# The Evolution of Bird Song: Comparative Analyses

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# The evolution of bird song: comparative analyses

ANDREW F. READ AND DANIEL M. WEARY†

*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.*

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## SUMMARY

Several ecological and behavioural factors are correlated with interspecific differences in the complexity and temporal arrangement of passerine songs. For example, song repertoires are larger in species where males provide more parental care; syllable repertoire sizes are greater in polygynous species; migrants have larger song and syllable repertoires; and more vocalization during a song bout is associated with higher fecundities and lower metabolic rates. These associations often differ at different taxonomic levels, suggesting that the factors causing divergence in song characters within genera are different from those responsible for divergence among more distantly related taxa. In general, correlates of greater song complexity can be interpreted as those factors likely to produce more intense inter- or intra-sexual selection (polygyny, migration, paternal care). Measures of song output are correlated with factors likely to be associated with species differences in energetic requirements (metabolic rate) or reproductive effort (fecundity). The ecological and behavioural correlates of within-song complexity differ from those of between-song complexity, suggesting that they are not alternative solutions to the same selective pressures.

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† Present address: Centre for Food and Animal Research, Agriculture Canada, Ottawa, Ontario, Canada K1A 0C6.

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## 1. INTRODUCTION

As exemplified by the tails of swallows, birds of paradise and peacocks, sexually selected traits vary enormously. Presumably this diversity has arisen because of interspecific differences in factors which constrain and promote sexual selection, a view which has had considerable success in explaining interspecific variation in traits used in male–male combat and sperm competition (e.g. body, antler, canine and testes size in various groups of mammals (Harvey and Bradbury 1991)). However, the factors responsible for generating interspecific variation in signalling systems associated with mate choice and non-contact antagonistic encounters have received surprisingly little attention from comparative biologists (Bradbury & Andersson 1987, Harper 1991).

Experimental evidence has demonstrated that song in passerines plays a role in mate attraction and male–male competition (Searcy & Andersson 1986, Catchpole 1987, Harper 1991, McGregor 1991), and is therefore a sexually selected trait. The temporal construction and complexity of songs vary enormously between species, even though males in all passerine species have to attract females and compete with other males for females and resources. Numerous hypotheses have been presented in an attempt to explain such variation (reviewed by Krebs 1977, Krebs & Kroodsma 1980, Slater 1981, Payne 1983, Harper 1991, McGregor 1991). Recent hypotheses have the common theme that sexual selection is involved, but there are different views on the relative strength and direction of intra- and inter-sexual selection on song, and on the relevance of psychological (see, for example, Hartshorne 1973), physiological (see, for example, Lambrechts & Dhondt 1988) or acoustical (see, for example, Wiley & Richards 1982) constraints.

Are species differences in ecology, behaviour, morphology and physiology associated with species differences in song? We attempt to answer that question for two aspects of song diversity: song complexity and the temporal organization of singing bouts.

## 2. PUTATIVE CAUSAL VARIABLES

### (*a*) *Costs*

Singing may be energetically expensive for birds (Brackenbury 1979). Several studies have reported circumstantial evidence that producing more song during a song bout (for example, with longer songs or shorter intersong intervals) is more expensive than producing less song (reviewed by Reid 1987, Cuthill & MacDonald 1990). Studies on anuran calling have demonstrated large physiological costs (Taigen & Wells 1984, Halliday 1987, Ryan 1988). Whether singing songs of greater complexity is also more costly is harder to determine, although some indirect evidence implies that it is. First, the ability to sing complex songs requires greater neuronal development (Nottebohm *et al.* 1981, Canady *et al.* 1984). Second, the size of song nuclei in the forebrain may fluctuate seasonally with the need to sing (Nottebohm *et al.* 1986). Finally, neural song control regions are sexually size dimorphic, as are repertoire sizes (Brenowitz & Arnold 1986).

Given these costs, sexual selection on song might be constrained in energetically marginal species (Halliday 1987, Partridge & Endler 1987, Ryan 1988). If so, small-bodied species with high metabolic rates will have less complex and less continuous songs.

### (*b*) *Benefits*

Darwin (1871) used evidence of an association between polygyny and elaborate ornamentation to support his theory of sexual selection. A variety of authors have suggested that polygyny in passerines also promotes greater song output and complexity. For example, within North American wrens (Troglodytidae), polygynous species ($n = 5$) generally sing with greater continuity and have more complex songs than do monogamous species ($n = 5$) (Kroodsma 1977). Similarly, in a comparison of two finch species, Payne (1983) found that the promiscuous species had a larger song repertoire. However, other tests have produced conflicting results. Monogamous species of *Acrocephalus* warblers ($n = 4$) and buntings from the genus *Emberiza* ($n = 4$) have longer, more complex songs than do polygynous congeneric species ($n = 2$, $n = 1$, respectively; Catchpole 1980, Catchpole & McGregor 1985). Among 56 species of wood warblers (Parulinae), Shutler & Weatherhead (1990) found no differences in song complexity or output associated with mating system ($n = 5$ regularly and $n = 11$ occasionally polygynous species). Among 17 species of New World blackbirds (Icterinae), there is no association between song and mating system (Irwin 1990).

Studies on other aspects of avian vocalizations suggest that mating systems can influence the evolution of vocal signalling systems. In a comparative analysis of vocalizations from one family of songbirds (Ploceidae), Loffredo & Borgia (1986) found that species which mate polygynously produced a greater numbers of buzzes, non-vocal sounds and noisy sounds of different types. Female songbirds are more likely to sing in monogamous species (Farabaugh 1982). Promiscuous birds of paradise ($n = 8$ species) have multi-note calls, whereas monogamous species ($n = 2$) have single-note calls (Pruett-Jones *et al.* 1990).

If females locate and choose males on the basis of secondary sexual characters, song may be more common in species in which other sexually selected traits, especially bright colours and elaborate plumes, are strongly selected against (e.g. by predation; Darwin 1871, Partridge & Endler 1987). The idea that song is elaborated in cryptic species has a long history in the literature (see, for example, Darwin 1871, Huxley 1938, Gilliard 1956, Lack 1968, Catchpole & McGregor 1985), but the generality of the idea has been formally tested in only one taxon (Shutler & Weatherhead 1990).

Few models predict the ecological characteristics of species in which female choice will lead to elaboration of male traits. One exception is Hamilton & Zuk's (1982) prediction that elaborate male traits should be found in species subject to high parasite pressure, since these traits may allow females to choose healthy mates as partners. Hamilton & Zuk reported a correlation across species between blood parasite prevalence and song, but recent analyses failed to find any such associations when phylogenetic associations were controlled for (Read & Weary 1990). Another exception is Catchpole's (1980, 1982) prediction that migrant species will have less time to obtain a territory and attract a mate, and this may lead to increased intersexual selection on song.

There are many predictions about the ecological and behavioural conditions which lead to male–male competition. Competition might be higher in hole-nesting species since nest sites are scarcer; in species with a high density of competing conspecifics, especially floating non-residents; in species where territory owners benefit from expanding their territories; and in migratory species, where rapidly obtaining a good territory to attract a mate may be crucial (Catchpole 1980, Craig & Jenkins 1982, Morton 1982, Kroodsma & Verner 1987). Many of these ideas lead to direct comparative predictions (e.g. differences in migratory behaviour and nest type should be correlated with interspecific song diversity), whereas others can be tested indirectly. For example, territory expansion may also be more crucial in small-bodied species with high metabolic rates, if food can be more easily acquired in larger territories (Morton 1982). Similarly, adult mortality rates should give an indication of territory turnover. Mortality rates in birds are difficult to obtain and are available (Saether 1988) for a rather small number of species for which song data are available. But annual fecundity in birds is known to be highly correlated with both adult and juvenile mortality (Saether 1988, Bennett & Harvey 1988), and so ought to be correlated with the rate at which territory ownership changes.

Differences in extrinsic mortality (mortality risk that is unrelated to reproductive rate (Sibly & Calow 1986)) may contribute to variation in the opportunity for sexual selection. Current reproductive effort (Gadgil & Bossert 1970) is expected to be higher in species which are less likely to breed again (Williams 1966, Patridge & Ender 1987). Song is a component of current reproductive effort, and thus may be greater in species with higher extrinsic mortality patterns. Because adult mortality rates and fecundity are correlated across bird species (Saether 1988, Bennett & Harvey 1988), differences in fecundity should also correlate with singing effort.

### (*c*) *Environmental constraints*

Of the ecological conditions which might constrain song evolution, species differences in habitat type has received the most attention. Many authors have suggested that song may differ among habitats because the acoustic properties of different habitats (in particular patterns of sound transmission) impose selection on the complexity and temporal organization of song (see, for example, Hunter & Krebs 1979, Wiley & Richards 1982, Shy 1983, Bowman 1983, Krebs & Dawkins 1984, Sorjonen 1986, Wiley 1991). Furthermore, song bird diversity and density undoubtedly varies with habitat. Signal detectability may therefore be decreased in some habitats because of noise levels from other singing birds. This could be countered by reducing repertoire sizes and increasing repetition (Wiley & Richards 1982). Reports of song differences associated with habitat differences are common (see, for example, Kroodsma 1977, Hunter & Krebs 1979, Wiley 1991).

## 3. THE COMPARABILITY PROBLEM

A number of possible factors which might promote and constrain the evolution of song can be identified, but with few exceptions (Sorjonen 1986, Read & Weary 1990, Shutler & Weatherhead 1990) these factors have not been subjected to comparative tests across a wide range of passerines (Harper 1991). A potential stumbling block is that measures of complexity may not be comparable between species. As an example of this 'comparability problem' (Krebs & Kroodsma 1980; Kroodsma 1982), consider the songs of winter wrens (*Troglodytes troglodytes*) and rock wrens (*Salpinctes obsoletus*). The former species repeats the same song several times before switching to another, has a repertoire of between three and ten songs, and each song is composed of around 70 different syllables. In contrast, the songs of rock wrens are composed of only one syllable type, but sequential song types are always different and they are drawn from a repertoire of around 100 songs (Kroodsma 1977). How can the songs of these species be compared? What if in both species the song patterns are the result of runaway selection through female choice (Fisher 1930; Lande 1981) initiated by the same social conditions (e.g. polygyny), but which has headed off in arbitrarily different directions? If this were the case, it would be an example of a problem common to all comparative analyses of adaptation: multiple solutions to the same selective pressures (Ridley 1983, Harvey & Pagel 1991). The existence of multiple solutions is intuitively compelling but difficult to prove: two species are likely to differ in ways not under investigation, so there may be very good undiscovered reasons why they differ. For example, the winter wren is polygynous, the rock wren monogamous; perhaps the balance of conflicting pressures of intra- and inter-sexual selection therefore differs in the two species, leading to different singing behaviour. Such logic suggests that the comparability problem may actually be a description of the phenomena under investigation rather than a difficulty for comparative biologists to overcome. We take the view that all differences should be seen as problems worth tackling, rather than arbitarily dismissing some as the outcome of factors which cannot be detected.

## 4. METHODS

### (*a*) *Song variables*

Species means for each of the following variables were extracted from the literature. Data on at least one song variable were gathered for 165 passerine species from five superfamilies (Tyrannoidea, Corvoidea, Fringilloidea, Sylvioidea, Turdoidea); collection methods and data are given in Appendix 1. Terminology follows Weary & Lemon (1988), who also provide definitions.

*Temporal organization*

(i) Song duration (s) (136 species); (ii) inter-song interval (s) (98 species); (iii) continuity (= song duration/(song duration + inter-song interval) (98 species)); and (iv) Song rate (= 60/(song duration + inter-song interval) (98 species)).

*Song complexity*

A variety of measures of song complexity are reported in the literature. We have attempted to partition complexity into three measures: (i) song repertoire size: the number of song types possessed by an individual (a measure of between-song complexity) (113 species); (ii) syllable repertoire size: the mean number of different syllable types within a song (a measure of within-song complexity) (143 species); and (iii) versatility: species were categorized as being either immediately versatile, where song types are rapidly switched (ABCDBDAC....), eventually versatile, where song types are repeated several times before switching (AAAABBBBCCCC....), or non-versatile, where a single song type is repeated through a song bout (AAAAAAA....) (108 species).

Note that our measure of syllable repertoire size differs from that used by some other authors (e.g. Catchpole 1980), who define syllable repertoire size as the total number of syllables in an individual's repertoire. Within particular taxa, such a measure may be a useful index of song complexity, but in broad analyses such as ours, it blurs the distinction between within and between-song complexity. Species with only a few different syllables in any song, but many different syllables in their repertoire, have in effect considerable between-song complexity and relatively little within-song complexity. Our measure of song repertoire size reflects total syllable repertoire size, as well as complexity arising from rearrangements of syllables.

In the analyses reported below, species with unmeasurably large song or syllable repertoire sizes, such as the North American robin (*Turdus migratorius*), were given a repertoire size equal to one greater than the maximum recorded in our data set. Versatility was treated as a continuous variable, but the conclusions are unaltered if it is treated as categorical variable.

### (*b*) *Putative causal variables*

Data sources are given in Read (1991), except where mentioned. For many species, there are population differences in some of the following variables. We assume that these are small compared with interspecific differences. If, for a discrete variable, a single species could be classified in more than one category, the predominant category was taken as the species value. If, for species found in both Europe and North America ($n = 8$), values differed in the two regions, the value was taken as missing for discrete variables and averaged for continuous variables. Communal nesting has arisen independently a minimum of six times in the species represented in the data set (a total of ten species). The remaining 155 species are territorial and so the effects of nest dispersion on song were not investigated.

*Body size*

Body mass (g) used as an index of size; data from P. Bennett (personal communication), sources are given in Bennett (1986).

*Resting metabolic rate (kcal/d)*

Data from Bennett & Harvey (1987), using only those data they included in their analyses (their Appendix 2). So that body mass and resting metabolic rate (RMR) estimates were from the same sources, Bennett & Harvey's estimates of body mass were used in analyses of RMR in which the effects of mass were controlled for.

*Reproductive rate*

Clutch size and annual fecundity (product of clutch size and broods per year) were used as measures of seasonal reproductive effort and survivorship. Data from sources given in Bennett (1986) and Trevelyan *et al.* (1990).

*Visual showiness*

The average of subjective scores by six ornithologists (who were unaware of the uses to which the data would be put; data from Read & Harvey 1989). For each species, males were scored on a showiness scale of 1 to 6, with 1 being very dull and 6 very striking. For discussion of the scoring procedure, see Read & Harvey (1989).

*Habitat*

Three variables were used to investigate habitat effects: habitat type, forested against open habitats, and nest type. (i) Habitat type: breeding habitat categorized (following Baker & Parker 1979, Bennett 1986) as forest; woodland; scrubland; tundra (also includes moorland and mountain lands); grassland (also includes steppe and savannah); marsh; freshwater (streams, rivers, lakes, ponds); and land (species living in more than one of: woodland, scrubland, tundra or grasslands). (ii) Open and forested habitat: a recategorization of habitat type, following several authors (e.g. Wiley & Richards 1978, Ryan & Brenowitz 1985, Wiley 1991) who report different sound transmission properties in forested habitats compared with more open habitats. Forested habitats were taken as a combination of forest and woodland, or scrub (if habitat descriptions suggested that the preferred scrub was in forests or woodlands), open habitats as the remainder. Where a species inhabits woodland and/or scrub, as well as more open habitats, they were categorized as living in open habitats if they spend the majority of their time there. (iii) Nest type: hole nests (including dome and roofed nests, and nests in crevices); ground nests (including raised nests in reeds and lakes); arboreal open nests.

*Behaviour*

(i) Male parental effort. Three variables: male contribution to nest building, to incubation, and to feeding young. Each was scored on a three point scale – only female, largely female or both sexes. In the results reported below, these variables were treated as continuous; the conclusions are the same if they are treated as discrete. (ii) Mating system. Categorized as monogamous or polygynous. See Read (1991) for sources, definitions, and a discussion of the difficulties of categorizing a species as monogamous. (iii) Migratory behaviour. Scored on a three point scale – resident, partial migrant, or migrant – and treated as a continuous variable in the analyses reported below. The conclusions are unaltered if the variable is treated as categorical.

### (*c*) *Controlling for phylogenetic associations*

It is well known that species cannot be considered as independent points in comparative analyses (Harvey & Mace 1982, Ridley 1983, Pagel & Harvey 1988, Harvey & Pagel 1991). The approach used here to control for phylogenetic associations is to look for evidence of an association within different radiations as recognized by monophyletic taxa (Felsenstein 1985, 1988, Pagel & Harvey 1988, Harvey & Pagel 1991). So long as each taxon is derived from a different common ancestor, these within-taxon associations are statistically independent. Three different tests were used; all three share this basic principle of controlling for phylogeny by looking within different taxa.

### (*d*) *Analysis*

Phylogeny was inferred from taxonomy following Howard & Moore (1980) for species and genera, and Sibley & Ahlquist (1985) at higher levels, except for the Sylviidae, where we follow Howard & Moore (1980) and Simms (1985). Body mass, RMR, clutch size, annual fecundity and all song variables were logarithmically transformed prior to analysis.

We used three methods to test for an association between variables. First, Pagel & Harvey's method of independent comparisons of incompletely resolved phylogenies (see Pagel & Harvey 1989, and especially Harvey & Pagel 1991, pp. 150–162). This method analyses covariance between two or more variables within taxa, by asking whether the variables are associated across species within genera, generic means within tribes, tribal means within subfamilies and so on. Each taxon that contains two or more subtaxa is equally weighted in the analysis. This method also allows relation between two variables to be examined when the effects of third variables are controlled for. For full discussion of this method, see Harvey & Pagel (1991), and Promislow (1991); for examples of its use, Trevelyan *et al.* (1990), Harvey *et al.* (1991*a*), and especially Promislow (1991) who gives worked examples.

To confirm that the $p$-value associated with the $F$-test was not unduly influenced by single outlying taxa (examples of this problem are given below), a second test for an association between variables was performed by calculating Spearman rank correlation coefficients to test for a correlation between the rank order of the linear contrasts. A second reason for testing the association non-parametrically is that there may be a nonlinear relation between the dependent and independent variables.

However, it is also possible that a particular relation is sufficiently nonlinear that even the rank orders of the linear contrasts are not correlated (e.g. if the sign of intra-taxon differences in the dependent variable is predicted by the sign of the differences in the independent variable, but not the magnitude of the differences). Thus, we performed a third test by calculating the number of taxa within which a particular correlation between two variables was positive and negative, and tested this against a null hypothesis of equality (Harvey & Pagel 1991, p. 160). Taxa within which there is no variation in the dependent variable despite variation in the independent variable should count in favour of the hypothesis of null association. We adopted the conservative solution of initially testing the hypothesis of equal proportions of positive and negative associations within only those taxa in which there is variation in both variables under consideration. Then, where this ratio was significantly different from unity, we counted the taxa with variation in the test variable but not the dependent variable as going against the most common direction. Where the direction of causality was not clear, the two variables were considered in turn as test variables.

It is possible that associations will differ among taxonomic levels (Pagel & Harvey 1988). For example, species within genera are more likely to be subject to similar selective pressures than are species in different families. Selective factors which differ between higher taxa may therefore obscure associations between song and other causal factors. To investigate this possibility, each of the three tests was performed within all taxa to search for any overall associations, and analyses were re-run using only the intra-generic comparisons, and then only intra-taxon comparisons from higher taxonomic levels.

In summary, three tests for an association between a song variable and a purported causal variable controlling for phylogenetic associations were conducted: (i) an $F$-test for association between intra-taxon differences (linear contrasts); (ii) a non-parametric test for association between the rank orders of the linear contrasts; and (iii) a sign test of positive and negative intra-taxon associations. In each case, for taxa with more than two subtaxa, the relevant test statistic was calculated for all taxa, all genera, and all taxa except genera.

## 5. RESULTS

### (*a*) *Body size*

Differences in body mass within taxa were not significantly associated with differences in the song

Table 1. *Associations between body mass and song variables*

(Tabulated values are ratio of positive to negative intra-taxon associations, and the *F*-value for the correlation between linear contrasts within taxa. Spearman rank correlation coefficients were also calculated to test for associations between linear contrasts; none were significant.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| song duration | 28:22 | $F_{1,49}=0.52$ | 17:10 | $F_{1,26}=2.85$ | 11:12 | $F_{1,21}=0.01$ |
| intersong interval | 24:16 | $F_{1,38}=0.53$ | 11:8 | $F_{1,17}=4.15$ | 13:8 | $F_{1,19}=0.02$ |
| continuity | 21:19 | $F_{1,38}=1.38$ | 12:7 | $F_{1,18}=0.52$ | 9:12 | $F_{1,19}=0.23$ |
| song rate | 15:25 | $F_{1,38}=0.11$ | 8:11 | $F_{1,17}=2.25$ | 7:14 | $F_{1,19}=0.08$ |
| song repertoire size | 24:10[a] | $F_{1,44}=0.36$ | 9:4 | $F_{1,22}=0.09$ | 15:6 | $F_{1,20}=0.10$ |
| syllable repertoire size | 28:25 | $F_{1,56}=0.17$ | 12:13 | $F_{1,27}=0.30$ | 16:12 | $F_{1,27}=0.07$ |
| versatility | 15:10 | $F_{1,43}=0.84$ | 6:0 | $F_{1,21}=0.02$ | 9:10 | $F_{1,20}=0.07$ |

[a] $p<0.05$, but see text for a discussion of this association.

variables (table 1). Within 24 of the 34 taxa within which both body size and song repertoire size vary, taxa characterized by heavier bodies have larger song repertoires (binomial $p=0.024$). However, there are 12 taxa within which there is variation in body mass but not song repertoire size and therefore there are positive associations in 24 taxa of 46 taxa, as expected by chance alone (binomial $p=0.88$). Thus, there is no strong evidence of an association between body mass and song.

### (*b*) *Metabolic rate*

Data on resting metabolic rate (RMR) and song are available for few species, limiting the number of within-taxa comparisons that can be made. Thus, only analyses within all taxa are reported in table 2.

Continuity is negatively associated with RMR within taxa significantly more often than expected by chance alone (table 2; binomial $p=0.013$). Thus, subtaxa with higher RMR are more likely to sing less continuously, but the magnitude of the differences in RMR are not associated with the magnitude of differences in song continuity. When intra-generic comparisons are excluded, the association between the magnitude of the intra-taxon differences in continuity and RMR is significant and negative ($F_{1,9}=5.54$, $p=0.043$). This is not due to one or a few isolated outliers: non-parametric analyses lead to the same conclusion ($r_s=-0.62$, $p=0.05$), and the association is still more commonly negative than positive (nine out of ten cases; binomial $p=0.021$). Thus, taxa characterized by continuous singers have lower resting metabolic rates.

Table 2. *Associations within all taxa between the song variables and resting metabolic rate* (RMR) *and* RMR *controlling for the effects of body mass*

(Tabulated values are ratio of positive to negative intra-taxon associations, and *F*-values for the association between linear contrasts within taxa.)

| | RMR | | RMR controlling for body mass |
|---|---|---|---|
| song duration | 9:14 | $F_{1,22}=0.06$ | $F_{1,21}=1.60$ |
| intersong interval | 12:5 | $F_{1,15}=3.65$ | $F_{1,14}=0.95$ |
| continuity | 3:14[a] | $F_{1,15}=0.03$ | $F_{1,14}=0.01$ |
| song rate | 5:12 | $F_{1,15}=0.30$ | $F_{1,14}=10.86$[b] |
| song repertoire size | 10:7 | $F_{1,18}=0.05$ | $F_{1,17}=0.16$ |
| syllable repertoire size | 15:14 | $F_{1,30}=0.27$ | $F_{1,29}=3.50$ |
| versatility | 9:6 | $F_{1,17}=0.72$ | $F_{1,16}=1.74$ |

[a] $p<0.05$.
[b] $p<0.01$.

But size may largely determine metabolic rate (Bennett & Harvey 1987), so we re-examined RMR once the effects of body size have been removed, and found a negative relation with song rate (table 2; non-parametric statistics support this conclusion: $r_s=-0.54$, $p=0.03$). That is, taxa with higher metabolic rates for their body mass tend to have lower song rates. No other song variable is significantly associated with relative RMR.

### (*c*) *Reproductive rate*

Within higher taxa, subtaxa with larger clutch sizes sing more continuously (table 3*a*; binomial $p=0.027$). This is different from the situation found within genera ($\chi^2_{[1]}=8.06$, $p=0.005$), where in most genera (table 3*a*; binomial $p=0.057$), species with larger clutches usually sing less continuously. These associations between clutch size and continuity are not linear: there is no significant association between the magnitude of differences in clutch size and the magnitude of the differences in continuity (table 3*a*). No other song variables were significantly associated with clutch size (table 3*a*).

Annual fecundity is negatively associated with intersong interval and positively associated with both continuity and song rate within higher taxa (binomial $p=0.041$, 0.041 and 0.012, respectively). These relations are also not linear (table 3*b*), and in each case the direction of the associations is opposite to that found within genera, though only significantly so for intersong interval and song rate ($\chi^2_{[1]}=5.44$, $p=0.02$; $\chi^2_{[1]}=2.37$, $p=0.12$; $\chi^2_{[1]}=5.09$, $p=0.024$, respectively). Thus, among higher taxa, subtaxa characterized by higher annual fecundities sing more continuously and at a faster rate.

Within genera, there is a significant association between the magnitude of differences in annual

Table 3. *Associations within taxa between the song variables and clutch size and annual fecundity (product of clutch size and number of broods per year)*

(Life-history data logarithmically transformed before analysis. Tabulated values are ratio of positive to negative intra-taxon associations, and *F*-values for the correlation between linear contrasts within taxa. Spearman rank correlation coefficients were also calculated to test for associations between linear contrasts; none were significant.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| Clutch size | | | | | | |
| song duration | 21:19 | $F_{1,39}=0.06$ | 10:7 | $F_{1,16}=0.10$ | 11:12 | $F_{1,21}=0.01$ |
| intersong interval | 17:18 | $F_{1,33}=0.29$ | 8:6 | $F_{1,12}=0.39$ | 9:12 | $F_{1,19}=0.23$ |
| continuity | 19:16 | $F_{1,33}<0.01$ | 3:11 | $F_{1,12}=0.05$ | 16:5[a] | $F_{1,19}=0.04$ |
| song rate | 20:15 | $F_{1,33}=0.58$ | 7:7 | $F_{1,12}=0.02$ | 13:8 | $F_{1,19}=3.64$ |
| song repertoire size | 11:18 | $F_{1,36}=0.34$ | 3:6 | $F_{1,15}=0.56$ | 8:12 | $F_{1,19}=0.05$ |
| syllable repertoire size | 25:20 | $F_{1,46}=1.88$ | 7:10 | $F_{1,17}=1.14$ | 18:10 | $F_{1,27}=0.39$ |
| versatility | 10:13 | $F_{1,36}=0.46$ | 3:1 | $F_{1,14}=0.17$ | 7:12 | $F_{1,20}=0.29$ |
| Annual fecundity | | | | | | |
| song duration | 20:20 | $F_{1,39}=2.24$ | 8:10 | $F_{1,17}=0.28$ | 12:10 | $F_{1,19}=2.47$ |
| intersong interval | 15:19 | $F_{1,32}<0.01$ | 10:4 | $F_{1,12}=0.05$ | 5:15[a] | $F_{1,18}=0.26$ |
| continuity | 21:13 | $F_{1,32}=2.84$ | 6:8 | $F_{1,12}=2.33$ | 15:5[a] | $F_{1,18}=0.63$ |
| song rate | 21:13 | $F_{1,32}=1.31$ | 5:9 | $F_{1,12}=0.91$ | 16:4[a] | $F_{1,18}=0.19$ |
| song repertoire size | 18:10 | $F_{1,34}=0.64$ | 6:3 | $F_{1,14}=5.07$[a] | 12:7 | $F_{1,18}=0.19$ |
| syllable repertoire size | 20:22 | $F_{1,45}=0.30$ | 9:7 | $F_{1,17}=0.23$ | 11:15 | $F_{1,26}=2.42$ |
| versatility | 15:8 | $F_{1,35}=0.03$ | 4:1 | $F_{1,14}=0.30$ | 11:7 | $F_{1,19}=0.03$ |

[a] $p<0.05$.

fecundity between species and the magnitude of differences in their song repertoire size, but this association is not significant when non-parametric statistics are used (table 3*b*), suggesting that outlying taxa are responsible for the associations. Indeed, two genera (*Phylloscopus* and *Troglodytes*) contain species which differ only slightly in fecundity but which have very large differences in repertoire sizes. If they are excluded, there is no significant association ($F_{1,12}=2.0$, $p=0.18$). No other associations between annual fecundity and song are significant (table 3*b*).

Neither clutch size nor annual fecundity are correlated with body mass in the taxa represented in this sample ($F_{1,59}=1.35$, $p=0.25$, negative associations within 19 of 48 taxa, binomial $p=0.19$; $F_{1,51}=0.17$, $p=0.69$, negative associations within 22 of 50 taxa, binomial $p=0.47$, respectively), so analyses of reproductive rate relative to body mass are unnecessary.

### (*d*) *Visual showiness*

For 15 of the 20 genera within which there is variation in both syllable repertoire size and visual showiness, species which are visually showier have smaller syllable repertoire sizes more often than expected by chance alone (binomial $p=0.041$; table 4). But there are an additional two genera within which there is variation in visual showiness but not in syllable repertoire size. These support the null hypothesis of no association. There is therefore a negative relation between song and colour in just over two thirds of genera, but this is not significantly different from that expected by chance alone (binomial $p=0.13$; there are also two genera within which there is variation in syllable repertoire size but not visual showiness, so the same conclusion applies even if the direction of causality is reversed). There is no such association within higher taxa, so the tendency for visually duller birds to have more complex songs is not found among more distantly related birds. No other song variables were significantly associated with visual showiness. Thus, there is no evidence for a general association between visual showiness and song.

### (*e*) *Habitat*

None of the song variables were significantly associated with variation in habitat type. There was too little intra-generic variation in habitat to allow meaningful analysis, and within higher taxa there were no significant associations. When each habitat was compared with all others, the only significant association was between song versatility and grassland habitats: taxa containing a large proportion of species living in grassland habitats are significantly more likely to contain less versatile singers than are related taxa containing fewer or no grassland-dwelling species (10 of 11 possible comparisons, binomial $p=0.012$).

When habitat types were pooled into forested habitats and open habitats, we found that songs in forests are produced at a faster rate and are more continuous (table 5). In neither case are these associations linear. The magnitude of differences in song rate within each taxon do not correlate significantly with the differences in the proportions of subtaxa within those taxa dwelling in open habitats, but the rank orders of the differences do ($r_s=-0.44$, $p=0.006$, $n=40$ intra-taxon comparisons). A similar association is found within genera ($r_s=-0.59$, $p=0.013$, $n=19$ intra-generic comparisons), but is not significant within higher taxa ($r_s=-0.37$, $p=0.10$, $n=21$ intra-taxon comparisons).

The relation between versatility and habitat is more complex. Within all taxa, subtaxa with higher mean

Table 4. *Associations between song and visual showiness*

(Visual showiness was scored on a subjective six-point scale (procedure described in text), with showier birds ranked higher. Tabulated values are ratio of positive to negative intra-taxon associations, and the value of $F$ for the association between linear contrasts within taxa. Spearman rank correlation efficients were also calculated to test for associations between linear contrasts; none were significant.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| song duration | 18:25 | $F_{1,42}=3.21$ | 8:13 | $F_{1,20}=1.87$ | 10:12 | $F_{1,20}=1.29$ |
| intersong interval | 18:15 | $F_{1,31}=0.13$ | 8:8 | $F_{1,14}=1.59$ | 10:7 | $F_{1,15}=0.81$ |
| continuity | 14:19 | $F_{1,31}=0.25$ | 6:10 | $F_{1,14}=2.47$ | 8:9 | $F_{1,15}=1.39$ |
| song rate | 19:14 | $F_{1,31}=0.05$ | 10:6 | $F_{1,14}=0.48$ | 9:8 | $F_{1,15}=0.08$ |
| song repertoire size | 15:15 | $F_{1,37}=0.61$ | 6:6 | $F_{1,18}=0.68$ | 9:9 | $F_{1,17}=1.75$ |
| syllable repertoire size | 18:28 | $F_{1,48}=0.32$ | 5:15[a] | $F_{1,20}=0.07$ | 13:13 | $F_{1,26}=0.54$ |
| versatility | 11:11 | $F_{1,37}=3.04$ | 2:3 | $F_{1,18}=0.13$ | 9:8 | $F_{1,17}=3.89$ |

[a] $p<0.05$, but see text for a discussion of this association.

Table 5. *Associations between song and the proportion of species living in open habitats*

(Tabulated values are ratio of positive to negative intra-taxon associations, and $F$-values for the correlation between linear contrasts within taxa. For song versatility, there was insufficient variation in habitats and versatility to allow meaningful analyses within genera.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| song duration | 17:13 | $F_{1,47}=0.05$ | 5:5 | $F_{1,24}=0.16$ | 12:8 | $F_{1,21}=1.12$ |
| intersong interval | 10:13 | $F_{1,38}=0.79$ | 1:5 | $F_{1,17}=0.81$ | 9:8 | $F_{1,19}=0.07$ |
| continuity | 11:12 | $F_{1,38}=3.35$[a] | 3:3 | $F_{1,17}=2.67$[a] | 8:9 | $F_{1,19}=0.74$ |
| song rate | 11:12 | $F_{1,38}=2.75$[b] | 3:3 | $F_{1,17}=1.56$[a] | 8:9 | $F_{1,19}=0.90$ |
| song repertoire size | 10:14 | $F_{1,33}=0.39$ | 3:2 | $F_{1,12}=1.34$ | 7:12 | $F_{1,19}=1.79$ |
| syllable repertoire size | 16:16 | $F_{1,50}=0.67$ | 3:4 | $F_{1,22}<0.01$ | 13:12 | $F_{1,26}=1.15$ |
| versatility | 4:15[c] | $F_{1,23}=0.46$ | — | | 2:15[d] | $F_{1,17}<0.01$ |

[a] Significant non-parametric correlation at $p<0.05$.

[b] Significant non-parametric correlation at $p<0.01$.

[c] $p<0.05$.

[d] $p<0.01$.

song versatilities are likely to contain a higher proportion of species living in forests (table 5; binomial $p=0.019$), but four taxa contain variation in habitat but not versatility. When these are counted against the hypothesis, open habitats are associated with less versatile singing in 15 of 23 taxa, which is not significantly different from that expected by chance alone (binomial $p=0.21$). Nevertheless, within only higher taxa, the association is significant (15 of 17 cases, binomial $p=0.002$), even when the taxa with variation in habitat but not versatility are included (15 of 19, binomial $p=0.029$).

Nest type, considered either as a three-category variable (hole nesting, open nesting or ground nest-

Table 6. *Associations between song and nest type (a three-category variable: hole, open and ground nesting) and hole against open nesting (i.e. ground nesters excluded)*

(There was too little variation in nest type within genera to attempt meaningful analyses. Tabulated $F$-values are for the correlation between the within-taxon linear contrasts. Ratios are of positive to negative intra-taxon associations between the proportion of a subtaxa that are hole nesters and a particular song variable (these ratios cannot be calculated for the three category variable). No $F$-values or ratios differed significantly from that expected by chance alone. For the hole against open nesters analysis, Spearman rank correlation coefficients were also calculated to test for associations between linear contrasts; none were significant.)

| | association with nest type | | hole against open nesting | | | |
|---|---|---|---|---|---|---|
| | within all taxa | within higher taxa | within all taxa | | within higher taxa | |
| song duration | $F_{2,42}=0.33$ | $F_{2,20}=0.11$ | 7:5 | $F_{1,33}=0.14$ | 6:5 | $F_{1,19}=0.03$ |
| intersong interval | $F_{2,37}=1.00$ | $F_{2,18}=0.03$ | 6:3 | $F_{1,26}=0.36$ | 6:3 | $F_{1,17}=0.35$ |
| continuity | $F_{2,37}=0.11$ | $F_{2,18}=1.12$ | 5:4 | $F_{1,26}=0.55$ | 5:4 | $F_{1,17}=0.51$ |
| song rate | $F_{2,37}=2.37$ | $F_{2,18}=0.58$ | 3:6 | $F_{1,26}=0.30$ | 3:6 | $F_{1,17}=0.29$ |
| song repertoire size | $F_{2,32}=0.06$ | $F_{2,18}=0.02$ | 3:7 | $F_{1,24}=0.92$ | 3:7 | $F_{1,17}=0.92$ |
| syllable repertoire size | $F_{2,50}=0.51$ | $F_{2,25}=0.94$ | 4:9 | $F_{1,35}=2.48$ | 3:9 | $F_{1,22}=2.09$ |
| versatility | $F_{2,22}=0.06$ | $F_{2,16}=0.04$ | 4:4 | $F_{1,19}=0.11$ | 4:4 | $F_{1,14}=0.14$ |

ing) or as a two-category variable (hole against open nesters, ground nesters excluded) was not significantly associated with any of the song variables (table 6).

### (*f*) *Male parental effort*

Taken together in a multiple regression, the three variables describing male parental effort at each stage of the nesting cycle predict significant amounts of variation in only two of the song variables (table 7), song rate within all taxa ($p=0.035$) and song repertoire size within higher taxa ($p=0.016$). The association with song rate is due to a single outlying genus (*Emberiza*) which contains large variation in both song rate and male parental effort, and is not significant if this genus is excluded ($F_{3,33}=0.64$, $p=0.59$).

How does the association between repertoire size and male parental effort arise? Controlling for the male contribution at the other two stages, there are significant associations with both male effort at nest building and feeding young, but not assistance during incubation (nest building, $F_{1,14}=5.89$, $p=0.027$; feeding young, $F_{1,14}=12.27$, $p=0.003$; incubation, $F_{1,14}=0.12$, $p=0.73$).

Each of the three variables describing male parental effort were tested separately for an association with the song variables following the procedure used for other single continuous variables above. The only significant association, apart from that just described, was between song versatility and feeding young. Within all taxa, and within higher taxa (there was insufficient variation in versatility and male feeding behaviour to allow meaningful analyses within genera), differences in male effort at provisioning the brood were positively associated with differences in versatility (16 of 21 cases, binomial $p=0.027$; 14 of 18 cases, binomial $p=0.031$, respectively). A similar association was found in the analyses reported in table 7 when variation in male contribution at other nesting stages were controlled (within all taxa: partial $r=+0.42$, $p=0.055$; within higher taxa: partial $r=+0.57$, $p=0.018$). Thus, increases in male contribution to feeding young are associated with increases in song versatility; this relation is linear when the effects of male contribution to other nesting stages are controlled for.

To summarize the effects of male parental care: greater male assistance with feeding young is associated with more versatile singing, and, within higher taxa, bigger song repertoires. For a given level of paternal provisioning of the young, greater male assistance with nest building is associated with smaller song repertoires within higher taxa.

### (*g*) *Mating system*

Lower song rates are associated with polygyny (table 8). Within all taxa this relation is significant (binomial $p=0.009$), but the trend is similar within genera (binomial $p=0.070$) and within higher taxa (binomial $p=0.096$) (in each case, there are no taxa with variation in mating system but not song rate). The rank orders of the differences are significantly associated within all taxa and within higher taxa ($r_s=-0.47$, $p=0.004$, $n=40$; $r_s=-0.51$, $p=0.024$, $n=21$, respectively).

Syllable repertoire size is positively associated with polygyny (table 8). That is, polygynous species and taxa containing a large proportion of polygynous subtaxa have more complicated songs (within all taxa binomial $p=0.0012$; within genera, binomial $p=0.065$, within higher taxa, binomial $p=0.015$; when taxa with variation in mating system but not in syllable repertoire are included, $p=0.005$, $p=0.146$ and $p=0.029$, respectively). Neither the magnitude of the differences in syllable repertoire sizes and polygyny, nor the rank order of the differences are correlated.

### (*h*) *Migratory behaviour*

Migration and continuity are associated within genera (table 9), but this association is due to a single genus, *Phylloscopus*, which contains both migratory and partly migrant species which differ widely in continuity. There is no consistent association within the other genera ($F_{1,16}=0.76$, $p=0.40$).

Species which are more migrant than their congeners have larger song repertoires. This intra-generic relation is not the result of one or a few outliers: the association between rank order of differences in song repertoire size and migratory behaviour is also signifi-

Table 7. *Associations between song and male parental effort*

(Tabulated *F*-values are from a multiple regression analysis of the intra-taxon linear contrasts of a song variable on to the intra-taxon linear contrasts of male contribution to nesting, incubation, and feeding of young. For each of these dependent variables, each species was scored on a three-point scale (none, less than female, same as female). There was insufficient variation in parental care and versatility within genera for meaningful analysis.)

| | within all taxa | within genera | within higher taxa |
|---|---|---|---|
| song duration | $F_{3,42}=0.42$ | $F_{3,19}=1.10$ | $F_{3,19}=0.37$ |
| intersong interval | $F_{3,34}=2.33$ | $F_{3,13}=2.75$ | $F_{3,17}=0.96$ |
| continuity | $F_{3,34}=0.22$ | $F_{3,13}=0.27$ | $F_{3,17}=0.82$ |
| song rate | $F_{3,34}=3.23^{a}$ | $F_{3,13}=2.90$ | $F_{3,17}=0.77$ |
| song repertoire size | $F_{3,28}=1.89$ | $F_{3,8}=1.62$ | $F_{3,16}=4.66^{a}$ |
| syllable repertoire size | $F_{3,45}=1.02$ | $F_{3,18}=2.2$ | $F_{3,23}=0.62$ |
| versatility | $F_{3,20}=1.54$ | — | $F_{3,15}=2.58$ |

[a] $p<0.05$.

Table 8. *Associations between song and mating system*

(Tabulated values are ratio of positive to negative intra-taxon associations between a song variable and the proportion of subtaxa that are polygynous, and $F$-values for the association between linear contrasts within taxa. There was insufficient variation in mating system and versatility within genera for meaningful analysis.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| song duration | 17:15 | $F_{1,47} = 0.31$ | 7:4 | $F_{1,24} = 0.59$ | 10:11 | $F_{1,21} = 0.02$ |
| intersong interval | 17:9 | $F_{1,38} = 1.41$ | 6:2 | $F_{1,17} = 1.06$ | 11:7 | $F_{1,19} = 0.36$ |
| continuity | 15:11 | $F_{1,38} = 0.39$ | 4:4 | $F_{1,17} = 0.01$ | 11:7 | $F_{1,19} = 0.66$ |
| song rate | 6:20[c] | $F_{1,38} = 3.99$[b] | 1:7 | $F_{1,17} = 0.99$ | 5:13 | $F_{1,19} = 3.49$[a] |
| song repertoire size | 12:13 | $F_{1,33} = 0.72$ | 3:3 | $F_{1,12} = 0.03$ | 9:10 | $F_{1,19} = 0.95$ |
| syllable repertoire size | 28:8[c] | $F_{1,50} = 0.48$ | 9:2 | $F_{1,22} = 4.09$ | 19:6[d] | $F_{1,26} = 0.48$ |
| versatility | 8:12 | $F_{1,23} = 0.02$ | — | | 5:12 | $F_{1,17} = 0.02$ |

[a] Non-parametric test for association significant at $p < 0.05$.
[b] Non-parametric test for association significant at $p < 0.01$.
[c] $p < 0.01$.
[d] $p < 0.05$.

cant ($r_s = 0.79$, $p = 0.005$). Migrants have more complicated songs: syllable repertoire size is associated with migratory behaviour within all taxa and within higher taxa (table 9; $p = 0.006$ and $p = 0.02$, respectively). Non-parametric analysis confirms this ($r_s = 0.28$, $p = 0.044$; $r_s = 0.53$, $p = 0.004$). There is no evidence of such a relation within genera (table 9; $r_s = 0.09$, $p = 0.65$).

## 6. CORRELATES OF SONG DIVERSITY

We have analysed morphological, behavioural and ecological correlates of song diversity (summarized in table 10). Our results suggest that the evolution of bird song relates to behaviour and ecology, and implies that at least some convergent evolution (genetic or cultural) in song has occurred.

### (*a*) ***Metabolic rate***

Energetic requirements might act as a constraint on song evolution, especially if greater song output or complexity is more costly (Halliday 1987, Partridge & Endler 1987). If so, output and complexity might be expected to be lower in species with higher energy requirements. There is no evidence that energetic requirements constrain song complexity: neither absolute nor relative RMR are associated with song complexity. However, both measures of song output (song rate and song continuity) are lower in taxa with higher metabolic rates, consistent with the idea that if higher RMR indicates greater energy requirements, song output is energy limited. Evidence from a number of intraspecific studies of alteration of song rates following experimental manipulation of food availability (reviewed by Reid 1987, Cuthill & MacDonald 1990), and of correlations between song rate and body condition (see, for example, Searcy 1979) and ambient temperature (see, for example, Reid 1987), supports this view.

We found no support for Morton's (1982) prediction of greater output and complexity in 'small-sized species with relatively high metabolism'. There is no association between absolute or relative metabolic rate or body mass and either song or syllable repertoire size. As far as song output goes, neither continuity nor song rate is significantly associated with body mass, and although they are associated with RMR, in both cases the association is in the opposite direction to that predicted. Thus, there is no comparative evidence in

Table 9. *Associations between song and migratory behaviour*

(Species were scored on a three-point scale (resident, partial migrant or migrant). Tabulated values are ratios of positive to negative intra-taxon associations between a song variables and the extent to which a species or taxon is migratory (treating the three-point scale as continuous), and $F$-values for the association between intra-taxon linear contrasts. There was insufficient variation in migratory behaviour and versatility within genera for meaningful analysis.)

| | within all taxa | | within genera | | within higher taxa | |
|---|---|---|---|---|---|---|
| song duration | 19:13 | $F_{1,48} = 0.18$ | 5:6 | $F_{1,25} < 0.01$ | 14:7 | $F_{1,21} = 0.55$ |
| intersong interval | 13:11 | $F_{1,38} = 0.02$ | 5:2 | $F_{1,17} = 0.15$ | 8:9 | $F_{1,19} = 1.57$ |
| continuity | 11:13 | $F_{1,38} = 1.23$ | 4:3 | $F_{1,17} = 4.70$[a] | 7:10 | $F_{1,19} = 0.05$ |
| song rate | 10:14 | $F_{1,38} = 0.11$ | 2:5 | $F_{1,17} = 0.01$ | 8:9 | $F_{1,19} = 0.20$ |
| song repertoire size | 18:11 | $F_{1,33} = 1.21$ | 7:2 | $F_{1,12} = 6.71$[b] | 11:9 | $F_{1,19} = 0.01$ |
| syllable repertoire size | 16:19 | $F_{1,51} = 8.08$[c] | 4:6 | $F_{1,23} = 0.22$ | 12:13 | $F_{1,26} = 10.13$[b] |
| versatility | 15:8 | $F_{1,23} < 0.01$ | — | | 12:7 | $F_{1,17} = 0.01$ |

[a] $p < 0.05$, but see text for discussion of this association.
[b] $p < 0.05$; non-parametric test for association significant at $p < 0.01$.
[c] $p < 0.01$; non-parametric test for association significant at $p < 0.05$.

Table 10. *Summary of associations found between putative causal variables and the song variables (controlling for phylogeny), tabulated by causal variable and by song variable*

| | |
|---|---|
| By causal putative variable | |
| Body size: | No associations with any song variable |
| Metabolic rate: | Higher RMR associated with less continuous singing<br>Higher RMR for a given body mass associated with lower song rates |
| Reproductive rate: | Larger clutches associated with more continuous songs[a]<br>Higher annual fecundity associated with shorter intersong intervals[a] and songs sung more continuously[a] and at a faster rate[a] |
| Visual showiness: | No associations with any song variable |
| Habitat: | No overall effect of habitat type, but grassland habitats associated with less versatile singing, and when habitats categorized as forested or open, forested habitats associated with faster song rates[a] and more versatile singing<br>No associations between nest type and any song variables |
| Behaviour: | Overall extent of male effort throughout nesting cycle associated with larger song repertoires. Greater contribution by male to provisioning young associated with larger song repertoires and more versatile singing. For a given level of paternal assistance with feeding the young, male assistance with nest building associated with smaller song repertoires<br>Polygyny associated with slower song rates and bigger syllable repertoires<br>Migration associated with bigger song[a] and syllable[a] repertoires |
| By song variable | |
| Song duration | No associations with any purported causal variable |
| Intersong interval | Short intervals associated with high annual fecundity[a] |
| Continuity | Greater continuity associated with lower RMR, larger clutch sizes[a] and higher annual fecundity[a] |
| Song rate | Faster song rates associated with monogamy, forested habitats[a], higher annual fecundity[a], and, for a given body size, lower RMR |
| Song repertoire size | Associated with the extent of male provisioning throughout the nesting cycle. In particular, larger repertoires associated with greater paternal provisioning of the young, and for a given level of male assistance with rearing the young, less assistance with nest building. Larger song repertoires associated with migration[a] |
| Syllable repertoire size | Larger syllable repertoires associated with polygyny, and migration[a] |
| Versatility | Song versatility is lower where males contribute little to raising offspring, in open and grassland habitats |

[a] Direction of association within genera qualitatively different from that within higher taxa: either the opposite direction or where absence of significance within one taxonomic level is not an obvious consequence of small sample sizes. Direction reported in the table is that which is most significant.

support of the predictions Morton derived from his 'ranging hypothesis'. McGregor (1991) summarizes experimental evidence which is also contrary to this hypothesis.

### (*b*) *Reproductive rate*

Within higher taxa, annual fecundity is positively associated with both measures of song output. Differences in clutch size between higher taxa are also associated with differences in continuity. These directions are significantly different from that found within genera, which is possibly a consequence of the fact that most variation in avian life history variables is found at higher taxonomic levels (Bennett 1986, Saether 1988). Differences in reproductive rate are therefore likely to be small within genera, and other factors may exert a greater influence.

Several explanations for the associations between annual fecundity and song output are suggested by the finding that fecundity is known to be strongly and negatively correlated with adult survivorship across and within avian taxa (Saether 1988, Bennett & Harvey 1988). Our analyses suggest that where adult survivorship rates are low, song output is high. If the costs of singing increase with song rate and song continuity, then this accords with the prediction from life history theory that current reproductive effort should be higher where the chances of surviving to breed again are lower (Williams 1966, Partridge & Endler 1987).

### (*c*) *Visual showiness*

Species with visually less showy males do not necessarily have more complex songs than those of their showier congenerics, in contrast to the widely held belief (see § 2*b*) that there is a negative relation between visual and vocal showiness. Our analysis supports Mayr's view (1963, p. 97) that the 'number of exceptions ... is too great for this to be accepted as a general rule'. This point emphasizes the problem of supporting general patterns by selected examples (e.g. North American wrens (Kroodsma 1977) and European warblers (Catchpole and McGregor 1985)). Clearly, there are many reasons why an association may not be found, one of which is the difficulties of assessing bird brightness (see, for example, Read & Harvey 1989).

Shutler & Weatherhead (1990) examined sexual dichromaticism and various measures of song output and complexity across 56 species of wood warblers (Parulinae) with mixed results. These are difficult to interpret, since the magnitude of sex differences in visual showiness need have nothing to do with song whatever the nature of any relation between male song and male colour. Sexual dichromaticism is likely to be a consequence of both natural and sexual selection acting independently on each sex, and on any genetic correlation between the sexes.

### (*d*) *Habitat*

Previous analyses of the effects of habitat on song evolution have dealt with frequency and finer details of temporal patterning of song than we have used. Nevertheless, consistent differences in song were found in different habitats. For the most part, these differences were only apparent when habitat types were categorized as open or forested (table 10). Song and syllable repertoire do not differ consistently with either of the habitat categorizations, but in forested habitats, song rates are higher and singing more versatile than in open habitats. Versatility is lower in grassland habitats than in the other seven habitat types.

One previous analysis of habitat and song data across diverse taxa reported similar findings. Sorjonen (1986) gathered song data on 49 species of European passerines. Although he made no attempt to control for phylogenetic associations, he too found that species living in forests had higher song rates and greater song versatility.

None of the other correlates of song rate and versatility found in this study (table 10) explain the habitat associations (association between song rate and open/forested habitats controlling for mating system as described above: $r_s = -0.43$, $p = 0.007$, $n = 40$; and there are no significant differences between open and forested habitats in relative RMR (described above); annual fecundity, $F_{1,48} = 0.02$, $p = 0.88$; male care of offspring, $F_{1,25} = 0.08$, $p = 0.79$; within all taxa in each case; non-parametric analyses and binomial tests give the same conclusion).

### (*e*) *Nest type*

There was no evidence for an association between song variation and nest type (table 6), suggesting that either male–male competition is no more intense where holes are one of the resources being fought over, or that if it is, this does not impose selection in a consistent direction on the song variables considered.

### (*f*) *Parental care*

If male singing performance is correlated with male vigour, then females could use song to assess male phenotypic quality (Catchpole 1980, Catchpole & McGregor 1985). If so, female choice based on characteristics of male song should be more common in species where males provide paternal assistance. There is no evidence of such an association with any of the measures of song output (table 10). There is, however, an association between the male's contribution to brood provisioning and both song repertoire size and versatility. For a given level of paternal care of the brood, males who provide the most help with nest building have smaller repertoires. It is possible that song repertoire sizes function secondarily in male–male competition, so only in species with limited male–male competition does it pay males to spend less time on territory defence and more on nest building.

The associations between song repertoire size and male care of young and nest building within higher taxa do not arise because of associations with other correlates of song repertoire size (table 10; feeding young, controlling for nest building and migration: $F_{1,15} = 13.38$, $p = 0.002$; nest building, controlling for feeding young and migration: $F_{1,15} = 5.35$, $p = 0.034$). Likewise, associations between paternal care of young and versatility cannot be due to habitat differences associated with versatility (table 5 and above; paternal care of young does not differ between open and forested habitats ($F_{1,17} = 0.59$, $p = 0.45$), nor does the level of paternal care of young in grassland habitats differ significantly from that found in other habitats ($F_{1,17} = 0.60$, $p = 0.45$); in all cases, reported statistics are for within higher taxa associations).

### (*g*) *Mating system*

Our results indicate that polygyny is associated with lower song rates. This is not a consequence of any of the other correlates of song rate (table 10). Song rate and mating system are still associated when the effects of open/forested habitats and annual fecundity are controlled for ($r_s = -0.48$, $n = 40$, $p = 0.003$; $r_s = -0.34$, $n = 35$, $p = 0.048$, respectively) and there is no significant association between mating system and RMR when the effects of body mass are removed ($r_s = 0.06$, $p = 0.81$, $n = 17$; in each of these analyses, reported associations are from within all taxonomic levels, use of parametric statistics does not alter the conclusions).

What explains the association between polygyny and song rate? One possibility is that females using song rate as a cue in mate choice would be most likely to obtain high quality males as fathers, and that male quality is relatively more important to females in monogamous species than in polygynous species. However, the fact that variation in song rate is not associated with male parental effort argues against this possibility. Perhaps song rates are faster in monogamous populations because males spend fewer days per breeding season singing and can therefore expend more energy per day than can males in polygynous populations, where singing does not stop after a male has attracted one female to his territory.

Within-song complexity is greater in polygynous species. However, there is no evidence of an association between mating system and between-song variability: neither song repertoire size nor versatility is significantly associated with mating systems. Why should polygyny be associated with greater song complexity? It is widely accepted that the strength of selection imposed by female choice will be much greater in polygynous populations (Darwin 1871; Fisher 1930; Bradbury & Andersson 1987), and if this is so, and song complexity is used as a cue in female choice, it should be more complex in polygynous populations. We note that previous comparative analyses have demonstrated that in some taxa, song complexity is greater in polygynous species, in others it is greater in monogamous species, and that in still others there is no association (§ 2b). While these studies demonstrate that in particular taxa, polygyny does not always result in greater song complexity, we believe our analysis is the first to investigate the association in a wide variety of different taxa.

The general association between complexity and polygyny contradicts the prediction (Catchpole 1980, 1982, Catchpole & McGregor 1985) that song complexity should be more complex in monogamous populations, given that male quality has a relatively greater effect on female reproductive success than territory quality, and that song complexity is an indicator of male quality.

The association between syllable repertoire size and mating system is not the result of an association between migration and syllable repertoire size (association between migration and syllable repertoire size: $F_{1,39}=0.64$, $p=0.43$; non-parametric statistics lead to the same conclusion).

### (*h*) *Migration*

Migratory behaviour is associated with larger song repertoires within genera, and with larger syllable repertoires within higher taxonomic levels. Why should larger song and syllable repertoire size be associated with migration? Catchpole (1980, 1982) suggested that migratory species have less time to obtain a territory and a mate than resident species, and that this would lead to more intense sexual selection and greater song complexity. The results reported here support this prediction.

These associations do not arise as a consequence of associations between migratory behaviour and other correlates (table 10) of song and syllable repertoire sizes (association between migration and syllable repertoire size remains significant when mating system is controlled for; $F_{1,24}=8.44$, $p=0.008$; there is insufficient intra-generic variation in the three paternal care variables and migration for meaningful analysis, but there is no association between paternal care and migration within all taxa; $F_{3,34}=0.44$, $p=0.73$).

## 7. GENERAL DISCUSSION

It is often pointed out that comparative analyses are only as good as the data on which they are based (see, for example, Harvey *et al.* 1991*b*). For that reason, we have appended the data used in our analyses. We have little doubt that these data could be refined (see Appendix), and it is clearly of interest to know whether we failed to find associations between some ecological and behavioural variables because of poor estimates of species values. However, it is often the case in comparative analyses that true differences between species are much greater than within-species variation or measurement error. Showing that some species values are not perfect does not invalidate our results; only further analyses constitute tests of the relations we have reported.

Many of the relationships which we have reported are found within genera but not when subtaxa within higher taxa are compared, or vice versa (table 10). For example, migratory species have larger syllable repertoires than less migratory congenerics, but taxa characterized by migratory species do not necessarily have higher average syllable repertoire sizes (table 9). The opposite is true for paternal brood provisioning: differences in parental effort by males are associated with song repertoire size when higher taxa are compared, but there is no such association when congeneric species are compared (table 7). In both cases, no associations are apparent when all intra-taxon comparisons are considered. How could such differences arise? Closely related species may share many similar selective factors, so that factors which do differ are more likely to produce detectable differences within genera, but be obscured by the effects of a greater number of other selective factors likely to differ between higher taxa. Similarly, there may be insufficient variation within genera in ecology or behaviour to produce any differences in song, but these could be revealed when higher taxa, which are more likely to differ, are compared. Where associations between a particular song variable and a putative causal variable within genera are in the opposite direction to that found within higher taxa (as is the case with song continuity and clutch size, for example; table 3*a*) the same ecological or behavioural variable must itself be associated with different conditions at different taxonomic levels. This does not mean the putative causal variable can not be involved, but an interactive effect with some other factor may be implicated.

In many cases, associations between a particular song and a putative causal variable are in the same direction significantly more often than expected by chance, but the magnitude of differences between species or subtaxa in the values of the variables are uncorrelated (table 10). Within a genera, for example, more fecund species are likely to have a higher song rate (table 3), but how much higher cannot be predicted from differences in fecundity (§ 5c). How could this situation arise? Many authors have suggested that sexually selected traits, and bird song in particular, may arise as a consequence of coevolution between signaller and receiver, or between signaller and signaller vying for a receiver's attention, and that this may lead to a runaway elaboration of song (e.g. Fisher 1930, Kroodsma 1977, Krebs & Kroodsma 1980, Catchpole 1980, Slater 1981, Craig & Jenkins 1982, Krebs & Dawkins 1984, Bradbury & Andersson 1987). If so, differences in a putative causal variable between species or higher taxa need not be linearly related to the magnitude of differences in a particular song variable. Indeed, if runaway elaboration has occurred often, the magnitude of intra-taxon differences in song variation may have more to do with those factors which halt elaboration than those which initiate it.

## 8. TOWARDS AN EXPLANATION OF INTERSPECIFIC SONG DIVERSITY

Several points emerge from our analyses which seem relevant to general explanations of bird song diversity. First, the idea that intra-sexual selection favours short, stereotyped songs and inter-sexual selection favours continuous output of complex songs, and that therefore song diversity is a consequence of interspecific variation in the relative importance of the two types of selection (Catchpole 1980, 1982, 1987, Slater 1981) does not easily incorporate the associations summarized in table 10. To a large extent, the ecological and behavioural correlates of song output differ from those associated with complexity. We see no compelling reason to consider male–male competition and female choice as imposing necessarily antagonistic selection on song. Indeed, several studies have shown that in species where song repertoire size is known to function in male–male competition, females are more likely to respond sexually to larger repertoires (see, for example, Baker *et al.* 1986, Searcy 1988).

A second general point to emerge from our analyses is that song and syllable repertoire sizes are associated with both the same and different ecological and behavioural correlates (table 10), suggesting that conditions which promote one form of complexity need not promote the other.

Third, given that song rate and continuity are known to be affected by energetic considerations, they might indicate male vigour and therefore be ideal cues in mate choice for good fathers and/or genes (Trivers 1972, Maynard Smith 1987) and for assessments of fighting ability in male–male competition. However, we found that neither song rate nor continuity are greater where more intense sexual selection might be expected (polygynous or migratory species). Instead, they are associated with resting metabolic rate and fecundity, which is consistent with the idea that the effort expended on singing depends on the energetic requirements of the species and on the costs of current reproductive effort on future reproduction.

Fourth, song repertoire size and versatility are higher where males contribute more to raising the brood. If song repertoire size is an indicator of phenotypic quality, then females choosing males with larger repertoires would obtain mates who are better fathers. If larger song repertoires evolved and are maintained as a result of female choice for high-quality phenotypes, they might also act as indicators of phenotypic quality in male–male competition. In any case, the association with male parental care is not predicted by the view that repertoire sizes are purely a consequence of the Fisherian runaway process (Fisher 1930, Lande 1981).

We suggest the following view of song evolution. The level of song output is set by the relative costs and benefits of advertising, with sexual selection always favouring increased output. Interspecific differences in the benefits of advertising are small relative to interspecific differences in costs, so that song output is associated with factors correlated with interspecific differences in the costs of singing. (Note that within species, measures of song output might still be associated with mate attraction or male–male competition, since they may be good indicators of male quality.) Larger song repertoire size and greater song versatility evolve where males play a larger role in rearing the offspring, supporting the idea (Catchpole 1980, 1982) that song repertoire size has evolved as an indicator of male phenotypic quality. Greater between-song complexity has thus evolved through female choice, although if it is an honest signal of phenotypic quality, it might also have arisen or play a role in male–male competition.

Interspecific variation in within-song complexity is not so easily accommodated in the same way. Unlike song repertoire size and versatility, syllable repertoire size does not correlate with paternal care. Rather, it is greater in those situations where sexual selection might be expected to be more intense (polygyny, migratory populations). If female choice is involved in generating interspecific differences in syllable repertoire size, then it is unlikely that females are choosing for quality of male care.

## 9. CONCLUSION

We have shown that aspects of interspecific song diversity are associated with differences in ecology, behaviour and physiology. However, we emphasize the exploratory nature of the exercise. Better data and more sensitive statistical methods may reveal additional associations. The essence of empirical testing is repeatability, and each of the correlations summarized in table 10 deserves to be tested on other species of song birds. It is in this spirit that we publish the raw data underlying our analyses (Appendix 1). Our hypotheses are amenable to testing by further comparative analyses or by intraspecific studies. As demonstrated here, the factors promoting and constraining song evolution are likely to vary from species to species, so we caution about generalizing from experiments or field studies on single populations, and urge the use of appropriate comparative analyses to test particular hypotheses.

Finally, it is likely that there are more factors influencing song diversity than those discussed in this paper. For example, when all the correlates of song repertoire size are considered together in a multiple regression, they explain only 22.3% of the variance in song repertoire sizes within all taxa. While this may be a reflection of the quality of the data and/or the comparability problem (§ 3), it seems probable that factors other than those included in this analysis remain to be discovered. There is enormous potential for further comparative analyses of song diversity, both of the variables considered here and others such as the proportion of the day spent singing and finer analyses of song structure (e.g. tonality, frequency).

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**APPENDIX.** Measures of temporal arrangement and complexity of songs of some species of European and North American passerines. Where data from the literature were available for the same species at different times of the year, we included data only on the advertising song during the pre-mating and laying periods. Song variables are defined in text; ∞ = unmeasurably large; — = missing data.

| | song duration/s | intersong interval/s | song repertoire size | syllable repertoire size | versatility | sources |
|---|---|---|---|---|---|---|
| *Empidonax difficilis* | 2 | 7 | 3 | 3 | 2 | Johnson 1980, Davis *et al.* 1963 |
| *Empidonax flaviventris* | — | — | — | 3 | — | Johnson 1980 |
| *Empidonax traillii* | 0.96 | — | 3 | 2 | — | Kroodsma 1984 |
| *Empidonax virescens* | — | — | — | 3 | — | Payne & Budde 1979 |
| *Myiarchus cinerascens* | 4 | — | — | 2 | — | Davis 1961 |
| *Myiarchus crinitus* | 3.5 | — | — | 2 | — | Davis 1961 |
| *Sayornis phoebe* | 0.4 | 1.7 | 2 | 2 | 2 | Kroodsma 1985 |
| *Lanius collurio* | — | — | — | 12 | — | Hindmarsh 1984 |
| *Vireo flavifrons* | 0.35 | 2.45 | 6 | 1.5 | 1 | Dobson & Lemon 1975, Borror 1972, James 1984 |
| *Vireo griseus* | 1 | 3 | 5.2 | 4 | 1 | Bradley 1980 |
| *Vireo olivaceus* | 0.35 | 1.42 | 43 | 2 | 2 | Dobson & Lemon 1975, Borror 1972, 1981 |
| *Vireo philadelphicus* | 0.4 | 2.25 | 25 | — | 2 | Dobson & Lemon 1975, Borror 1972 |
| *Vireo solitarius* | 0.34 | 2.3 | 15 | 2 | 2 | Dobson & Lemon 1975, Borror 1972, James 1981 |
| *Alauda arvensis* | — | — | — | 15 | — | Hindmarsh 1984 |
| *Cardinalis cardinalis* | 1.8 | 6.9 | 9 | 1 | 0 | Dobson & Lemon 1975, Lemon 1965, Lemon & Herzog 1969 |
| *Passerina ciris* | 1.91 | 7.37 | 4 | — | 2 | Dobson & Lemon 1975, Thompson 1968 |
| *Passerina amoena* | 2.13 | 8.61 | 1 | 9 | 0 | Dobson & Lemon 1975, Thompson 1968, Emlen *et al.* 1975 |
| *Passerina cyanea* | 2.2 | 8.59 | 1 | 9 | 0 | Dobson & Lemon 1975, Thompson 1968, Emlen *et al.* 1975 |
| *Pheucticus ludovicianus* | 3.7 | 10.5 | ∞ | 10 | 2 | Dobson & Lemon 1975, Lemon & Chatfield 1973, Borror 1961 |
| *Aimophila aestivalis* | 0.55 | 10 | 20 | 2 | 2 | Borror 1971 |
| *Ammodramus maritimus* | 1 | 4.4 | 4 | 3 | — | Post & Greenlaw 1975 |
| *Calcarius lapponicus* | 2.25 | — | 1 | 16 | — | Borror 1961 |
| *Emberiza calandra* | 1.6 | 10.9 | 2 | 20 | 1 | McGregor 1980 |
| *Emberiza cia* | 1.5 | 6 | — | — | — | Györgypál 1980 |
| *Emberiza cirlus* | 0.43 | 0.32 | 3 | 2 | 1 | Kreutzer 1979 |
| *Emberiza citrinella* | 2.1 | — | 2.05 | 3 | 1 | Hiett & Catchpole 1982, Helb 1985 |
| *Emberiza hortulana* | 1.5 | — | 2.5 | 3 | — | Conrads 1976, Catchpole & McGregor 1985 |
| *Emberiza schoeniclus* | — | — | 20 | 3 | — | Ewin 1976 |
| *Junco hyemalis* | 1.4 | 4.5 | 5 | 1 | 1 | Williams & MacRoberts 1977 |
| *Melospiza georgiana* | 2 | — | 3.5 | 3.5 | 1 | Falls & D'Agincourt 1982, Borror 1961 |
| *Melospiza lincolnii* | — | — | — | — | 1 | Borror 1961 |
| *Melospiza melodia* | 2.62 | 6.07 | 15 | 5 | 1 | Dobson & Lemon 1975, Reynard 1963, Mulligan 1963, Harris & Lemon 1972 |
| *Passerculus sandwichensis* | 2.25 | 6.3 | 1 | 5 | 0 | Bradley 1977 |
| *Passerella iliaca* | 2.2 | — | 3.2 | 7 | 2 | Martin 1977 |
| *Pipilo erythrophthalmus* | 0.83 | 4.39 | 6 | 1 | 1 | Dobson & Lemon 1975, Kroodsma 1971, Borror 1961 |
| *Pipilo fuscus* | 1.52 | 10.4 | 6 | 1 | 1 | Marler & Isaac 1960 |
| *Pooecetes gramineus* | 2.7 | — | 6.4 | 6.6 | — | Ritchison 1981 |
| *Spizella pallida* | 1.75 | 6.25 | 1 | 1 | 0 | Knapton 1981 |
| *Spizella passerina* | 2.61 | 6.79 | 1 | 1 | 0 | Dobson & Lemon 1975, Reynard 1963, Marler & Isaac 1960 |
| *Spizella pusilla* | 3 | — | 1 | 2 | 0 | Falls & D'Agincourt 1981, Goldman 1973 |
| *Zonotrichia albicollis* | 2.87 | 5.83 | 1 | 4 | 0 | Dobson & Lemon 1975, Borror & Gunn 1965 |
| *Zonotrichia leucophrys* | 1.9 | 11 | 1 | 4 | 0 | Dobson & Lemon 1975, Marler & Tamura 1962, Baptista *et al.* 1981, Smith & Reid 1979 |
| *Agelaius phoeniceus* | 1.25 | 14 | 6 | 3 | 1 | Beletsky & Corral 1983 |

**APPENDIX** (*contd*)

| | song duration/s | intersong interval/s | song repertoire size | syllable repertoire size | versatility | sources |
|---|---|---|---|---|---|---|
| *Icterus galbula* | 1.4 | 10.6 | 6.5 | 10.7 | 2 | Dobson & Lemon 1975 |
| *Sturnella magna* | 1.28 | — | 70 | 5 | 1 | Falls & D'Agincourt 1981, 1982, D'Agincourt & Falls 1983, Lanyon 1957 |
| *Sturnella neglecta* | 2 | 8 | 8 | 8 | 1 | Falls & D'Agincourt 1981, Falls & Krebs 1975 |
| *Xanthocephalus xanthocephalus* | 2.75 | 46 | — | 3 | — | Orians & Christman 1968 |
| *Dendroica castanea* | 1 | 5 | 2 | 2 | 1 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Dendroica coronata* | 1.5 | 11.1 | 2 | 1.9 | 2 | Weary & Lemon 1988 |
| *Dendroica fusca* | 1.5 | 4.4 | 2 | 3.2 | 1 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Dendroica magnolia* | 0.9 | 8.3 | 2 | 3.1 | 1 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Dendroica nigrescens* | 1.4 | — | 2 | 4 | 1 | Morrison & Hardy 1983a |
| *Dendroica pensylvanica* | 1.3 | 7.1 | 5 | 3.5 | 2 | Weary & Lemon 1988, Lein 1978 |
| *Dendroica petechia* | 1.3 | 7.1 | 4 | 3.7 | 2 | Weary & Lemon 1988, Morse 1966 |
| *Dendroica tigrina* | 1 | 5.9 | 3 | 1.2 | 2 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Dendroica townsendi* | 1.4 | — | — | 3 | — | Morrison & Hardy 1983b, Stein 1962 |
| *Dendroica virens* | 1.5 | 8.3 | 2 | 2.4 | 2 | Weary & Lemon 1988, Stein 1962 |
| *Geothlypis philadelphia* | 1.3 | 7.1 | 1 | 2.4 | 0 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Geothlypis trichas* | 1.9 | 5.6 | 1 | 4.9 | 0 | Weary & Lemon 1988, Wunderle 1979 |
| *Mniotilta varia* | 2 | 6.3 | 2 | 3.6 | 1 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Parula americana* | 1.6 | 5.3 | 2 | 2.7 | 1 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Seiurus aurocapillus* | 2.7 | 4.8 | 1 | 3 | 0 | Weary & Lemon 1988, Falls 1963 |
| *Seiurus noveboracensis* | 1.8 | 7.7 | 1 | 3.8 | 0 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Setophaga ruticilla* | 0.9 | 5.3 | 4 | 1.6 | 2 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Vermivora peregrina* | 2.9 | 3.6 | 1 | 4.5 | 0 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Vermivora pinus* | 2.6 | — | 2 | 2 | — | Ficken & Ficken 1967, Kroodsma *et al.* 1984 |
| *Vermivora ruficapilla* | 1.9 | 5.9 | 1 | 2.7 | 0 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Wilsonia canadensis* | 1.5 | 4.2 | 5 | 12.1 | 2 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Wilsonia pusilla* | 1.2 | 4 | 3 | 2 | 2 | Weary & Lemon 1988, Lemon *et al.* 1983 |
| *Piranga ludovicana* | — | — | ∞ | 5 | 2 | Shy 1984 |
| *Piranga olivacea* | 2.75 | 9.5 | ∞ | 5.5 | 2 | Shy 1983*a*, Prescott 1965 |
| *Piranga rubra* | 21 | — | ∞ | 10.7 | 2 | Shy 1985, 1983*a*,*b*, 1984 |
| *Acanthis flammea* | ∞ | — | — | — | — | Borror 1961 |
| *Carduelis chloris* | ∞ | — | ∞ | 3 | 1 | Hindmarsh 1984, Güttinger 1976 |
| *Carduelis spinus* | ∞ | — | — | 15 | — | Borror 1961, Hindmarsh 1984 |
| *Carduelis tristis* | ∞ | — | — | — | — | Borror 1961 |
| *Carpodacus mexicanus* | 1.9 | 4.9 | 4.5 | 1.3 | 2 | Bitterbaum & Baptista 1979 |
| *Carpodacus purpureus* | 2 | — | — | 15 | — | Borror 1961 |
| *Coccothraustes coccothraustes* | — | — | — | 6 | — | Hindmarsh 1984 |
| *Loxia leucoptera* | 5 | — | — | — | — | Borror 1961 |
| *Spiza americana* | 1.5 | — | 1 | 2 | 0 | Borror 1961 |
| *Fringilla coelebs* | 2.1 | 8.1 | 2.5 | 5 | 1 | Dobson & Lemon 1975, Barber 1959, Marler 1956, Falls & D'Agincourt 1981 |
| *Anthus campestris* | 0.4 | — | 1 | 3 | 0 | Neuschultz 1986 |
| *Anthus trivialis* | — | — | — | 6 | — | Hindmarsh 1984 |
| *Motacilla alba* | — | — | — | 9 | — | Hindmarsh 1984 |
| *Passer montanus* | — | — | — | 6 | — | Hindmarsh 1984 |
| *Prunella modularis* | 3 | — | 4 | 12 | 1 | Snow & Snow 1983 |
| *Delichon urbica* | — | — | — | 4 | — | Hindmarsh 1984 |
| *Petrochelidon pyrrhonota* | 7 | — | — | — | — | Samuel 1971 |
| *Hirundo rustica* | 6 | 6 | — | 12 | — | Hindmarsh 1984, Samuel 1971 |

**APPENDIX** (*contd*)

| | song duration/s | intersong interval/s | song repertoire size | syllable repertoire size | versatility | sources |
|---|---|---|---|---|---|---|
| *Progne subis* | 3 | 17 | 1 | 10 | 0 | Brown 1984 |
| *Parus ater* | 2.1 | — | 3 | 2 | 1 | Latimer 1977 |
| *Parus atricristatus* | 1.27 | 3.75 | 9 | 1 | 0 | Dobson & Lemon 1975, Lemon 1968, Latimer 1977 |
| *Parus bicolor* | 1.4 | 1 | 13.7 | 1.5 | 1 | Latimer 1977, Gaddis 1983 |
| *Parus caeruleus* | 2.4 | 4.6 | 3 | 2 | 1 | Latimer 1977 |
| *Parus carolinensis* | 1.2 | 3 | — | 4 | — | Robbins *et al.* 1986, Latimer 1977 |
| *Parus cristatus* | 3.2 | — | — | 2 | — | Latimer 1977 |
| *Parus inornatus* | 2.5 | 1 | 11 | 1.5 | 1 | Gaddis 1983 |
| *Parus major* | 3 | — | 4.5 | 2 | 1 | Latimer 1977, Falls & D'Agincourt 1981 |
| *Parus montanus* | 1 | — | 1 | 1 | 0 | Lewis 1985, Latimer 1977 |
| *Parus palustris* | 1.5 | 3.5 | 4 | 2 | 0 | Latimer 1977 |
| *Sitta carolinensis* | 2 | — | 2 | 1 | — | Ritchison 1983 |
| *Acrocephalus arundinaceus* | 3.2 | 2 | ∞ | 5 | 2 | Catchpole 1980, Simms 1985 |
| *Acrocephalus palustris* | ∞ | 0.01 | ∞ | 90 | 2 | Catchpole 1980 |
| *Acrocephalus schoenobaenus* | 19.5 | 1.31 | ∞ | 7.7 | 2 | Catchpole 1976 |
| *Acrocephalus scirpaceus* | ∞ | 0.01 | ∞ | 80 | 2 | Catchpole 1980 |
| *Cettia cetti* | 2 | 17.5 | — | 4 | — | Simms 1985 |
| *Cisticola juncidus* | 1.2 | 1.6 | 1 | 2 | 0 | Simms 1985 |
| *Hippolais icterina* | — | — | — | 1.5 | — | Simms 1985 |
| *Hippolais polyglotta* | 14 | — | — | 12 | 2 | Simms 1985 |
| *Locustella luscinioides* | 46 | — | 1 | 1 | 0 | Simms 1985 |
| *Locustella naevia* | 51 | 1.5 | 1 | 1 | 0 | Simms 1985 |
| *Phylloscopus bonelli* | 0.7 | 8 | 5 | 1 | 1 | Bremond 1975 |
| *Phylloscopus collybitus* | 4 | 2.7 | 1 | 2 | 0 | Simms 1985 |
| *Phylloscopus sibilatrix* | 3.4 | — | 2 | 1.5 | 2 | Temrin 1986 |
| *Phylloscopus trochilus* | 3.31 | 7.28 | 31 | 9 | 2 | Dobson & Lemon 1975, Schubert 1967 |
| *Regulus ignicapillus* | 2 | 5.5 | 1 | 4 | 0 | Simms 1985 |
| *Regulus regulus* | 3.7 | 6.3 | 1 | 6 | 0 | Simms 1985 |
| *Sylvia atricapilla* | 5 | 4.2 | — | 25 | — | Simms 1985 |
| *Sylvia borin* | 3.5 | 1.55 | — | 20 | — | Simms 1985 |
| *Sylvia communis* | 2.5 | 5 | — | 15 | — | Simms 1985 |
| *Sylvia curruca* | 1.75 | 9 | — | 8 | — | Simms 1985, Hindmarsh 1984 |
| *Sylvia hortensis* | 4 | 6 | — | — | — | Simms 1985 |
| *Sylvia nisoria* | 6 | 11 | — | — | — | Simms 1985 |
| *Certhia familiaris* | 1.2 | — | 1 | 5 | 0 | Baptista & Johnson 1982 |
| *Campylorhynchus brunneicapillus* | 2.9 | 7.8 | — | 1 | 1 | Kroodsma 1977 |
| *Catherpes mexicanus* | 4.6 | — | 3 | 3 | 1 | Kroodsma 1977 |
| *Salpinctus obsoletus* | 1.5 | 3.5 | 9.4 | 1 | 2 | Kroodsma 1977 |
| *Cistothorus platensis* | 1.5 | 2.1 | 110 | 66 | 2 | Kroodsma 1977, Kroodsma & Verner 1978 |
| *Thryomanes bewickii* | 1.71 | 6.22 | 16 | 4 | 1 | Dobson & Lemon 1975, Borror 1964, Kroodsma 1977 |
| *Thryothorus ludovicianus* | 1.6 | 3.6 | 28 | 2.5 | 1 | Dobson & Lemon 1975, Borror 1956, Grant 1966, Simpson 1984 |
| *Troglodytes aedon* | 1.7 | — | ∞ | 6 | 1 | Kroodsma 1977 |
| *Troglodytes troglodytes* | 6.3 | 5.6 | 6.5 | 47 | 1 | Kroodsma 1977 |
| *Cinclus cinclus* | — | — | — | 12 | — | Hindmarsh 1984 |
| *Dumetella carolinensis* | 0.27 | 0.19 | ∞ | ∞ | 2 | Dobson & Lemon 1975, Thompson & Jane 1969 |

**APPENDIX** (*contd*)

| | song duration/s | intersong interval/s | song repertoire size | syllable repertoire size | versatility | sources |
|---|---|---|---|---|---|---|
| *Mimus polyglottos* | 3.06 | 1.1 | ∞ | ∞ | 2 | Dobson & Lemon 1975, Wildenthal 1965 |
| *Sturnus vulgaris* | — | — | — | 15 | — | Hindmarsh 1984 |
| *Erithacus luscinia* | 5.6 | — | — | 5 | — | Sorjonen 1983 |
| *Erithacus megarhynchos* | 3.12 | 3.78 | 220 | 7.5 | 2 | Hultsch & Todt 1981, 1982 |
| *Erithacus rubecula* | 2.18 | 3.27 | ∞ | 4 | 2 | Hoelzel 1986 |
| *Erithacus svecica* | 5 | — | — | 5 | — | Bergmann 1977 |
| *Oenanthe oenanthe* | — | — | — | 18 | — | Hindmarsh 1984 |
| *Phoenicurus phoenicurus* | — | — | — | 18 | — | Hindmarsh 1984 |
| *Saxicola rubetra* | — | — | — | 15 | — | Hindmarsh 1984 |
| *Ficedula hypoleuca* | — | — | — | 9 | — | Hindmarsh 1984 |
| *Catharus fuscescens* | 1.84 | 4.56 | 2 | 3 | 2 | Dobson & Lemon 1975, Borror 1964, Weary *et al.* 1986 |
| *Catharus guttatus* | 1.59 | 3.71 | 13 | 4 | 2 | Borror 1964, Dobson & Lemon 1975 |
| *Catharus minimus* | 2.14 | 6.43 | 3 | — | 2 | Borror 1964, Dobson & Lemon 1975 |
| *Catharus ustulatus* | 2 | 5 | 5 | 6 | 2 | Dobson & Lemon 1977 |
| *Hylocichla mustelina* | 1.56 | 3.04 | 18 | 4 | 2 | Borror 1964, Dobson & Lemon 1975, Lanyon 1979 |
| *Turdus iliacus* | 0.9 | 8.49 | 1 | 2 | 0 | Bjerke & Bjerke 1985 |
| *Turdus merula* | 2.4 | 1.6 | 32 | 6 | 2 | Dobson & Lemon 1975, Dabelsteen 1984 |
| *Turdus migratorius* | 1.93 | 2.28 | ∞ | — | 2 | Dobson & Lemon 1975 |
| *Turdus philomelos* | 0.6 | 0.9 | 171 | 9 | 2 | Dobson & Lemon 1975, Hindmarsh 1984 |
| *Turdus viscivorus* | 1 | 1.6 | ∞ | 3.5 | 2 | Issac & Marler 1963, Lanyon 1979 |

We hope that the publication of this Appendix will stimulate others to expand on our data set and to refine our estimates. These data were originally collected in order to test the parasite hypothesis of sexual selection (Read & Weary 1990), and we therefore searched for data only on species for which we had parasite data. Data were collected by systematically searching Zoological Record 1980–1987 and the indexed reprint collection of the Alexander Library at the Edward Grey Institute of Field Ornithology. Other literature was less systematically surveyed. We made no attempt to collect all the published estimates for each species, nor did we make any systematic attempt to collect the most recent estimates. Recorded species means are those given by the cited authors; where those authors did not give estimates of some values (e.g. syllable repertoire size), we estimated those from sonograms given in the cited reference(s).

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