensis*, *A. vaughani*, *Buteo galapagoensis*, *Gallinula mortieri*, *Geospiza scandens*, *Hymenolaimus malachorhynchus*, *Loxioides bailleui*, *Notiomystis cincta*, *Petroica australis*, *Phoebastria irrorata*, *Serinus canaria*, and *Zosterops lateralis*). Hence, we repeated all analyses with these species excluded to check whether their inclusion affected the results. In no instances did results differ qualitatively from those reported below.

To improve normality, the proportion of EPP and SI were arcsine-squareroot transformed prior to analysis, sample size was log-transformed, and all variables were treated as continuous.

Comparative analyses

Species are not statistically independent data points, by default of their shared phylogenetic history (reviewed by Harvey and Pagel, 1991; Harvey and Purvis, 1991). Hence, similarity due to common descent needs to be controlled for when testing for correlated evolution of traits across species. In this study, Felsenstein's (1985) independent contrasts method was implemented using the CRUNCH algorithm of the CAIC (Comparative Analysis by Independent Contrasts) 2.6.2b software package (Purvis and Rambaut, 1995). Based on a phylogeny of n taxa, CAIC computes for the traits of interest the difference in the taxa subtended by each node, thus producing $n - 1$ phylogenetically independent linear contrasts that, once standardized, may be entered into conventional statistical analyses. Standardization of contrasts is dependent on branch lengths, which may be estimated under alternative models of evolution. In a recent comparative study of mating systems in birds, Dunn et al. (2001)

demonstrated that results were sometimes inconsistent under different evolutionary assumptions and thus recommended that multiple methods be used to test the dependence of conclusions drawn on a particular evolutionary model. We therefore report results from analyses performed (1) under the assumption of a punctuated mode of evolution, with branch lengths set to be equal (Harvey and Pagel, 1991), and (2) assuming a gradual mode of evolution, with branch lengths calculated as proportional to the number of species in the clade (Grafen, 1989). This may be especially important given that tests of the statistical and evolutionary assumptions of the comparative procedure, as recommended by Garland et al. (1992), revealed in a few cases significantly negative relationships between absolute values of standardized contrasts and their standard deviations and positive ones with their estimated nodal values. To reduce the consequent problem of heterogeneity of variance, any extreme outliers (contrasts with Studentized residuals >3) were excluded from subsequent analyses (Dunn et al., 2001; Jones and Purvis, 1997), and (2) analyses were repeated with the independent variable expressed in ranks. In neither instance did these verifications change any of the conclusions reported below, unless otherwise stated.

The complete phylogenetic hypothesis on which the comparative analysis was based is reported in Figure 1. Higher nodes for the nonpasserines were drawn from the DNA-DNA hybridization phylogeny of Sibley and Ahlquist (1990) and predominantly from Barker et al. (2001) for Passeriformes. Where these phylogenies did not offer sufficient resolution, we resolved polytomies as far as possible on the assumption that genera defined in Sibley and Monroe (1990) are monophyletic and by using other published phylogenies (Corvidae: Cibois and Pasquet, 1999; Laridae: Crochet et al., 2000; Grapputo et al., 2001; Icteridae: Johnson and Lanyon, 1999; *Acrocephalus*: Leisler et al., 1997; Procellariiformes: Nunn and Stanley, 1998; Emberizidae: Patten and Fugate, 1998; *Parus*: Sheldon et al., 1992; Hirundinidae: Sheldon and Winkler, 1993; Suhonen et al., 1994; *Falco*: Wink et al., 1998). To test whether the results reported here were dependent on this topology, analyses were repeated using a phylogeny constructed from a standard taxonomy of birds (Howard and Moore, 1991). Results were qualitatively unchanged from the results reported below.

Because the null expectation for a contrast at any given node is zero, all regressions were forced through the origin (Harvey and Pagel, 1991). Where appropriate, multivariate analyses were performed to control for confounding variables and were performed in JMP 4.0.4 (SAS Institute, Cary, North Carolina).

RESULTS

Bivariate regressions indicated that various measures of latitude are good predictors of breeding synchrony index (Table 1 and Figure 2), lending credence to the use of latitude as an index of breeding synchrony. Mean latitude and absolute mean latitude do not measure the same parameter: mean latitude represents mean distance along the earth's surface from one pole to another (with the South Pole at -90 and the North Pole at 90), whereas absolute mean latitude reflects average distance from the equator, independent of hemisphere. Hence, given that all the Southern Hemisphere species for which SI data were available were tropical or south-temperate, the stronger correlation between mean latitude and SI than between absolute mean latitude and SI is as expected from the well-documented phenomenon that south-temperate species generally exhibit life-history traits

Table 1
Bivariate correlations between phylogenetically independent contrasts of synchrony index and different measures of latitude

	Punctuated		Gradual	
	r^2	p	r^2	p
Mean latitude	.714	<.001	.756	<.001
Absolute mean latitude	.644	<.001	.665	<.001
Maximum latitude	.615	<.001	.688	<.001
Southern limit of range	.593	<.001	.704	<.001
Northern limit of range	.732	<.001	.793	<.001

The relationship was positive, and the sample size was 33 or 34 contrasts in all cases.

more similar to tropical species than to north-temperate species (e.g., Martin, 1996).

As previously reported by Stutchbury (1998b), SI is a good predictor of the proportion of EPP (punctuated model of evolution: $F = 17.77$, $df = 1,32$, $r^2 = .357$, $p < .001$, slope [SE] = 0.636 [0.150]; gradual model of evolution: $F = 22.38$, $df = 1,32$, $r^2 = .412$, $p < .001$, slope = 0.672 [0.142]), at least among the 37 largely north-temperate taxa (all passerine but 2) for which SI estimates have been published. In this subset of species, EPP was also strongly positively correlated with absolute mean latitude (punctuated model of evolution: $F = 14.54$, $df = 1,32$, $r^2 = .312$, $p < .001$, slope = 0.009 [0.002]; gradual model of evolution: $F = 33.43$, $df = 1,32$, $r^2 = .511$, $p < 0.001$, slope = 0.011 [0.002]), as well as other latitudinal measures.

Using the full EPP data set, EPP was significantly positively correlated with both absolute mean latitude (Figure 3) and maximum latitude. Up to 7.3% of the variance in EPP was explained (absolute mean latitude, punctuated: $F = 6.24$, $df = 1,173$, $r^2 = .035$, $p = .013$, slope [SE] = 0.0024 [0.0010]; absolute mean latitude, gradual: $F = 13.54$, $df = 1,173$, $r^2 = .073$, $p < .001$, slope = 0.0037 [0.0010]; maximum latitude, punctuated: $F = 7.52$, $df = 1,173$, $r^2 = .042$, $p = .0068$, slope = 0.0023 [0.0008], maximum latitude, gradual: $F = 13.33$, $df = 1,173$, $r^2 = .072$, $p < .001$, slope = 0.0032 [0.0009]). Relative to other latitudinal measures, the stronger relationship between absolute mean latitude and EPP than between absolute mean latitude and SI can probably be explained by a bias in the data set, in that EPP but not SI data were available for a number of Southern Hemisphere species at extreme latitudes (Antarctic and Subantarctic), which, unlike south-temperate species, are not expected to exhibit tropical life histories. Hence, we used absolute mean latitude (analogous to distance from the equator, given that distances over the earth's surface between successive lines of latitude are constant) as an index of breeding synchrony in subsequent analyses, unless stated otherwise. As Stutchbury and Morton (1995, 2001) and Stutchbury et al. (1998) point out, there are exceptions to this latitudinal trend, and these could be informative because it is breeding synchrony per se, and not latitude, that is predicted to affect EPP. We thus tested whether, among the subset of species with SI information, SI explains additional variance in EPP independently of latitude. If latitude is a good predictor of synchrony, we should expect to find little variance in residual EPP explained by breeding synchrony after controlling for latitude. In accordance with this, a regression against SI of the residuals from the regression of EPP on latitude was nonsignificant and explained little additional variance (punctuated model: $F = 0.93$, $df = 1,32$, $r^2 = .028$, $p = .34$; gradual model: $F = 0.10$, $df = 1,32$, $r^2 = .003$, $p = .75$).

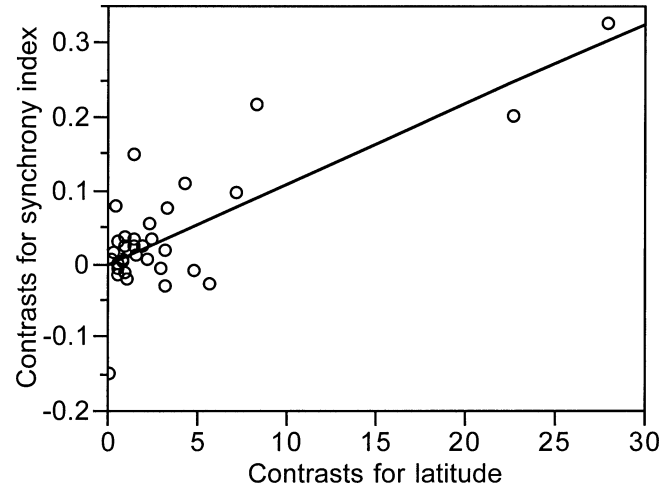


Figure 2
 Absolute mean latitude as a predictor of breeding synchrony index (Kempnaers, 1993). The line is a regression line forced through the origin ($F = 63.65$, $df = 1,32$, $r^2 = .665$, $p < .001$, slope [SE] = 0.0109 [0.0014]). Data points are phylogenetically independent standardized linear contrasts calculated under a gradual model of evolution (Grafen, 1989). Exclusion of the two extreme values at right did not affect the direction or significance of the relationship.

We predicted that migratory species should breed relatively synchronously and, independently, experience elevated levels of EPP. Bivariate analyses of phylogenetically independent contrasts revealed, first, that species with the longest migrations indeed tended to be more synchronous breeders (regression of SI on migration distance: punctuated model: $F = 29.60$, $df = 1,33$, $r^2 = .473$, $p < .001$, slope [SE] = 0.046 [0.008], gradual model: $F = 42.66$, $df = 1,33$, $r^2 = .564$, $p < .001$, slope = 0.051 [0.008]) and, second, that they tended to occur at relatively high latitudes (absolute mean latitude: punctuated model: $F = 63.92$, $df = 1,171$, $r^2 = .272$, $p < .001$, slope = 3.00 [0.375]; gradual model: $F = 52.74$, $df = 1,171$, $r^2 = .236$, $p < .001$, slope = 2.605 [0.359]; maximum latitude: punctuated model: $F = 78.13$, $df = 1,172$, $r^2 = .312$, $p < .001$, slope = 3.617 [0.409], gradual model: $F = 71.51$, $df = 1,172$, $r^2 = .294$, $p < .001$, slope = 3.322 [0.393]).

Species with longer migrations experienced, on average, higher levels of EPP (punctuated: $F = 10.46$, $df = 1,173$, $r^2 = .057$, $p = .0015$, slope [SE] = 0.018 [0.006]; gradual: $F = 16.74$, $df = 1,173$, $r^2 = .088$, $p < .001$, slope = 0.023 [0.006]; Figure 4). When species were taken as data points, migratory species had significantly higher EPP than sedentary species (mean [SE], migratory = 0.298 [0.021], sedentary = 0.196 [0.029]; $t = -2.33$, $df = 184$, $p = .0053$).

To evaluate whether migration is able to explain the latitudinal trend in EPP, we tested whether latitude explained additional variance in EPP after controlling for migration distance. A regression on latitude of the residuals of the regression of EPP on migration distance revealed that the proportion of variance explained by latitude alone was greatly reduced, statistically significant only under one model of evolution (punctuated model: $F = 1.51$, $df = 1,173$, $r^2 = .009$, $p = .22$; gradual model: $F = 4.98$, $df = 1,172$, $r^2 = .028$, $p = .027$, slope [SE] = 0.002 [0.001]), and in the latter instance not robust to ranking of the independent variable. This suggests that migration distance is able to statistically explain the latitudinal trend in EPP.

However, not all birds are migratory. If migration provides a good general explanation for latitudinal variation in EPP across all bird species, then no latitudinal trend should be present among sedentary species. We tested this by restricting

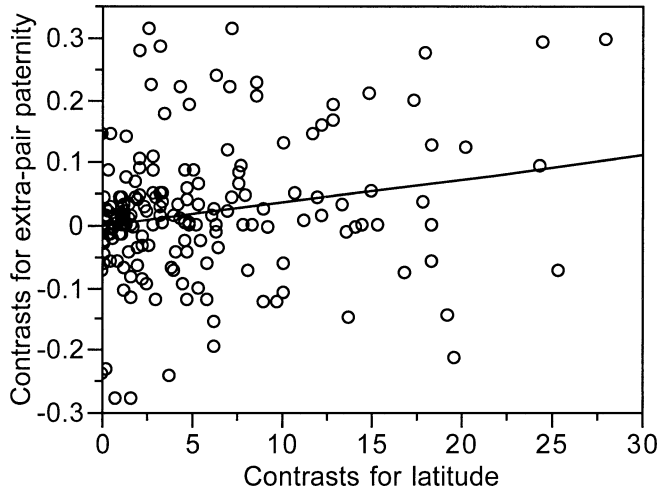


Figure 3

Extrapair paternity in birds in relation to absolute mean latitude. The line is a regression line forced through the origin ($F = 13.54$, $df = 1, 173$, $r^2 = .0073$, $p < .001$, slope [SE] = $0.0037 [0.0010]$) and contrasts were generated under a gradual model of evolution.

the analysis to sedentary species only. A strict definition of a sedentary species was applied: only those species with a migration score of 0 were included (which excludes, for example, partial migrants). Results were inconsistent between the two evolutionary models: no latitudinal trend in EPP was detectable in sedentary species under a punctuated model, but after exclusion of extreme outliers a trend emerged under a gradual model (punctuated: $F = 1.40$, $df = 1, 63$, $r^2 = .022$, $p = .241$; gradual: $F = 5.93$, $df = 1, 61$, $r^2 = .089$, $p = .018$). However, the latter result was not robust because it was dependent on the inclusion of a single extreme data point (Studentized residual = 2.86; results with this contrast omitted: $F = 1.77$, $df = 1, 60$, $r^2 = .020$, $p = .188$), and no significant trend was detected when the independent variable was expressed in ranks.

DISCUSSION

The breeding synchrony hypothesis seeks to explain variation in EPP by providing a process that could account for consistent variation in the relative costs and benefits of female choice, and it predicts a positive interspecific correlation between latitude and EPP. We first tested the geographical and phylogenetic generality of this previously reported correlation (Stutchbury, 1998a,b; Stutchbury and Morton, 1995, 2001). The present analysis of latitudinal trends in EPP expands on previous largely north-temperate and Neotropical coverage (Stutchbury, 1998a,b; Stutchbury and Morton, 1995) by including the broad range of south-temperate and Subantarctic species for which paternity estimates now exist. Furthermore, the continuous latitudinal measure used may be more biologically meaningful than previous discrete tropical/temperate comparisons. Average latitude explained up to 7% of interspecific variation in EPP across 186 species (Figure 3), not altering previous conclusions. The proportion of variance explained was reduced relative to regressions using synchrony index.

Although latitude is not always an accurate predictor of breeding synchrony (see, e.g., Stutchbury and Morton, 2001), this discrepancy probably reflects the broader selection of species considered in the present study. This is suggested by the observations that, first, latitude was a much stronger predictor of EPP in the geographically restricted subset of

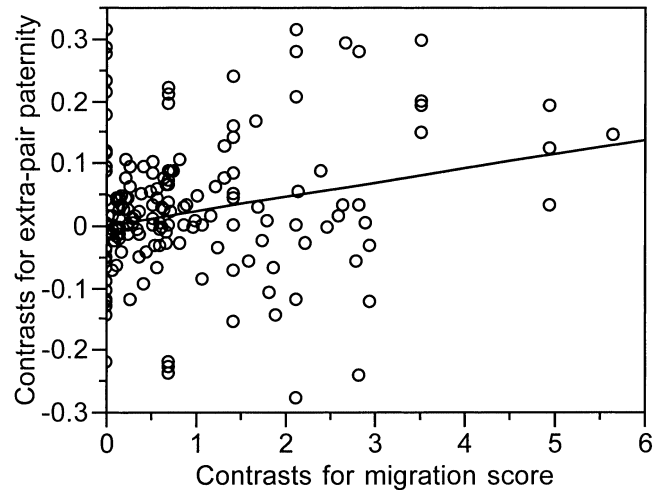


Figure 4

Extrapair paternity in birds in relation to an index of mean migration distance. The line is a regression line forced through the origin ($F = 16.74$, $df = 1, 173$, $r^2 = .088$, $p < .001$, slope [SE] = $0.023 [0.006]$) and contrasts were generated under a gradual model of evolution.

species for which synchrony index data were available than in the complete data set and, second, that synchrony index was unable to explain significant additional variance in EPP after controlling for latitude. It was also shown that the reported relationship exists across a phylogenetically diverse selection of species. This confirms the generality of previous comparative analyses that considered a limited selection of passerines, which are known to exhibit greater variance in EPP than other birds (e.g., Birkhead and Møller, 1996).

Although this relationship is consistent with the breeding synchrony hypothesis, it is not exclusive to it (Weatherhead and Yezerinac, 1998). We investigated an alternative factor, migration, which covaries with latitude in the same way as breeding synchrony but provides alternative benefits to female choice at a given latitude or implicit level of seasonality. Females of migratory species could be expected to experience greater benefits from pursuing EPCs than sedentary species, if migration is associated with (1) hasty or (2) inaccurate choice of social mate due to constraints during territory settlement (Weatherhead and Yezerinac, 1998), (3) migration allows females more accurately to assess potential extrapair mates, given that arrival time on the breeding grounds is condition dependent and strongly selected by female choice (e.g., Møller, 1994, 2001a), or (4) migratory species exhibit more variance in male genetic quality (Fitzpatrick, 1994, 1998). Some causal relationships implied by these hypotheses are illustrated in Figure 5. It seems reasonable to predict that these effects should be most pronounced for long-distance migrants, which are likely to experience the most constrained breeding seasons, incur the greatest costs of migration, and thus be most strongly selected for early arrival.

We showed that species with longer migrations exhibit higher levels of EPP, with average migration distance explaining up to 9% of the interspecific variance in EPP (Figure 4). When migration distance was statistically controlled, the amount of residual variance in EPP explained by latitude alone was greatly reduced and not statistically robust. Further, when only completely sedentary species were considered ($n = 66$), the latitudinal trend in EPP was weak and inconsistent. These findings suggest that migration can to a large extent explain the latitudinal trend in EPP. A tendency for migratory species to experience high EPP has not previously been demonstrated, although it was implicit from the findings that

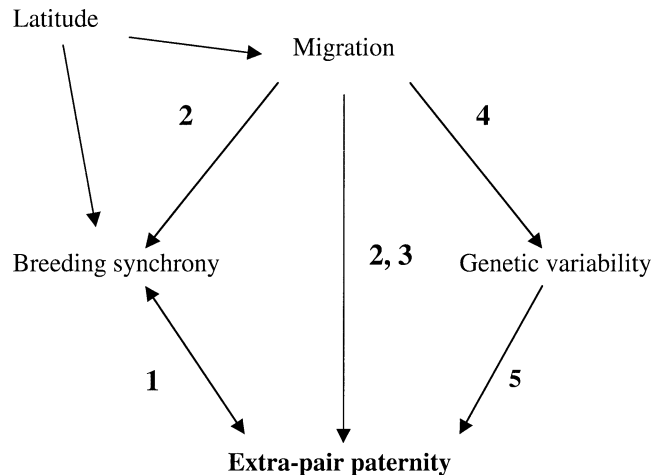


Figure 5
Hypothetical causal relationships considered in this study. References to the individual relationships are as follows: 1. Stutchbury and Morton (1995); 2. Weatherhead and Yezerinac (1997); 3. Møller (2001), this study; 4. Fitzpatrick (1994), and 5. Petrie et al. (1998).

migratory taxa are generally more sexually dichromatic than resident taxa (Fitzpatrick, 1994, 1998), and that sexual dichromatism is associated with EPP (Dunn et al., 2001; Møller and Birkhead, 1994; Petrie et al., 1998).

These analyses suggest that latitudinal variation in EPP can be explained by factors not necessarily related to breeding synchrony. However, like previous interspecific analyses of breeding synchrony, they suffer from the limitation that causality cannot be inferred. We cannot distinguish between the foregoing four hypotheses proposing causal associations between migration and EPP or between these and a common correlation with breeding synchrony. Careful intraspecific tests (such as those suggested by Weatherhead and Yezerinac, 1998) are needed to determine whether these effects are independent.

The possibility of a relationship between migration behavior and genetic variability deserves further investigation. There is little evidence for a relationship between migration

distance and genetic diversity as estimated by neutral minisatellite variability (Møller and Spottiswoode, unpublished data); however, neutral markers such as minisatellites are not necessarily good indices of the additive genetic variation under selection by female choice (Storfer, 1996), and these findings might not reflect biologically significant phenomena. There are several reasons to expect that migration could be associated with the generation of additive genetic variation. First, migratory populations could maintain higher genetic diversity if they encounter greater environmental heterogeneity at climatically variable high latitudes, in addition to those conditions experienced on the nonbreeding grounds. Second, given that migration behavior in birds is under genetic control (reviewed by Berthold, 1991), variance in male genetic quality could be generated continuously by variance in optimal migration routes due to climatic fluctuations, thus selecting for stronger female choice and hence EPP (Fitzpatrick, 1994). Third, genetic variance might also be generated by exposure to a second and diverse parasite fauna on the nonbreeding grounds (Møller and Erritzøe, 1998; but see Zuk, 1991). All of these processes could select for strong female choice and hence EPP, and thus potentially mediate a relationship between EPP and migration. Thus, the existence of a latitudinal trend in EPP that is independent of breeding synchrony per se would also be supported.

We have shown here that migration covaries with latitude and EPP in the same way as breeding synchrony and have discussed reasons that migration could provide alternative benefits to female choice at a given latitude or implicit level of seasonality. These hypotheses need not be exclusive and are difficult to distinguish comparatively with available data because they are linked by interrelated variables that are also difficult to manipulate experimentally. These findings also emphasize the need to take into account alternative processes leading to consistent geographical variation in the costs and benefits of female choice when attempting to explain differences in life histories. For example, breeding asynchrony and hence high mate fidelity has been suggested to be an important selective force behind elevated paternal investment in offspring care in the tropics (Stutchbury and Morton, 2001). If selection pressures on female choice in temperate regions are independent of breeding synchrony, then alternative pathways to such patterns could be considered.

APPENDIX A

Meta-analysis of intraspecific studies of breeding synchrony and extrapair paternity in birds

Species	N	Effect size	Variance	Reference
<i>Agelaius phoeniceus</i>	68	0.155	0.015	Gray (1996)
<i>Agelaius phoeniceus</i>	269	0.009	0.004	Weatherhead (1997)
<i>Agelaius phoeniceus</i>	175	0.001	0.006	Westneat and Gray (1998)
<i>Anser caerulescens</i>	23	-0.633	0.050	Dunn et al. (1999)
<i>Anser rossi</i>	24	0.161	0.048	Dunn et al. (1999)
<i>Anthus spinoletta</i>	258	-0.259	0.004	Reyer et al. (1997)
<i>Dendroica petechia</i>	50	-0.191	0.021	Yezerinac and Weatherhead (1997)
<i>Geothlypis trichas</i>	30	-0.641	0.037	Thusius et al. (2001)
<i>Hirundo rustica</i>	52	-0.356	0.020	Saino et al. (1997)
<i>Nectarinia osea</i>	18	1.201	0.067	Zilberman et al. (1999)
<i>Parus caeruleus</i>	37	0.232	0.029	Kempnaers (1997)
<i>Prunella modularis</i>	17	0.385	0.071	Hartley et al. (1995)
<i>Setophaga ruticilla</i>	29	-0.204	0.038	Perreault et al. (1997)
<i>Sialia sialis</i>	21	-0.428	0.056	Meek et al. (1994)
<i>Tachycineta bicolor</i>	34	0.326	0.032	Dunn et al. (1994)
<i>Turdus grayi</i>	19	0.412	0.063	Stutchbury et al. (1997)
<i>Wilsonia citrina</i>	85	0.183	0.012	Stutchbury et al. (1998)

The data were analyzed using the method outlined in Jennions et al. (2001), resulting in a significant mean weighted effect size of $r = -0.049$ (95% CI: -0.107 – 0.010).

APPENDIX B

Information used on extrapair paternity (%), latitudinal parameters, breeding synchrony index (SI), sexual dichromatism, migration score, and sample size for extrapair paternity in birds (EPP)

Species	EPP (%)	Southern limit of range	Northern limit of range	Absolute mean latitude	Migration score	SI (%)	Sexual dichromatism	N for EPP	References for EPP
<i>Accipiter gentilis</i>	1.30	17.63	70.31	43.97	0		1	122	Gavin et al. (1998)
<i>Accipiter nisus</i>	5.40	26.00	70.00	48.00	1		1		Newton I and McGrady MI (unpublished data)
<i>Acrocephalus arundinaceus</i>	4.02	18.40	63.04	40.72	8	30.0	0	1069	Hasselquist et al. (1996); Leisler et al. (2000); Wink M (unpublished data)
<i>Acrocephalus paludicola</i>	39.10	45.81	57.41	51.61	5		0	340	Leisler and Wink (2000); Schulze-Hagen et al. (1993)
<i>Acrocephalus palustris</i>	3.05	36.99	62.86	49.92	9		0	131	Leisler and Wink (2000)
<i>Acrocephalus schoenobaenus</i>	7.85	37.27	70.63	53.95	8		0	344	Buchanan and Catchpole (2000); Langefors et al. (1998)
<i>Acrocephalus sechellensis</i>	0	-4.33	-4.33	4.33	0		0	55	Richardson et al. (2001)
<i>Acrocephalus vaughani</i>	0	-24.14	-24.09	24.11	0		0	23	Brooke and Hartley (1995)
<i>Aegolius funereus</i>	5.00	36.06	73.41	54.74	0		0		Hakkalainen et al. (1996)
<i>Aethia pusilla</i>	0	51.35	65.68	58.51	2		0		Byrd and Williams (1993)
<i>Aethia pygmaea</i>	11.10	51.35	65.68	58.51	1		0		Byrd and Williams (1993)
<i>Agelaius phoeniceus</i>	28.27	10.21	67.03	38.62	5	36.0	2.5	1245	Gray (1996); Weatherhead and Boag (1995); Westneat (1993)
<i>Alectura lathami</i>	27.70	-33.50	-10.50	22.00	0		1	65	Birks (1997)
<i>Anas platyrhynchos</i>	3.00	30	72.70	51.35	2		2.5	298	Evarts and Williams (1987)
<i>Anser caerulescens</i>	5.00	52.70	80	66.35	4	66.1	0	80	Dunn et al. (1999)
<i>Anser rossi</i>	2.41	52.70	70.86	61.78	4	70.3	0	83	Dunn et al. (1999)
<i>Anthus spinoletta</i>	5.23	35.90	70.94	53.42	1	28.0	0	1052	Reyer et al. (1997)
<i>Aphelocoma coerulescens</i>	0	26.11	29.21	27.66	0		0	139	Quinn et al. (1999)
<i>Apus apus</i>	5.00	31.59	69.83	50.71	8		0	88	Blakey J et al. (unpublished data)
<i>Asio otus</i>	0	27.50	67.07	47.28	1		0	59	Marks et al. (1999)
<i>Athene noctua</i>	0	5.00	57.50	31.25	0		0	53	Müller et al. (2001)
<i>Branta leucopsis</i>	0	68.11	80	74.05	3		0	153	Choudhury et al. (1993); Larsson et al. (1995)
<i>Bubulcus ibis</i>	13.00	-40	50	5.00	2		0		Schwagmeyer et al. (1999)
<i>Bucephala clangula</i>	0	45.68	70.31	57.99	2		2.5		Eadie et al. (1995)
<i>Bucephala islandica</i>	0	42.02	66.00	54.01	2		2.5		Eadie (2000)
<i>Buteo galapagoensis</i>	0	-1.40	0.66	0.37	0		0	24	Faaborg et al. (1995)
<i>Calcarius ornatus</i>	17.64	36.38	52.50	44.44	2		1.5	85	Hill DP et al. (unpublished data)
<i>Calcarius pictus</i>	37.5	54.08	69.60	61.84	4		1.5	114	Briskie et al. (1998)
<i>Calidris maritima</i>	1.22	58.41	82.00	70.20	2		0	82	Pierce and Liffield (1998)
<i>Calonectris diomedea</i>	0	14.76	43.33	29.05	8		0	46	Swatschek et al. (1994)
<i>Campylorhynchus griseus</i>	4.6	2.46	12.32	7.39	0		0	222	Haydock et al. (1996)
<i>Campylorhynchus nuchalis</i>	1.40	6.45	11.69	9.07	0		0	69	Rabenold et al. (1990)
<i>Cardellina rubrifrons</i>	60	22.89	36.06	29.48	2		3		Barber P (unpublished data)
<i>Cardinalis cardinalis</i>	13.51	16.28	46.30	31.29	0	18.0	2	37	Ritchison et al. (1994)
<i>Carduelis flammea</i>	4.55	44.17	71.35	57.76	2		1.5		Angst (1998)
<i>Carduelis tristis</i>	14.29	31.40	56.49	43.94	2		3	70	Gissing et al. (1998)
<i>Carpodacus mexicanus</i>	8.40	16.56	50	33.28	1	17.0	2	119	Hill et al. (1994)
<i>Catharacta lonnbergi</i>	0	-67.97	-37.55	52.76	2		0	45	Millar et al. (1994)
<i>Catharacta maccormicki</i>	7.14	-81.35	-60.43	70.89	9		0	14	Millar et al. (1997)
<i>Cercomacra tyrannina</i>	0	-10	9.14	0.43	0	8.0	0	15	Fleischer et al. (1997)
<i>Charadrius hiaticula</i>	0	48.00	83.00	65.50	12		0	57	Wallerander et al. (2001)
<i>Charadrius seminellus</i>	4.55	42.63	76.39	59.51	8		-1	44	Owens et al. (1995)
<i>Charadrius semipalmatus</i>	4.71	41.24	72.05	56.65	10		0.5	85	Zharikov and Nol (2000)
<i>Coragyps atratus</i>	0	-40	40.54	0.27	0		0	36	Decker et al. (1993)
<i>Corcorax melanoramphos</i>	0	-39.08	-19.47	29.27	0		0	51	Heinsohn et al. (2000)
<i>Corvus monedula</i>	0	30.67	66.33	48.50	1		0	74	Henderson et al. (2000)
<i>Cygnus columbianus</i>	0	54.49	74.20	64.35	4		0		Rees et al. (1996)
<i>Cygnus cygnus</i>	0	51.25	74.00	62.63	2		0		Rees et al. (1996)
<i>Dacelo novaeguineae</i>	0	-39.02	-10.21	24.62	0		0	140	Legge and Cockburn (2000)

APPENDIX B, continued

Species	EPP (%)	Southern limit of range	Northern limit of range	Absolute mean latitude	Migration score	SI (%)	Sexual dichromatism	N for EPP	References for EPP
<i>Delichon urbica</i>	17.04	20.27	70.17	45.22	8	60.0	0	135	Riley et al. (1995); Whittingham and Lifjeld (1995)
<i>Dendrocopus major</i>	1.20	18.18	68.67	43.42	0		1	176	Michalak and Winkler (1997)
<i>Dendroica caerulescens</i>	27.20	33.87	49.41	41.64	2	27.0	3	125	Chuang et al. (1999)
<i>Dendroica petechia</i>	31.14	17.13	70.54	43.83	6	47.0	2	537	Yezerinac et al. (1996, 1999)
<i>Dolichonyx oryzivorus</i>	14.60	32.15	53.65	42.90	8	35.0	2.5	840	Bollinger and Gavin (1991)
<i>Emberiza calandra</i>	4.55	29.62	59.26	44.44	1	18.0	0	38	Hartley et al. (1993)
<i>Emberiza citrinella</i>	37.40	38.57	70.67	54.62	1		1.5	123	Sundberg and Dixon (1996)
<i>Emberiza schoeniclus</i>	54.63	34.46	71.17	52.82	1	34.0	1	216	Dixon et al. (1994)
<i>Emberiza yessoensis</i>	24.00	33.45	47.86	40.66	2		1	28	Nagata H and Sodhi NS, (unpublished data)
<i>Erithacus rubecula</i>	4.00	27.69	70.33	49.01	2		0		Tobias (1996)
<i>Eudypetes schlegeli</i>	4.00	-54.77	-54.47	54.62	2		0	26	St Clair et al. (1995)
<i>Euplectes orix</i>	17.60	-34.74	0	17.37	0		3	432	Friedl and Klump (1999)
<i>Falco columbarius</i>	0	42.15	71.17	56.66	4		1.5	66	Warkentin et al. (1994)
<i>Falco eleonorae</i>	0	29.17	43.13	36.15	7		2	60	Swatschek et al. (1993)
<i>Falco naumanni</i>	3.44	31.34	55.56	43.45	8		1		Negro et al. (1996)
<i>Falco peregrinus</i>	0	-55.00	77.80	11.40	8		1	54	Nesje et al. (2000)
<i>Falco sparverius</i>	11.20	-55.00	67.03	6.01	4		1	89	Villarroel et al. (1998)
<i>Falco tinnunculus</i>	1.88	-34.20	70.65	18.22	7		1	319	Korpimäki et al. (1996)
<i>Ficedula albicollis</i>	15.47	38.91	57.96	48.44	7		1	459	Sheldon and Ellegren (1999)
<i>Ficedula hypoleuca</i>	7.98	30.89	70.67	50.78	5	44.0	1.5	614	Brün et al. (1996); Ellegren et al. (1995); Gelter and Tegelström (1992); Lifjeld et al. (1991); Rätti et al. (1995)
<i>Fregata minor</i>	1.09	-24.80	20	2.40	2		2.5	92	Dearborn et al. (2001)
<i>Fringilla coelebs</i>	17.00	27.78	70	48.89	3		2	47	Sheldon and Burke (1994)
<i>Fulmarus glacialis</i>	0	44.64	81.75	63.20	3		0	19	Hunter et al. (1992)
<i>Gallinula chloropus</i>	0	-34.20	66.00	15.90	2		0	150	McRae (1996); McRae and Burke (1996)
<i>Gallinula mortieri</i>	0	-43.15	-40.65	41.90	0		0	26	Gibbs et al. (1994)
<i>Gavia immer</i>	0	43.23	68.72	55.98	4		0	58	Piper et al. (1997)
<i>Geospiza scandens</i>	7.55	-1.40	0.66	0.37	0		1	159	Petren et al. (1999)
<i>Geothlypis trichas</i>	20.30	20	66.00	43.00	5	25.5	2	153	Peterson et al. (2001)
<i>Grallina cyanoleuca</i>	2.91	-39.02	-6.14	22.58	0		0	103	Hall and Magrath (2000)
<i>Haematopus ostralegus</i>	1.54	35.00	71.27	53.13	4		0	65	Heg et al. (1993)
<i>Hirundo ariel</i>	13.79	-39.13	-13.54	26.34	1	13.0	0	203	Magrath and Elgar (1997)
<i>Hirundo rustica</i>	28.78	18.62	70.38	44.50	9		1	592	Møller and Tegelström (1997); Saino et al. (1997); Wellbourn et al. (unpublished data)
<i>Hymenolaimus malachorhynchus</i>	0	-46.54	-38.00	42.27	0		0	14	Triggs et al. (1991)
<i>Icteria virens</i>	21.00	21.06	50	35.53	3		2	29	Eckerle and Thompson (2001)
<i>Icterus galbula</i>	32.18	30.54	58.11	44.32	3		3		Richardson and Burke (1999)
<i>Jacana jacana</i>	10.20	-39.35	11.57	13.89	0		2	235	Emlen et al. (1998)
<i>Junco hyemalis</i>	28.34	27.17	67.57	47.37	3		0	187	Ketterson et al. (1998)
<i>Lagopus lagopus</i>	9.40	48.11	75.68	61.89	0		2	256	Freeland et al. (1995)
<i>Lanius bucephalus</i>	10.10	30.92	50	40.46	3		0	99	Yamagishi et al. (1992)

APPENDIX B, continued

Species	EPP (%)	Southern limit of range	Northern limit of range	Absolute mean latitude	Migration score	SI (%)	Sexual dichromatism	N for EPP	References for EPP
<i>Lanius collurio</i>	5.26	32.68	66.33	49.51	9		1.5	19	Fornasari et al. (1994)
<i>Lanius minor</i>	0	28.00	55.58	41.79	7		1		Hoi H (unpublished data)
<i>Larus argentatus</i>	0.50	27.73	76.19	51.96	2		0		Gilbert (1996)
<i>Larus canus</i>	3.64	46.11	71.25	58.68	2		0	56	Bukacinska et al. (1998)
<i>Larus occidentalis</i>	0	27.00	46.63	36.82	0		0	33	Gilbert et al. (1998)
<i>Loxioides bailleui</i>	0	19.30	19.96	19.63	0		0	20	Fleischer et al. (1994)
<i>Luscinia svecica</i>	31.37	32.81	71.33	52.07	5	66.0	2	312	Krokene et al. (1996); Questiau et al. (1999)
<i>Malurus cyaneus</i>	66.99	-43.57	-22.08	32.83	0		4.5	309	Dunn and Cockburn (1999)
<i>Malurus splendens</i>	62.10	-37.72	-18.23	27.97	0		4	91	Brooker et al. (1990)
<i>Manorina melanocephala</i>	0	-42.86	-16.60	29.73	0		0	85	Pöldmaa et al. (1995)
<i>Manorina melanophrys</i>	4.20	-38.00	-23.00	30.50	0		0	24	Pöldmaa et al. (1995)
<i>Melanerpes formicivorus</i>	0	11.60	45.65	28.62	0		0	51	Dickinson et al. (1995)
<i>Melospiza melodia</i>	8.80	20.76	62.70	41.73	2		0		Smith (1991)
<i>Merops apiaster</i>	0.70	-34.59	57.59	11.50	6		0	100	Jones et al. (1991)
<i>Merops bullockoides</i>	1.31	-29.76	4.05	12.85	0		0	97	Wrege and Emlen (1987)
<i>Merops viridis</i>	0	-8.75	29.00	10.13	2		0		Stader (1994)
<i>Mimus polyglottos</i>	8.00	15.64	51.34	33.49	1	24.0	0		Derrickson and Breitwisch (1992)
<i>Nectarinia osea</i>	26.00	4.05	33.48	18.77	0		4.5	90	Zilberman et al. (1999)
<i>Notiomystis cincta</i>	35.00	-36.22	-36.16	36.19	0		0		Ewen et al. (1999)
<i>Oceanites oceanicus</i>	0	-73.41	-46.27	59.84	9		0	63	Quillfeldt et al. (2001)
<i>Oceanodroma leucorhoa</i>	0	26.63	67.83	47.23	6		0	48	Mauck et al. (1995)
<i>Oenanthe oenanthe</i>	10.96	30.89	80	55.45	9		1.5	73	Currie et al. (1998)
<i>Oporornis formosus</i>	43.00	29.67	41.40	35.54	3	35.0	2		McDonald (1998)
<i>Otus asio</i>	0	22.17	50.22	36.20	0		0		Lawless et al. (1997)
<i>Panurus biarmicus</i>	14.40	36.75	59.07	47.91	0	50.0	1	187	Hoi and Hoi-Leitner (1997)
<i>Parus ater</i>	25.32	27.86	67.33	47.60	0		0	158	Lubjuhn et al. (1999a)
<i>Parus atricapillus</i>	8.91	36.06	65.68	50.87	0	53.0	0	359	Otter et al. (1998)
<i>Parus caeruleus</i>	11.18	27.64	67.50	47.57	0	57.0	1	2946	Gullberg et al. (1992); Kempnaers et al. (1997); Krokene et al. (1998); Leech et al. (2001)
<i>Parus cristatus</i>	12.40	35.96	67.00	51.48	0		0	121	Lens et al. (1997)
<i>Parus major</i>	10.04	-10.91	71.25	30.17	0		1	3815	Blakey (1994); Gullberg et al. (1992); Krokene et al. (1998); Lubjuhn et al. (1999b); Strohbach et al. (1998); Verboven and Mateman (1997)
<i>Parus montanus</i>	0.96	31.00	70.63	50.81	0		0	112	Orell et al. (1997)
<i>Passer montanus</i>	10	-8.75	71.69	31.47	0		0		Summers-Smith (1997)
<i>Passerculus sandwichensis</i>	23.10	15.87	71.35	43.61	4	34.0	0	160	Freeman-Gallant (1997)
<i>Passerina cyanea</i>	36.37	26.02	50.27	38.15	5	17.0	2.5	320	Westneat (1987, 1990)
<i>Perisoreus canadensis</i>	0	33.76	68.67	51.22	0		0		Strickland and Ouellet (1993)
<i>Perisoreus infaustus</i>	0	50	70.38	60.19	0		0	40	Ekman et al. (1994); Lillandt et al. (2001)
<i>Petroica australis</i>	0	-47.27	-37.68	42.47	0		2	62	Ardern et al. (1997)
<i>Phalacrocorax aristotelis</i>	9.30	27.73	71.25	49.49	0		0		Graves et al. (1993)
<i>Phalacrocorax carbo</i>	16.19	-43.70	71.00	13.65	1		0	186	Piertney et al. (2003)
<i>Phalaropus fulicarius</i>	8.57	60	79.58	69.79	10		-1.5	70	Dale et al. (1999)
<i>Phalaropus tricolor</i>	0	36.70	60.93	48.82	9		-1.5	51	Delehanty et al. (1998)
<i>Philetairus socius</i>	17.00	-29.44	-18.53	23.99	0		0		Marsden (1999)
<i>Phoebastria irrorata</i>	25.00	-1.45	-1.25	1.35	1		0	16	Huyvaert et al. (2000)
<i>Phoeniculus purpureus</i>	0	-34.11	17.16	8.48	0		0		Du Plessis MA (unpublished data)

APPENDIX B, continued

Species	EPP (%)	Southern limit of range	Northern limit of range	Absolute mean latitude	Migration score	SI (%)	Sexual dichromatism	N for EPP	References for EPP
<i>Phylloscopus sibilatrix</i>	0	38.91	68.33	53.62	6		0	56	Gyllensten et al. (1990)
<i>Phylloscopus trochilus</i>	18.52	43.33	71.25	57.29	9	69.0	0	297	Bjørnstad and Lifjeld (1997); Fridolfsson et al. (1997); Gyllensten et al. (1990)
<i>Pica pica</i>	4.89	18.21	71.25	44.73	0		0	184	Parrott (1995)
<i>Picoides borealis</i>	1.25	25.87	37.13	31.50	0		1	80	Haig et al. (1994)
<i>Plocepasser mahali</i>	0	-30	7.70	11.15	0		0	36	McRae SB (unpublished data)
<i>Porphyrio porphyrio</i>	0	-47.27	46.84	0.21	0		0	73	Jamieson et al. (1994)
<i>Progne subis</i>	23.90	20	56.25	38.13	7	28.0	0.5	190	Morton et al. (1990); Wagner et al. (1996)
<i>Promerops cafer</i>	43.18	-34.67	-31.63	33.15	0		3	44	Henderson (2000)
<i>Prunella collaris</i>	0	27.00	57.04	42.02	1		0	127	Hartley et al. (1995); Heer (1996)
<i>Prunella modularis</i>	0.80	35.14	70.63	52.88	2		0	133	Burke et al. (1989)
<i>Psaltirparus minimus</i>	0	14.46	51.35	32.90	0		0	50	Bruce et al. (1996)
<i>Puffinus tenuirostris</i>	10.84	-43.57	-32.50	38.04	10		0	83	Austin and Parkin (1996)
<i>Pygoscelis adeliae</i>	6.05	-78.47	-54.26	66.37	2		0	22	Hunter F (unpublished data); Pilastro et al. (2001)
<i>Pygoscelis antarctica</i>	0	-68.55	-54.16	61.36	2		0	38	Moreno et al. (2000)
<i>Remiz pendulinus</i>	6.97	30.82	60.18	45.50	2		1.5	201	Schleicher et al. (1997)
<i>Riparia riparia</i>	14.37	24.09	70.63	47.36	8		0	167	Alves and Bryant (1998)
<i>Rissa tridactyla</i>	0.96	43.33	81.00	62.17	2		0	104	Danchin E et al. (unpublished data)
<i>Sayornis phoebe</i>	11.84	28.92	64.86	46.89	3		0	76	Conrad et al. (1998)
<i>Sericornis frontalis</i>	5.70	-39.02	-17.55	28.29	0		0	137	Whittingham et al. (1997)
<i>Serinus canaria</i>	0	27.73	39.69	33.71	0		2		Voigt (1997)
<i>Serinus serinus</i>	9.35	27.78	59.81	43.80	1		2	139	Hoi-Leitner et al. (1999)
<i>Setophaga ruticilla</i>	39.81	30.33	64.46	47.39	2		3	108	Perreault et al. (1997)
<i>Sialia mexicana</i>	16.90	18.62	52.48	35.55	2		2.5	207	Dickinson and Akre (1998)
<i>Sialia sialis</i>	8.43	12.55	52.57	32.56	2	18.0	2.5	83	Meek et al. (1994)
<i>Speotyto cunicularia</i>	7.50	17.61	53.78	35.70	2		0		Haug et al. (1993)
<i>Spheniscus humboldti</i>	0	-33.00	-5.00	19.00	0		0	49	Schwartz et al. (1999)
<i>Spizella pusilla</i>	15.10	30	49.35	39.67	1		0		Carey et al. (1994)
<i>Sterna caspia</i>	0	-47.27	66.03	9.38	5		0		Gilbert (1996)
<i>Sterna hirundo</i>	2.94	5.00	71.00	38.00	12		0	102	González-Solís et al. (2001)
<i>Sturnus unicolor</i>	15.90	29.50	43.75	36.63	0		0	334	Cordero et al. (2003)
<i>Sturnus vulgaris</i>	9.09	25.08	71.25	48.17	2		0	154	Pinxten et al. (1993); Smith and von Schantz (1993)
<i>Tachycineta albilinea</i>	15.73	-7.79	29.38	10.79	0	8.0	0	97	Moore et al. (1999)
<i>Tachycineta bicolor</i>	54.06	32.39	68.24	50.32	5	46.0	0	640	Barber et al. (1996); Dunn et al. (1994); Kempnaers et al. (1999)
<i>Taeniopygia guttata</i>	2.40	-38.70	-13.83	26.26	0		2.5	92	Birkhead et al. (1990)
<i>Tetrao tetrix</i>	0	41.44	70	55.72	0		1.5	66	Alatalo et al. (1996)
<i>Thalassoica antarctica</i>	9.52	-68.54	-65.61	67.07	2		0	42	Lorentsen et al. (2000)
<i>Thryothorus ludovicianus</i>	0	22.07	43.10	32.58	0		0	84	Haggerty et al. (2001)
<i>Tockus monteiri</i>	0	-23.11	-12.97	18.04	0		0		Stanback et al. (1999)
<i>Tringa macularia</i>	9.90	32.72	68.92	50.82	7		0	111	Oring et al. (1992)
<i>Troglodytes aedon</i>	8.35	30	59.46	44.73	3		0	790	Soukup and Thompson (1997)
<i>Turdoides squamiceps</i>	0	12.64	32.17	22.40	0		0	186	Lundy et al. (1998)
<i>Turdus grayi</i>	37.84	5.74	27.07	16.40	0	25.0	0	37	Stutchbury et al. (1998)

APPENDIX B, continued

Species	EPP (%)	Southern limit of range	Northern limit of range	Absolute mean latitude	Migration score	SI (%)	Sexual dichromatism	N for EPP	References for EPP
<i>Turdus merula</i>	17.77	5.95	71.09	38.52	1		2	467	Creighton (2000); Rasa A (unpublished data)
<i>Turdus migratorius</i>	53.00	16.06	70.54	43.30	3		0		Montgomerie in Briskie et al. (1997)
<i>Tyrannus tyrannus</i>	45.84	26.34	65.27	45.81	7	40.0	0	124	McKittrick (1990); Rowe et al. (2001)
<i>Upupa epops</i>	7.58	5.95	60	32.97	5		0.5	132	Martín-Vivaldi (1997)
<i>Uria aalge</i>	7.80	37.44	78.89	58.17	2		0	77	Birkhead et al. (2001)
<i>Vireo olivaceus</i>	57.89	29.13	67.03	48.08	6	43.0	0	19	Morton et al. (1998)
<i>Vireo solitarius</i>	2.70	34.46	62.03	48.24	3	23.0	0	37	Morton et al. (1998)
<i>Wilsonia citrina</i>	26.69	28.26	43.66	35.96	2	33.0	1.5	356	Stutchbury et al. (1997)
<i>Wilsonia pusilla</i>	32.00	34.52	71.35	52.93	4		1.5	59	Bereson R et al. (unpublished data)
<i>Zonotrichia albicollis</i>	12.80	41.06	65.41	53.23	2		0		Tuttle (1993)
<i>Zonotrichia leucophrys</i>	36.00	19.74	69.04	44.39	3	35.0	0	110	Sherman and Morton (1988)
<i>Zosterops lateralis</i>	0	-52.25	-10.21	31.23	0	12.0	0	122	Robertson et al. (2001)

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