Phylogenetic distributions of British birds of conservation concern

Gavin H. Thomas*

NERC Centre for Population Biology & Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK

Recent studies suggest that species' life histories and ecology can be used to forecast future extinction risk. Threatened species often share similar traits such that if a trait predisposing a species to decline or extinction is evolutionarily conserved, then close relatives of threatened species are themselves likely to be at risk. The phylogenetic distribution of current threat has been argued to provide insight into the species that could be threatened in the future when trait data are not available. Conservation criteria are typically based on multiple indices that capture different symptoms of threat including population trends and range contraction. However, there is no reason to assume consistent phylogenetic distributions of different symptoms. I construct a molecular phylogeny of 249 species of British birds (more than 93% of the breeding and wintering species) and use this to show that the species that are threatened due to population declines are phylogenetically more closely related than expected by chance alone. However, species that are listed for other reasons, including range contraction, are distributed randomly with respect to phylogeny. I suggest that while phylogeny can be informative with respect to identifying clades that are susceptible to some measures of extinction risk, such patterns are likely to be idiosyncratic with respect to symptom and taxa.

Keywords: phylogeny; British birds; population decline; range contraction

1. INTRODUCTION

Is phylogeny a useful aid in predicting extinction risk? Recent studies have advocated the use of life-history and ecological data as a tool to forecast future, or 'latent', risk (Cardillo *et al.* 2004). Indeed, numerous studies have found correlations between species' traits and measures of extinction risk (Purvis *et al.* 2000; Fisher *et al.* 2003; Koh *et al.* 2004; Thomas *et al.* 2006; Long *et al.* 2007; Cooper *et al.* 2008). Although the indices of extinction risk do not themselves evolve along the branches of phylogenetic trees, the fact that their correlates often do (Cardillo *et al.* 2006) suggests that where traits predict extinction risk, there will be phylogenetic clustering of threatened species (Lockwood *et al.* 2002; Bielby *et al.* 2006). More generally, close relatives of threatened species are expected to be at risk more often than distant relatives (Mace *et al.* 2003). Consequently, the extent of phylogenetic clustering of current threat has been advocated as a means of predicting species that may be vulnerable in the future, particularly where data on species' biology are lacking (Lockwood *et al.* 2002; Corey & Waite 2008).

Indices of extinction risk, such as the IUCN red list criteria, capture multiple symptoms of threat by incorporating information, such as population trend, abundance and range size. Yet, the biological correlates and phylogenetic distribution of different threat symptoms need not always be the same. For instance, although abundance and range size are consistently positively correlated (Brown 1984; Hanski *et al.* 1993; Gaston *et al.* 2000; Thomas *et al.* 2004), it is possible to envisage

cases where the relationship may break down or be nonlinear (Schonewald-Cox & Buechner 1991; Gaston 1994; Freckleton *et al.* 2005) such that phylogenetic patterns of the two symptoms could differ. For example, persecution or climate change could result in population decline without local extinction (i.e. no range decline), whereas habitat loss in low-density areas could result in substantial loss of range but negligible declines in population size (Gaston 2003). Each symptom of threat may result in clustered distributions of species on a phylogenetic tree when considered in isolation. However, since different species may display different symptoms, the combined set of threatened or at-risk species may be phylogenetically random. Differences in the correlates and phylogenetic distribution of alternative symptoms of threat have largely been ignored. Yet, it is clear that if the different symptoms of threat are to some degree decoupled from one another, then phylogenetic approaches that use combinatorial extinction risk metrics may fail as tools for understanding and predicting species vulnerability.

The British avifauna represents an excellent test case to examine phylogenetic patterns in multiple symptoms of threat. Using expert knowledge and long-term data, British birds have been classified according to the degree of conservation concern (Gregory *et al.* 2002). Classification as a species of high (red list) or moderate (amber list) conservation concern is made on the basis of a range of different criteria including range contraction and population decline. Surprisingly, for such an otherwise well-known group, a phylogeny is lacking. Here, I construct the first comprehensive molecular phylogeny of the British avifauna and test for phylogenetic clustering in species of conservation concern.

*g.thomas@imperial.ac.uk

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0549> or via <http://journals.royalsociety.org>.

2. MATERIAL AND METHODS

(a) *Taxon sampling and sequence alignment*

The British bird checklist contains 572 species of which 266 are classed as resident or migrant breeders or wintering birds; the remaining 306 species are classed as passage or scarce migrants, vagrants or former breeders (Dudley *et al.* 2006). I used GENEIOUS v. 2.0 (Drummond *et al.* 2006b) to search GenBank (Benson *et al.* 2007) for sequence data on the 266 breeding and wintering birds. I obtained data from 12 mitochondrial protein-encoding genes (*ATP6*, *ATP8*, *Cyt b*, *ND1*, *ND2*, *ND3*, *ND4*, *ND5*, *ND6*, *COI*, *COII* and *COIII*), with at least one gene sequence for each of 248 species (the lowest number of nucleotides any species was represented by was 300). In addition, I used a published cytochrome *b* sequence for whinchat *Saxicola rubetra* (Wink *et al.* 2002). I used non-British congeners as surrogates for three species (little bittern *Ixobrychus minutus*, European bee-eater *Merops apiaster* and European golden plover *Pluvialis apricaria*) for which sequence data were not otherwise available. I used the ostrich *Struthio camelus* as an out-group. I aligned the sequences for each gene by eye using SE-AL v. 2.0a11 (Rambaut 2002) and removed start and stop codons prior to concatenation. The total length of the concatenated sequence was 10 989 base pairs. The sequence accession numbers for all species (except *S. rubetra*) and justification of the choice of surrogates and out-group are provided as electronic supplementary material.

(b) *Phylogenetic analyses*

I used a relaxed clock Bayesian inference method (Drummond *et al.* 2006a) implemented in BEAST v. 1.4.5 (Drummond & Rambaut 2007) for phylogenetic analyses. I used a codon-specific substitution model (GTR+CP₁₁₂+I+Γ, following the nomenclature of Shapiro *et al.* 2006), in which rate variation among adjacent branches was assumed to follow an uncorrelated lognormal distribution (Drummond *et al.* 2006a) with a Yule speciation process prior on branching rates. Long mitochondrial sequences have been shown to perform well in phylogenetic analyses of family level relationships in birds (Paton & Baker 2006). However, although the total length of sequences in the dataset is long (10 989 base pairs), the data are patchy and most species are missing from several genes. A combination of such patchiness and nucleotide saturation could be problematic for resolving deep nodes. To overcome this problem, I applied a defined tree prior in which 11 nodes were constrained (out of possible 248 nodes for a fully bifurcating tree). The fixed nodes defined order level and higher clades as follows: Anseriformes, Charadriiformes, Columbiformes, Falconiformes, Gruiformes, Galliformes, Passeriformes, Podicipediformes, Strigiformes, Galloanserae and Neognathae (figure 1). These constraints reflect generally well-supported and widely accepted divisions in the avian phylogeny (Ericson *et al.* 2006; Slack *et al.* 2007). I did not constrain the ages of any nodes in the tree. The XML-format BEAST input file, specifying all prior parameter estimates and constraints, was produced using BEAUTI v. 1.4.5 (Drummond & Rambaut 2007) and is available as electronic supplementary material.

In addition, and in part owing to the large size and patchiness of the sequence alignment, I treated all 12 genes as a single partition in order to ensure an acceptable computation time. An initial run of 15 million generations indicated that only one of the four chains was approaching

convergence. I therefore ran four further independent chains for 20 million generations with parameter estimates and the final tree from the initial chain with the highest posterior probability as priors. The log and tree files from the four runs were combined using LOGCOMBINER v. 1.4.5 (Drummond & Rambaut 2007). Convergence was assessed by visual examination of plots of the parameters and on the basis of effective sample size (ESS; Drummond *et al.* 2006a) using TRACER v. 1.3 (Rambaut & Drummond 2007). An ESS greater than 200 for a continuous parameter indicates that the chain has been run for an adequate length (Drummond *et al.* 2006a). After discarding the first two million generations of each chain as burn-in, the combined results of the four independent chains had ESS values greater than 200 for all parameters with the exception of the node age estimate for the constrained Charadriiformes clade that had an ESS greater than 130. The ESS' for the tree likelihoods and for the posterior probability were all greater than 2300.

For visual purposes, I summarized the posterior distribution of trees as a maximum credibility tree in which clades with a posterior probability less than 50% are collapsed to polytomies and node ages are the median of the posterior distribution (figure 1 and the electronic supplementary material) using TREEANNOTATOR (Drummond & Rambaut 2007). The maximum credibility tree finds the tree with the maximum product of posterior clade probabilities. Unlike majority rule consensus methods, the maximum credibility tree is always drawn from the posterior distribution. A subset of the posterior distribution of trees is available as electronic supplementary material and the full distribution is available on request. Note that branch lengths are based on a mean substitution rate of 0.01 per site per million years (Weir 2006).

(c) *Population status of British birds*

Gregory *et al.* (2002) classified 247 British birds into species of high conservation (the red list; 40 species), medium conservation (the amber list; 121 species) and no current conservation (the green list; 86 species) concern. I placed the 181 resident and migrant breeding birds (out of 189 listed by Gregory *et al.* 2002) that are included in the phylogeny into conservation concern categories based on Gregory *et al.* (2002). In addition, I classified species according to their range size rarity (data from Gibbons *et al.* 1993) and population size (data from Baker *et al.* 2006): species among the lower decile of (i) range size and (ii) population size were scored 1 and the remaining species were scored 0. The conservation concern categories are summarized in table 1 and full details are available as electronic supplementary material.

(d) *Phylogenetic uncertainty and the distribution of birds of conservation concern*

To quantify the phylogenetic distribution of British birds of conservation concern, I first calculated the mean phylogenetic distance (MPD, Webb *et al.* 2002). This is simply the mean of the phylogenetic distance between each pair of species and is commonly used to assess the extent of phylogenetic over- or underdispersion of ecological communities or assemblages. Next, I calculated the amount of branch length lost (phylogenetic diversity (PD)) from the phylogeny when species from each conservation concern category are pruned from the tree. This type of approach has been advocated as an alternative biodiversity metric to species richness to capture feature diversity of species (Faith 1992),

Figure 1. A phylogeny of British birds. The phylogeny is the maximum credibility tree (see text for details) from the posterior distribution of trees. Nodes marked with a filled circle contain species that were constrained to be monophyletic *a priori*. Nodes with posterior probabilities less than 50% are collapsed to polytomies. Species marked with asterisks are species for which non-British congeners were used as surrogates (see text for details).

as a means of assessing the 'evolutionary heritage' of species within geopolitical units (Mooers & Atkins 2003) and as a tool to identify parts of the world that can better preserve the evolutionary potential of floras and faunas (Forest *et al.* 2007). I calculated the median value of both MPD and PD across 1000 trees drawn from the posterior distribution of possible trees. The use of a subset rather than the complete posterior distribution of trees was necessary because the file size of the full posterior distribution caused the software to crash.

To assess whether the values of MPD and PD were over- or underdispersed I conducted 10 000 randomizations. In each randomization, one tree was selected at random from the posterior distribution of 1000 trees and then the relevant numbers of species (e.g. 32 for red-listed species) were

randomly drawn without replacement from the pool of 181 species. Thus, the null hypothesis incorporated uncertainty in the phylogeny. The values of MPD and PD for the set of species were then calculated. I then compared the median observed value of MPD and PD against the null distribution of values that are expected at random. A high value for MPD relative to the null distribution indicates that species are more distantly related to one another than expected by chance, whereas a low value indicates that species are more closely related to one another than expected by chance. A high value for PD lost indicates that more branch length is lost from the phylogeny than expected by chance, whereas a low value indicates that less branch length is lost from the phylogeny than expected by chance. All calculations and randomizations were carried out in R v. 2.4.

Table 1. Conservation concern categories for British birds (after Gregory *et al.* 2002).

conservation concern status	conservation concern category	number of species
red list	all red-listed species	32
	historical population decline during 1800–1995	8
	≥50% decline in UK breeding population over last 25 years	22
	≥50% contraction in UK breeding range over last 25 years	6
amber list	all amber red-listed species	121
	historical population decline during 1800–1995, but recovering	5
	25–49% decline in UK breeding population over last 25 years	27
	25–49% contraction in UK breeding range over last 25 years	10
	5-year mean population size of 1–300 breeding pairs	21
	≥20% of European breeding population in UK	14
	≥50% of UK breeding population in ≤10 sites, but not rare breeders	28
	≥50% decline in UK breeding population but not over last 25 years	20
	≥50% decline in UK breeding range but not breeding over last 25 years	4
green list	all green-listed species	60
other	lowest decile of population size	18
	lowest decile of range size	18

3. RESULTS

(a) *Phylogeny*

A summary of the posterior distribution of phylogenetic trees, the most complete molecular phylogeny of British birds to date, is provided in figure 1. The phylogeny retained the monophyly of the majority of tribes and families described in taxonomically less complete earlier phylogenies (Sibley & Ahlquist 1990) as well as being overwhelmingly consistent with the taxonomic assignment of species to genera. The only notable exception was the placement of the wood warbler *Phylloscopus sibilatrix* in a polytomy with the long-tailed tit *Aegithalos caudatus*, Cetti's warbler *Cettia cetti* and a clade of *Sylvia* warblers. There was also a lack of resolution among some of the deeper nodes, though this is an issue that has not yet been resolved even with extensive gene sequencing (Poe & Chubb 2004).

(b) *Phylogenetic clustering of threat symptoms*

I found that when all the red- or amber-listed species are considered irrespective of the different threat symptoms, the relatedness among species is indistinguishable from random. There was significant phylogenetic clustering among red-listed species with population declines ($P < 0.05$, $n = 22$; figure 2a) but although suggestive of a trend, clustering among amber-listed species does not differ significantly from the null distribution ($P < 0.1$, $n = 49$; figure 2a). By contrast, the phylogenetic relatedness of red- and amber-listed species with range contractions is indistinguishable from random (figure 2a; see table S1 in the electronic supplementary material). Several species that are red- or amber listed for population declines are also listed for range contractions. When species listed for range contractions are excluded, the pattern of phylogenetic clustering for species red- and amber-listed for population declines becomes stronger ($P < 0.01$ for red-listed species, $n = 20$; $P < 0.05$ for amber-listed species, $n = 40$). In addition to population decline listed species, species with highly concentrated populations (50% or more of UK breeding population in 10 sites or less) are phylogenetically clustered ($P < 0.05$, $n = 28$; figure 2a). The MPD of all other conservation concern criteria was indistinguishable from the null distribution.

(c) *Threatened evolutionary heritage*

In contrast to the patterns for MPD, there is little evidence to suggest that species of conservation concern represent unusually large amounts of evolutionary heritage (figure 2b; see table S1 in the electronic supplementary material). Indeed, the only criterion in which the observed value for PD differs significantly from the null expectation is for species in the lower decile of range size ($P < 0.05$, $n = 9$): loss of species with small ranges would lead to the loss of unexpectedly large amounts of PD (figure 2b; see table S1 in the electronic supplementary material). Note that this result holds if the fifth percentile is used as a cut-off for range restriction but not if the lower quartile is used.

4. DISCUSSION

My results clearly show that there is no unusual phylogenetic clustering of species of conservation concern among British birds. This implies that either there are no common attributes shared by red- or amber-listed species, that any relevant species attributes are decoupled from evolutionary history, or different symptoms have different distributions on the phylogeny. I suggest that the latter is likely since some symptoms are clustered, while others are not. Most notably, population-declining species tend to be phylogenetically clustered. The list of British birds that have suffered recent population declines is dominated by passerines and more generally by species that are associated with farmland or woodland. Some clades, in particular, were more likely to be listed due to population declines than others. For instance, three of four members of the *Emberiza* genus are red listed owing to population declines. This implies that the ciril bunting *Emberiza cirilus*, a species that is already red listed owing to recent range contraction, is likely to suffer future population declines. Even widespread green-listed species, such as common blackbird *Turdus merula*, appear to be future candidates for population decline given that they have several close relatives that are red listed, including the previously abundant but now declining common starling *Sturnus vulgaris*.

It is perhaps surprising, given the typically tight relationship between range size and population size (Brown 1984; Hanski *et al.* 1993; Gaston *et al.* 2000;

Figure 2. The phylogenetic distribution of British birds of conservation concern. (a) The null and observed distributions of relatedness (MPD) among species and (b) the null and observed distributions of PD lost. Light grey areas show the distribution of null values (see text for details). Dark grey indicates the range of the 95th percentiles, mid-grey indicates the range of the 99th percentiles and light grey shows the extent of the randomized data. MPD or PD lost values for red- and amber-listed species sets that lie in the dark grey area have distributions that are indistinguishable from random, whereas values outside this range indicate underdispersion (low values) or overdispersion (high values). Note that the category labelled 'red list range declines only' is the one with species that are also on the red or amber list for population decline removed, and the category 'red list population declines only' is the one with species that are also on the red or amber list for range decline removed. Red diamonds, red list; amber diamonds, amber list; green diamonds, green list; red down triangles, red list historical decline; red circles, red list range decline; red up triangles, red list population decline; black up triangles, small population size; black circles, small range size; pluses, more than 20% European population; asterisks, small range, more than 50% UK population; crossed circles, red list range declines only; crossed diamonds, red list population declines only.

Thomas *et al.* 2004), that the pattern of clustering among population declining species was not also found among range-contracting species. In contrast to the list of species

that have suffered population declines, range-contracting species appear idiosyncratic with respect to their biological characteristics. For example, habitat use by range declining species varies from reed beds (bittern *Botaurus stellaris*) and heathland (nightjar *Caprimulgus europaeus*), to woodland (hawfinch *Coccothraustes coccothraustes*) and a range of agricultural land types (e.g. stone curlew *Burhinus oedipnemus*). The differences in the lists of population and range declining species could arise if the loss of local populations also results in reductions in abundance throughout the rest of the species range (Gaston 2003). This generates a lag in the decline of range size relative to population size (Gaston 2003). In terms of categorizing species as being of conservation concern, it is obvious that a lag could result in species being listed for population declines more readily than they would be for range contraction for data collected over the same time period. Consistent with this pattern, concurrent losses of local populations alongside reductions in density of the remaining populations have been documented among British farmland birds (Gates & Donald 2000). An alternative though not mutually exclusive explanation for such a lag is that the data used to red- or amber list species for population declines do not come from the same period as the data for range contraction. Population trend data are derived from several sources (e.g. Common Bird Census, Waterways Bird Survey, Breeding Bird Survey), all of which include data that run at least to 1999. By contrast, the breeding range data used for conservation categorization are based on the changes in the distribution of species taken from two atlases of breeding birds (Sharrock 1976; Gibbons *et al.* 1993), of which the more recent (Gibbons *et al.* 1993) only includes data up to 1990. Thus, any lag in the relationship between changes in population size and range size could be artefact.

As outlined above, a lag in the decline of range size relative to population size could lead to species being placed on the red list for population declines more often than for range contraction. However, it seems reasonable to expect that there would still be substantial overlap between the two lists of red-listed species. This is not the case for British birds: out of 22 species red listed for population declines, only two are also red listed and a further five amber listed for range contraction. This substantial discrepancy might be better explained by a decoupling of abundance from occupancy. It has been widely reported for British birds that locally abundant species are also widespread (e.g. Gaston *et al.* 1999a,b). An intraspecific parallel where individual species are more widespread in years when they are locally abundant has also been documented (Freckleton *et al.* 2006). However, the strength of this relationship among British farmland and woodland birds declined markedly between 1968 and 1999, and this trend was driven by the decoupling of abundance and occupancy in rare and declining species (Webb *et al.* 2007).

The phylogenetic distribution of species with population declines or range contractions cannot be used to separate a lag effect (real or artefact) from the decoupling of abundance and occupancy, yet the fact that the patterns differ has important conservation implications. Since measures of conservation concern or extinction risk are typically based on indices of multiple symptoms, conservation listing of species will inevitably capture a

combination of different patterns. It seems obvious that this can lead to apparently random phylogenetic distributions of species that mask potentially important patterns in the data. For British birds, using the red list in its entirety masks the clustering of both population declining species and species with small ranges that are not rare breeders. While the former includes many farmland species (see above), the latter is dominated by coastal and colony-nesting species (e.g. razorbill *Alca torda*, Manx shearwater *Puffinus puffinus*, gannet *Morus bassanus*, little tern *Sternula albifrons*). Clearly, conservation strategies for these two sets of species would be very different.

Despite the need for caution when interpreting phylogenetic distributions of conservation concern indices, this does not mean that they are uninformative. Phylogenetic patterns can provide insight into the sorts of threats that make some species more vulnerable to decline or extinction than others (Lockwood *et al.* 2002; Bielby *et al.* 2006). Moreover, phylogenetic approaches can be used to examine continuous measures of extinction risk (e.g. the rate of population change) and need not be restricted to lists of species that are threatened (or not) as I have used here. Where geographical distributions are also available, phylogenetic clustering of extinction risk may be used to identify areas that are most vulnerable. Corey & Waite (2008) used the phylogenetic clumping of extinction risk in amphibians to propose that a shift from species to clade-based conservation prioritization of geographical areas may be beneficial. This type of approach has parallels with the concept of evolutionary heritage (Mooers & Atkins 2003; Mooers *et al.* 2005). For British birds, small-ranged species represent an unusually large amount of evolutionary heritage and as such might be considered as conservation priorities (Mooers *et al.* 2005; Redding & Mooers 2006; Isaac *et al.* 2007). However, it is not clear whether evolutionary heritage reflects evolutionary potential. If PD is a reliable indicator of phenotypic diversity, then prioritizing based on evolutionary heritage may be an effective means of capturing feature diversity (Forest *et al.* 2007). Yet, low, rather than high, evolutionary heritage may better reflect evolutionary potential since short branches may imply shorter waiting times to speciation. Thus, it is not straightforward to choose between conservation of old taxa that have high evolutionary heritage but low evolutionary potential, or young taxa that have low evolutionary heritage but high evolutionary potential.

For British birds with population declines it may be possible to predict population declines from species' traits. However, as demonstrated by the conflict with the phylogenetic distribution of species with contracting ranges, the generality of such inference is likely to be limited, especially where pattern is in some way decoupled from process. Taken together, my results suggest that while phylogeny has the potential to provide an insight into the types of species that are likely to be susceptible to extinction risk or decline in some cases, a degree of caution is required where different, and potentially conflicting, conservation metrics are lumped into single indices.

I thank Michael Wink for kindly providing whinchat sequence data, and Georgina Mace, Shai Meiri, Albert Phillimore and two anonymous reviewers for their insightful comments on this manuscript.

REFERENCES

- Baker, H., Stroud, D. A., Aebischer, N. J., Cranswick, P. A., Gregory, R. D., McSorley, C. A., Noble, D. & Rehfisch, M. M. 2006 Population estimates of birds in Great Britain and the United Kingdom. *British Birds* **99**, 25–44.
- Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J. & Wheeler, D. L. 2007 GenBank. *Nucleic Acids Res.* **35**, D1–D25. (doi:10.1093/nar/gkm484)
- Bielby, J., Cunningham, A. A. & Purvis, A. 2006 Taxonomic selectivity in amphibians: ignorance, geography or biology? *Anim. Conserv.* **9**, 135–143. (doi:10.1111/j.1469-1795.2005.00013.x)
- Brown, J. M. 1984 On the relationship between abundance and distribution of species. *The Am. Nat.* **124**, 255–279. (doi:10.1086/284267)
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. 2004 Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914. (doi:10.1371/journal.pbio.0020197)
- Cardillo, M., Mace, G. M., Gittleman, J. L. & Purvis, A. 2006 Latent extinction risk and the future battlegrounds of mammal conservation. *Proc. Natl Acad. Sci. USA* **103**, 4157–4161. (doi:10.1073/pnas.0510541103)
- Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. 2008 Macroecology and extinction risk correlates of frogs. *Global Ecol. Biogeogr.* **17**, 211–221. (doi:10.1111/j.1466-8238.2007.00355.x)
- Corey, S. J. & Waite, T. A. 2008 Phylogenetic autocorrelation of extinction threat in globally imperilled amphibians. *Divers. Distributions* **14**, 614–629. (doi:10.1111/j.1472-4642.2007.00448.x)
- Drummond, A. & Rambaut, A. 2007 BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**, 214. (doi:10.1186/1471-2148-7-214)
- Drummond, A., Ho, S. Y. W., Phillips, M. J. & Rambaut, A. 2006a Relaxed phylogenetics and dating with confidence. *PLoS Biol.* **4**, e88. (doi:10.1371/journal.pbio.0040088)
- Drummond, A., Kearse, M., Heled, J., Moir, R., Thierer, T., Ashton, B. & Wilson, A. 2006b GENEIOUS v. 2.0. Available from <http://www.geneious.com/>.
- Dudley, S. P., Gee, M., Kehoe, C. & Melling, T. M. 2006 The British list: a checklist of birds of Britain. *Ibis* **148**, 526–563. (doi:10.1111/j.1474-919X.2006.00603.x)
- Ericson, P. G. P. *et al.* 2006 Diversification of Neoaves: integration of molecular sequence data and fossils. *Biol. Lett.* **2**, 543–547. (doi:10.1098/rsbl.2006.0523)
- Faith, D. P. 1992 Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61**, 1–10. (doi:10.1016/0006-3207(92)91201-3)
- Fisher, D. O., Blomberg, S. P. & Owens, I. P. F. 2003 Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. R. Soc. B* **270**, 1801–1808. (doi:10.1098/rspb.2003.2447)
- Forest, F., Grenyer, R., Rouget, M., Davies, T. J., Cowling, R. M., Faith, D. P., Hedderson, T. A. J. & Savolainen, V. 2007 Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **445**, 757–760. (doi:10.1038/nature05587)
- Freckleton, R. P., Gill, J. A., Noble, D. & Watkinson, A. R. 2005 Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. *J. Anim. Ecol.* **74**, 353–364. (doi:10.1111/j.1365-2656.2005.00931.x)
- Freckleton, R. P., Noble, D. & Webb, T. J. 2006 Distribution of habitat suitability and the abundance–occupancy relationship. *The Am. Nat.* **167**, 260–275. (doi:10.1086/498655)
- Gaston, K. J. 1994 Geographic range sizes and trajectories to extinction. *Biodivers. Lett.* **2**, 163–170. (doi:10.2307/2999657)

- Gaston, K. J. 2003 *The structure and dynamics of geographic ranges*. Oxford Series in Ecology and Evolution. Oxford, UK: Oxford University Press.
- Gaston, K. J., Blackburn, T. M. & Gregory, R. D. 1999a Intraspecific abundance–occupancy relationships: case studies of six bird species in Britain. *Divers. Distributions* **5**, 167–212. (doi:10.1046/j.1472-4642.1999.00054.x)
- Gaston, K. J., Gregory, R. D. & Blackburn, T. M. 1999b Intraspecific relationships between abundance and occupancy among species of Paridae and Sylviidae in Britain. *Ecoscience* **6**, 131–142.
- Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M. & Lawton, J. H. 2000 Abundance–occupancy relationships. *J. Appl. Ecol.* **37**, 39–59. (doi:10.1046/j.1365-2664.2000.00485.x)
- Gates, S. & Donald, P. F. 2000 Local extinction of British farmland birds and the prediction of further loss. *J. Appl. Ecol.* **37**, 806–820. (doi:10.1046/j.1365-2664.2000.00549.x)
- Gibbons, D. W., Reid, J. B. & Chapman, R. A. 1993 *The new atlas of breeding birds in Britain and Ireland: 1988–1991*. London, UK: T. & A.D. Poyser.
- Gregory, R. D., Wilkinson, N. I., Noble, D. G., Robinson, J. A., Brown, A. F., Hughes, J., Proctor, D., Gibbons, D. W. & Galbraith, C. A. 2002 The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–2007. *British Birds* **95**, 410–448.
- Hanski, I., Kouki, J. & Halkka, A. 1993 Three explanations of the positive relationship between distribution and abundance of species. In *Species diversity in ecological communities: historical and geographical perspectives* (eds R. E. Ricklefs & D. Schluter), pp. 108–116. Chicago, IL: University of Chicago Press.
- Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. 2007 Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One* **2**, e296. (doi:10.1371/journal.pone.0000296)
- Koh, L. P., Sodhi, N. S. & Brook, B. W. 2004 Ecological correlates of extinction proneness in tropical butterflies. *Conserv. Biol.* **18**, 1571–1578. (doi:10.1111/j.1523-1739.2004.00468.x)
- Lockwood, J. L., Russell, G. J., Gittleman, J. L., Daehler, C. C., McKinney, M. L. & Purvis, A. 2002 A metric for analyzing taxonomic patterns of extinction risk. *Conserv. Biol.* **16**, 1137–1142. (doi:10.1046/j.1523-1739.2002.01152.x)
- Long, P. R., Székely, T., Kershaw, M. & O'Connell, M. 2007 Ecological factors and human threats both drive wildfowl population declines. *Anim. Conserv.* **10**, 183–191. (doi:10.1111/j.1469-1795.2006.00087.x)
- Mace, G. M., Gittleman, J. L. & Purvis, A. 2003 Preserving the tree of life. *Science* **300**, 1707–1709. (doi:10.1126/science.1085510)
- Mooers, A. O. & Atkins, R. A. 2003 Indonesia's threatened birds: over 500 million years of evolutionary heritage at risk. *Anim. Conserv.* **6**, 183–188. (doi:10.1017/S1367943003003226)
- Mooers, A. O., Heard, S. B. & Chrostowski, E. 2005 Evolutionary heritage as a metric for conservation. In *Phylogeny and conservation* (eds A. Purvis, J. L. Gittleman & T. Brooks), pp. 120–138. Oxford, UK: Oxford University Press.
- Paton, T. A. & Baker, A. J. 2006 Sequences from 14 mitochondrial genes provide a well-supported phylogeny of charadriiform birds congruent with nuclear RAG-1 tree. *Mol. Phylogenet. Evol.* **39**, 657–667. (doi:10.1016/j.ympev.2006.01.011)
- Poe, S. & Chubb, A. L. 2004 Birds in a bush: five genes indicate explosive evolution of avian orders. *Evolution* **58**, 404–415. (doi:10.1554/03-037)
- Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. B* **267**, 1947–1952. (doi:10.1098/rspb.2000.1234)
- R Core Development Team 2007 R: a language and environment for statistical computing.
- Rambaut, A. 2002 SE-AL v. 2.0a11: sequence alignment program. (<http://tree.bio.ed.ac.uk/software/seal/>)
- Rambaut, A. & Drummond, A. 2007 TRACER v. 1.3, Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Redding, D. W. & Mooers, A. O. 2006 Incorporating evolutionary measures into conservation prioritization. *Conserv. Biol.* **20**, 1670–1678. (doi:10.1111/j.1523-1739.2006.00555.x)
- Schönewald-Cox, C. & Buechner, M. 1991 Housing viable populations in protected habitats: the value of a coarse-grained geographic analysis of density patterns and available habitat. In *Species conservation: a population-biological approach* (eds A. Seitz & V. Loeschke), pp. 213–226. Basel, Switzerland: Birkhäuser Verlag.
- Shapiro, B., Rambaut, A. & Drummond, A. 2006 Choosing appropriate substitution models for the phylogenetic analysis of protein-coding sequences. *Mol. Biol. Evol.* **23**, 7–9. (doi:10.1093/molbev/msj021)
- Sharrock, J. T. R. 1976 *The atlas of breeding Birds in Britain and Ireland*. London, UK: T. & A.D. Poyser.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Slack, K. E., Delsuc, F., McLenachan, P. A., Arnason, U. & Penny, D. 2007 Resolving the root of the avian mitogenomic tree by breaking up long branches. *Mol. Phylogenet. Evol.* **42**, 1–13. (doi:10.1016/j.ympev.2006.06.002)
- Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T. & Lawton, J. H. 2004 Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881. (doi:10.1126/science.1095046)
- Thomas, G. H., Lanctot, R. B. & Székely, T. 2006 Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Anim. Conserv.* **9**, 252–258. (doi:10.1111/j.1469-1795.2006.00029.x)
- Webb, C. O., Ackerly, D. D., McPeck, M. A. & Donoghue, M. J. 2002 Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505. (doi:10.1146/annurev.ecolsys.33.010802.150448)
- Webb, T. J., Noble, D. & Freckleton, R. P. 2007 Abundance–occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *J. Anim. Ecol.* **76**, 123–134. (doi:10.1111/j.1365-2656.2006.01192.x)
- Weir, J. T. 2006 Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* **60**, 842–855. (doi:10.1554/05-272.1)
- Wink, M., Kuhn, M., Sauer-Gürth, H. & Witt, H.-H. 2002 A molecular phylogeny of stonechats and related turdids. In *Stonechats* (ed. E. Urquhart), pp. 23–30. London, UK: A and C Black.