

LETTER

Common European birds are declining rapidly while less abundant species' numbers are rising

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Abstract

Biodiversity is undergoing unprecedented global decline. Efforts to slow this rate have focused foremost on rarer species, which are at most risk of extinction. Less interest has been paid to more common species, despite their greater importance in terms of ecosystem function and service provision. How rates of decline are partitioned between common and less abundant species remains unclear. Using a 30-year data set of 144 bird species, we examined Europe-wide trends in avian abundance and biomass. Overall, avian abundance and biomass are both declining with most of this decline being attributed to more common species, while less abundant species showed an overall increase in both abundance and biomass. If overall avian declines are mainly due to reductions in a small number of common species, conservation efforts targeted at rarer species must be better matched with efforts to increase overall bird numbers, if ecological impacts of birds are to be maintained.

Keywords

Abundance, avian, biomass, birds, common, conservation, declines, ecosystem services, rare, rarity.

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INTRODUCTION

That a relatively small number of species are common while a far greater number are less abundant has been termed a 'law' of ecology as it has been observed in all communities that have been studied (Gaston 1994; McGill *et al.* 2007; Henderson & Magurran 2010). Global biodiversity is undergoing unprecedented decline (Butchart *et al.* 2010) and conservation efforts to reverse or at least slow the rate have focused foremost on the less abundant species, which by definition face the greatest extinction threats (Caughley & Gunn 1995; Baillie *et al.* 2004; Gaston 2010). Considerably less attention has been given to declines in more common species, which is troubling because these are important in the delivery of absolute levels of ecosystem function and of ecosystem goods and services (Grime 1998; Geider *et al.* 2001; Gaston 2008, 2011). Indeed, although they may constitute a small proportion of the species richness, common species often define the structure, character and dynamics of ecosystems (Ellison *et al.* 2005; Gaston 2010). Even relatively small proportional declines in the abundances of common species will often result in the loss of large numbers of individuals and substantial amounts of biomass, with dramatic ecosystem consequences (Ellison *et al.* 2005; Gaston 2010). This suggests that a key issue in the strategic allocation of inevitably limited conservation resources is how directional change in population sizes is distributed amongst common and rare species, and particularly whether there are any systematic patterns of variation.

Birds provide an excellent opportunity to investigate possible asymmetries in population changes between common and less abundant species as they vary widely in abundance and have been the subject of intensive monitoring programmes for a number of decades, thus providing geographically wide-ranging, robust, long-term data sets (Gregory *et al.* 2005; Gregory & van Strien 2010). Potential declines in common birds are also important as a growing body of evidence suggests that birds play vital roles in the structuring and functioning of ecosystems and that declines in their numbers will likely reduce key ecosystem processes and services including decomposition, pest control, pollination and seed dispersal (Sekercioglu *et al.* 2004; Whelan *et al.* 2008; Wenny *et al.* 2011; Gangoso *et al.* 2013). In this study, we utilise data from the Pan-European Common Bird Monitoring Scheme (PECBMS) to construct a 30-year data set across 25 countries (Fig. S1), for 144 bird species, and examine how population trajectories (both in terms of abundance and biomass) differ between species based on their abundance.

MATERIALS AND METHODS

Bird abundance estimates

Two data sources, population estimates from Birdlife International and European population indices from The Pan-European Common Bird Monitoring Scheme (PECBMS), were used

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to calculate bird abundance estimates used in the analysis. BirdLife International (2004) provides estimated numbers of breeding pairs for 520 species in 52 European countries and regions. Estimates for 144 species and 25 countries covered by PECBMS were extracted. These are based on survey data with a mean starting year of 1997 and a mean end year of 2000, and hence, we assume that the population estimates reflect the population size in the year 2000. The population estimates consist of a minimum and maximum population size, in breeding pairs, for each country, of which a geometric mean was taken and multiplied by two to give an abundance estimate for each species and country. As these estimates are based on the number of breeding pairs they do not take into account the non-breeding population, although we assume the breeding population reflects the size of the actual population. A single abundance estimate was then produced for each species by summing population estimates across all countries. PECBMS collects survey data from all participating countries and incorporates these data into a single supranational European index for each species for the period 1980–2009. The number of countries contributing to the scheme, and the number of years covered by the data has been increasing since its inception, meaning that in the earlier years a smaller number of countries were used to produce the indices. Missing data were estimated using existing data from other countries within the same region that share socioeconomic, environment and environmental pressures. The European Bird Census Council website (<http://www.ebcc.info/index.php?ID=509>) provides full details of the methods used to calculate indices and their associated caveats. These indices were then applied to the population estimates calculated from the Birdlife international data to produce abundance estimates each for species from 1980–2009. Biomass estimates were calculated using body mass data (a mean of male and female masses) were taken from Snow & Perrins (1998), Dunning (2007) and BirdLife International (2012). Both data sets are publically available and our derived data set is available on request.

For 28 species, we did not have indices of change for some of the earlier years (ranging from 8 to 19 years (mean = 14.07, SD = 4.25), see Table S1). In these cases, we calculated the population estimates for the missing years based on the abundances for the years for which indices of change were available. Three methods were utilised, taking the geometric mean of the available abundance and using this value for the missing years, and linear regression/exponential regression of the available abundances then using the predictions from the regression to fill the missing years. In addition, we repeated the analysis with the interpolated data removed. Finally, to reduce the noise associated with annual fluctuations, the data were smoothed using a generalised additive model with degrees of freedom 0.3 times the number of years in the data set (Fewster *et al.* 2000). The effects of interpolation method and of smoothing the data were examined by calculating R^2 values and parameter estimates for the different data manipulations (Table S2). After the data had been smoothed the best model fit was achieved using data where linear regression had been used to interpolate the data for missing years and hence these data were used in all subsequent analysis.

Factors affecting species population trajectories

To detect differences in directional changes in population sizes between common and less common species, we assigned all species of bird to a quartile based on their abundance, with the least abundant species occupying quartile one and the most abundant in quartile four (from here termed Q1, Q2, Q3 & Q4). Species were assigned to both variable and fixed quartiles. For variable quartiles assignment was performed on a yearly basis allowing species to move between quartiles as their abundance changed, hence the species composition of the quartiles was dynamic. Full details of assignment to, and movement between, quartiles are available (Table S3). For fixed quartiles, species were assigned to quartiles based on abundance in year 1 of the study.

For each bird species, we also identified three additional factors likely to affect their population trajectories: major feeding guild, habitat and body size. Feeding guild was based on feeding preferences used for the majority of the year, not including seasonal variation (taken from Snow & Perrins 1998; Handbook of the Birds of the World Alive 2013): aerial insectivore ($n = 9$), carnivore ($n = 5$), granivore ($n = 32$), herbivore ($n = 6$), insectivore ($n = 79$) & omnivore ($n = 13$). Habitat type was taken from the PECBMS: farmland ($n = 36$), forest ($n = 32$), inland water ($n = 8$) and other habitat ($n = 68$).

To investigate the role of different variables in determining changes in abundance of species within the study, we used general linear mixed effects models with a Gaussian error structure. All models were fitted with the R (v3.0.2) language and environment (R Core Team 2012), using the package 'lme4' (Bates *et al.* 2013). Abundance was used as the dependent variable in the model, with one data point for each species ($n = 144$) per year ($n = 30$). As abundance rank is formulated from the absolute abundance they are obviously correlated. To minimise this correlation, we z-transformed each species' abundance independently using species-specific means and standard deviations, the resulting standardised abundances approximated a Gaussian distribution and were used in subsequent analysis. Fixed factors included in the maximal models were time (year, continuous integer variable) major feeding guild (six-level categorical variable), habitat (four-level categorical variable), and body mass (continuous variable). All fixed effects were also standardised using the 'arm' package (Gelman *et al.* 2013) to ensure they were on a common scale, which increases the interpretability of the parameter estimates particularly when interactions are involved (Schielzeth 2010). In all cases models with variable quartiles were found to be better in terms of parsimony (based on AIC) and variance explained (see below), hence this method was used for all the subsequent mixed effect models. The fixed effects structure included two-way interactions of year with each other variable. Species was modelled with a random slope (by time) and intercept.

To evaluate the variance explained we calculated R^2 values of the global model, i.e. the model containing all the parameters of interest, using the methods of Nakagawa & Schielzeth (2013). We calculated $R^2_{GLMM(m)}$, the marginal R^2 which describes the variance explained by the fixed factors, and

$R^2_{\text{GLMM}(c)}$, the conditional R^2 which is concerned with the variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013).

Model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Burnham & Anderson (2002) and Grueber *et al.* (2011). We used the package ‘MuMin’ (Barton 2011) to produce all subsets of models based on the global model and rank them based on AIC_c . Following Richards (2008), and to be 95% sure that the most parsimonious models were maintained within the best supported model set, we retained all models where $\Delta AIC_c < 6$. When multiple equally feasible models were found in the candidate model set, we used model averaging to produce the averaged parameter estimates and relative importance (RI) of each parameter (Burnham & Anderson 2002).

Two sets of sensitivity analyses were carried out to explore the robustness of the models. First, to examine how sensitive the models were to the composition of species within the analysis, species were randomly removed from the data set, the global model was re-run and the $R^2_{\text{GLMM}(m)}$ was calculated for 100 iterations. This process was repeated with between 1 and 50 species being removed (a total of 5000 model runs). Second, our abundance data are based on population estimates, with associated variation and uncertainty which remain unknown, thus excluding the calculation of confidence intervals around the data. Therefore, to simulate the

Table 1 Changes in estimated avian abundance (number of individuals) within Europe between 1980 and 2009. (a) Total changes and changes by quartile when species composition of each quartile is allowed to vary with time. (b) Changes by quartile when species composition of each quartile is fixed in year 1. (c) Number of species increasing or decreasing and the number of species for which these changes were statistically significant ($\alpha = 0.05$)

Quartile	Year 1	Year 30	Change	Proportion of total change
(a)				
All	2063173982	1641329711	-421844271	
Q1	13576444	13597987	21543	0.000
Q2	88694609	79127422	-9567187	0.023
Q3	293659205	232800545	-60858660	0.144
Q4	1667243724	1315803757	-351439967	0.833
Quartile	Year 1	Year 30	Change	Proportion of total change
(b)				
Q1	13576444	18390981	4814537	0.011
Q2	88694609	91421345	2726736	0.006
Q3	293659205	266209319	-27449886	0.063
Q4	1667243724	1265308066	-401935658	0.920
	Increase	Decrease	Significant increase	Significant decrease
(c)				
Total	74	70	55	62
Q1	24	12	17	8
Q2	21	15	17	14
Q3	17	19	11	18
Q4	12	24	10	22

effects of variation in the data set, we randomly altered each abundance estimate, re-ran the models and calculated the $R^2_{\text{GLMM}(m)}$ for 100 iterations (a total of 3000 model runs). The magnitude of the alteration was chosen randomly from a uniform distribution from between 1 and up to 30% of the estimated abundance for each species and year (See Supporting Information, Sensitivity analysis methods and R code for full details). Abundance and biomass estimates calculated within the simulations were used to provide variability around the mean estimates.

To determine whether there were differences in the number of species demonstrating significant population declines or increases between abundance quartiles, we produced linear regression models (abundance against year) for each species individually as we were unable to determine significance for the species-specific slopes from the mixed effects model. General additive models used to illustrate the trends on plots were carried out using package ‘gam’. F and P values were calculated using Satterthwaite (1946) approximations to determine denominator degrees of freedom in package ‘lmerTest’ (Kuznetsova *et al.* 2013).

RESULTS

Overall trends

Summing all species, we found a negative trend in total estimated bird abundance between 1980 and 2009, resulting in a decrease of 421 million individuals (Table 1, Fig. 1a). Generalised linear models highlight steep declines during the first half of the study (1980–1994) followed by a period of greater stability during the second half (Fig. 1a). When these estimated abundances were converted to biomass there was a total decrease of over 7000 tonnes (Table 2; Fig. 2b). Similar to the abundance data, avian biomass declined during the first 20 years (1980–1999) of the study, but showed recovery in the final 10 years. See Fig. S2 for individual species abundance plots.

Factors affecting population trajectories

The global model explained around 82% of the variation in the data ($R^2_{\text{GLMM}(c)} = 0.817$) of which around 30% was explained by the fixed factors, and their interactions ($R^2_{\text{GLMM}(m)} = 0.299$). We produced a candidate model set consisting of all simplified versions of the global model and compared them based on their AIC_c . The 11 models with $\Delta AIC_c < 6$ (Table S4) were used to produce model averaged parameter estimates.

Relative importance of parameters

Abundance quartile, time and body mass were all retained in each model within the candidate model set having a RI of 1 in the final average model. Feeding guild was retained in 82% of top models with a RI of 0.97. Habitat, however, was only retained in 46% of the top models with a RI of 0.18. The interaction of time and the other main effects was used to determine how abundance changed with time in relation to these factors. The interaction of abundance quartile with time was retained in

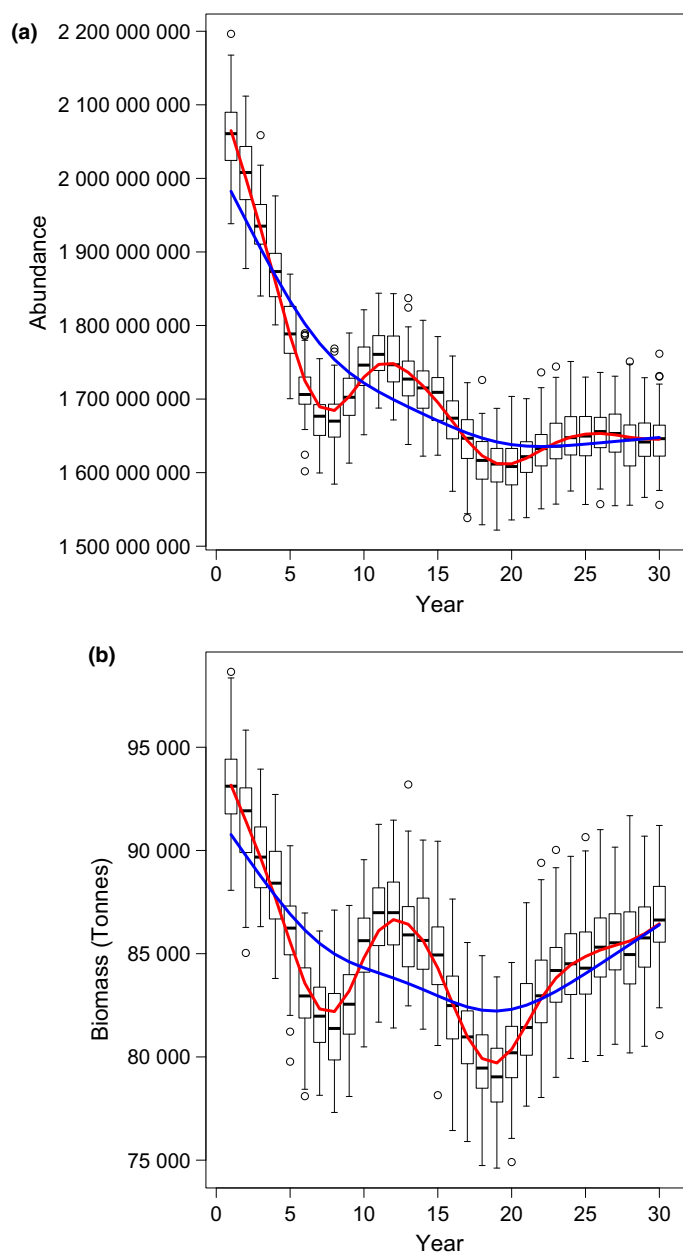


Fig. 1 Total changes in abundance and biomass of birds considered by the PECBMS. Each point represents the totalled abundance estimates of 144 species from 1980 to 2009. Lines represent the fitted values from a general additive model (red – degrees of freedom = 10, blue – degrees of freedom = 3). Linear regression reveals a significant decrease in both abundance ($\beta = -9.89 \times 10^6$, $t = -6.127$, $P < 0.0001$) and biomass ($\beta = -133.51$, $t = -2.074$, $P = 0.0474$) over the 30 year study period. Box and whisker plots represent the variation generated by randomly altering each abundance estimate ± 1 & 20% for 100 iterations.

all models with a RI of 1, while the interaction of feeding guild and time was found in 36% of the models (RI = 0.43), and the interaction of body mass and time was also retained in 56% of the models but with a RI of 0.46. Finally, the interaction between habitat and time was retained in 9% of the candidate model set (RI = 0.01). These results suggest that abundance quartile is a better predictor of population trajectory than major feeding guild, habitat type or body mass.

Table 2 Changes in estimated avian biomass (Tonnes) within Europe between 1980 and 2009 (a) Total changes and changes by quartile when species composition of each quartile is allowed to vary with time. (b) Changes by quartile when species composition of each quartile is fixed in year 1

Quartile	Year 1 (Tonnes)	Year 30 (Tonnes)	Change (Tonnes)	Proportion of change
(a)				
Total	93084	86037	-7047	
Q1	3476	4274	798	0.092
Q2	9225	7637	-1588	0.184
Q3	18223	13141	-5082	0.588
Q4	62159	60986	-1174	0.136
(b)				
Q1	3476	5298	1823	0.102
Q2	9225	11066	1841	0.103
Q3	18223	19988	1765	0.099
Q4	62159	49685	-12475	0.697

Model averaged parameter estimates

The model averaged parameter estimates also highlight how changes in abundance with time are strongly affected by abundance quartile (Table S5; Quartile and time interaction), with the steepest declines being in Q4 ($\beta = -1.56$, $SE = 0.24$) followed by Q3 ($\beta = -0.761$, $SE = 0.222$) and Q2 ($\beta = -0.505$, $SE = 0.191$) (Q1 as the base level), while species within Q1 showed an increase in abundance with time ($\beta = 0.718$, $SE = 0.139$, Q2 as base level). All quartile interactions with time were significant (at $\alpha = 0.001$), and reflect the patterns in the actual data (Fig. 2) with declines within Q2, Q3 & Q4 and increases in Q1 when variable quartiles were used. When considered by feeding guild, while we found considerable decreases in granivores we found no statistically significant changes in abundance with time (Table S5; Fig. S3). In terms of habitat type, we found no significant changes in abundance with time (Table S5; Fig. S4). To ensure that our results were not biased in anyway by the use of interpolated data for the 28 species with some missing data, we ran the models with these data omitted and found no change to our general conclusions (Table S6).

Sensitivity analysis

The models proved to be very robust to both the species composition used within the analysis and random changes in the abundance estimates used in the models. Removing up to 50 species reduced the $R^2_{GLMM(m)}$ from 0.299 (SD = 0.0006) to 0.282 (SD = 0.075) (Fig. S5, Table S7). Altering all of the abundance estimates between 1 and up to a maximum of 30% (the change in abundance was chosen randomly between 1 and the maximum at each of 100 iterations) reduced $R^2_{GLMM(m)}$ from 0.249 (SD = 0.101) to 0.210 (SD = 0.006) (Fig. S6, Table S8).

Changes by quartile

When quartile was assigned on a yearly basis (variable quartiles) 69 species stayed in the same quartile, 67 species occupied 2 quartiles and 8 species occupied three quartiles, over the 30 year study period. Of those that did move between quar-

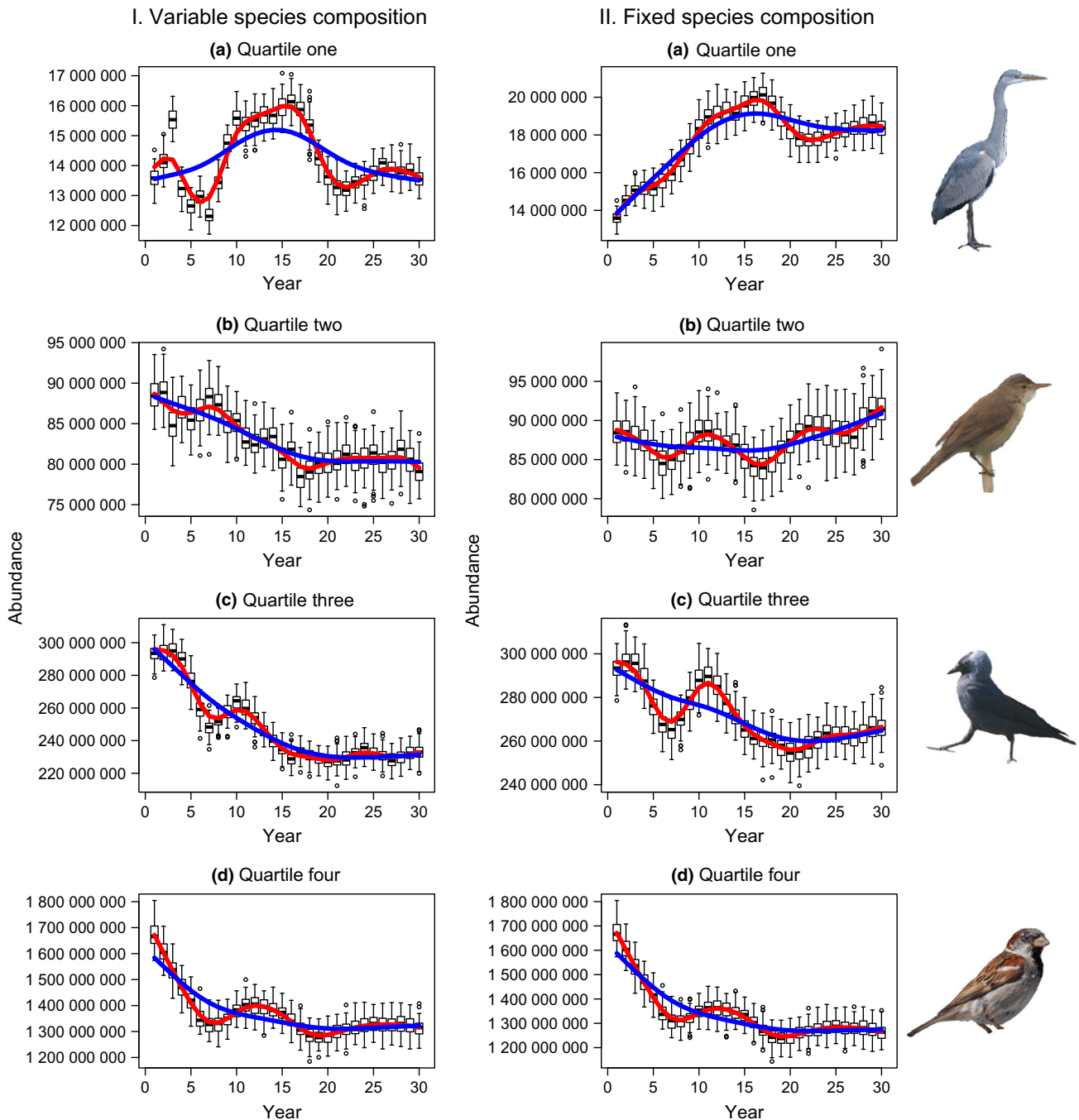


Fig. 2 Total estimates of abundance separated into quartiles. (I) Quartiles based on abundance on a yearly basis hence quartiles have a variable species composition. (II) Quartiles based on abundance in year 1 of the study (1980) hence quartiles have a fixed species composition. Lines represent the fitted values from a general additive model (red – degrees of freedom = 10, blue – degrees of freedom = 3). Species representing each quartile are; Q1 Grey Heron (*Ardea cinerea*), Q2 Reed Warbler (*Acrocephalus scirpaceus*), Q3 Jackdaw (*Corvus monedula*) & Q4 House Sparrow (*Passer domesticus*). Box and whisker plots represent the variation generated by randomly altering each abundance estimate ± 1 & 20% for 100 iterations.

tiles, 33 species were in the same quartile in the final year as at the start of the study. Twenty-two species moved into a more abundant quartile and 19 species moved into a less abundant quartile. When considered by abundance quartile and as predicted by our model there were considerable asymmetries in population trajectories between the different abundance quartiles.

The vast majority of the changes in abundance and biomass were driven by changes in the most common, Q4, species, accounting for 83% of the total abundance decline when the species composition was variable (method one, Table 1, a, Fig. 2I d). When species were fixed to their year 1 quartile, Q4 changes accounted for 92% of the total change in abundance (Table 1b, Fig. 2II d). Of the 36 most common species,

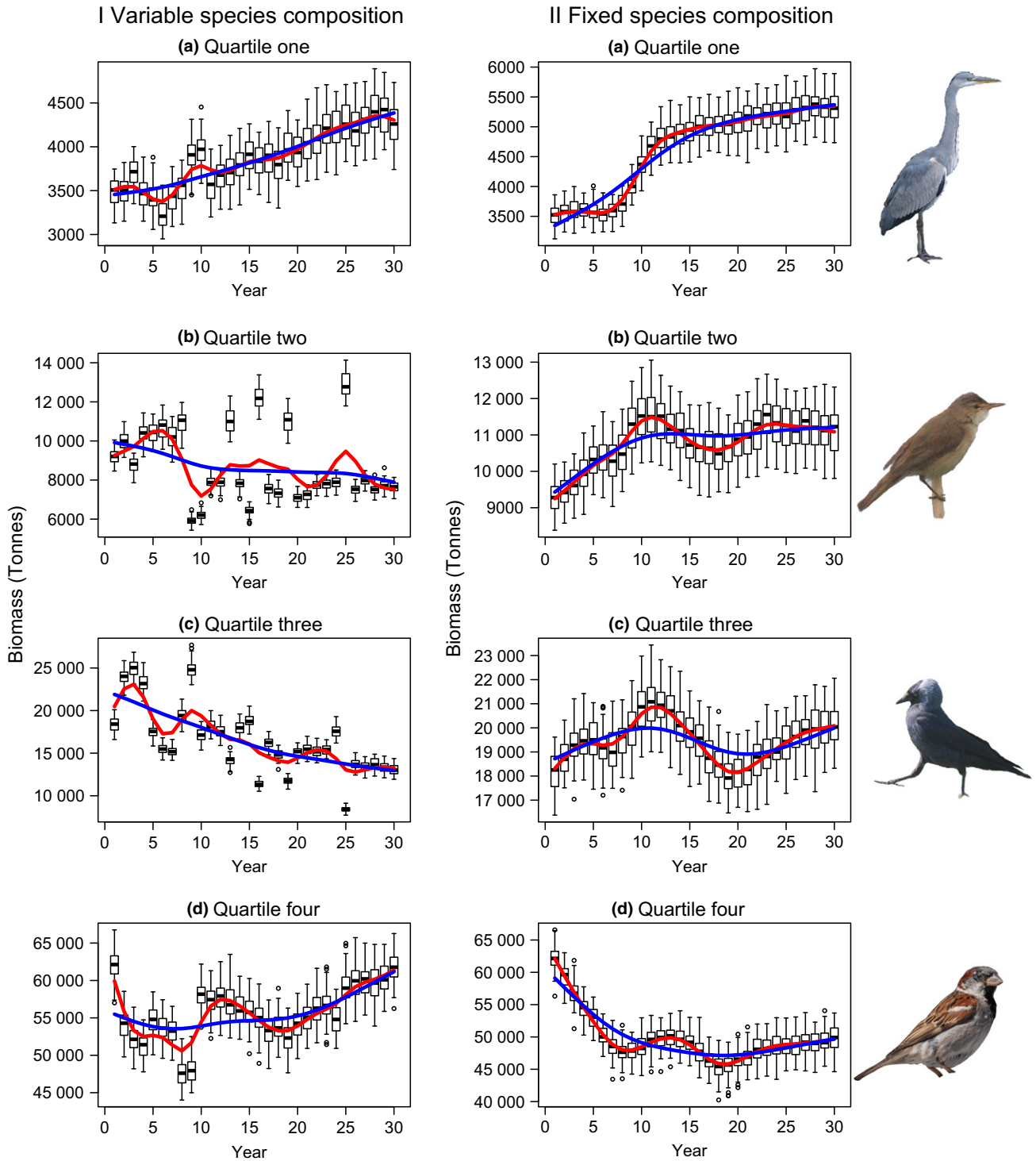


Fig. 3 Total estimates of biomass separated into quartiles. (I) Quartiles based on abundance on a yearly basis hence quartiles have a variable species composition. (II) Quartiles based on abundance in year 1 of the study (1980) hence quartiles have a fixed species composition. Lines represent the fitted values from a general additive model (red – degrees of freedom = 10, blue – degrees of freedom = 3). Box and whisker plots represent the variation generated by randomly altering each abundance estimate ± 1 & 20% for 100 iterations.

24 were decreasing (22 statistically significantly $\alpha = 0.05$) and 12 showed increases (10 significantly, Table 1c). Species belonging to Q3, representing the second most abundant group, also demonstrated an overall decline, although these changes represent only a small fraction of the overall decline

(Table 1a, c and Fig. 2I, II c). When quartile composition was flexible, Q2 species also showed declines (Table 2a and Fig. 2I b). When however quartiles were fixed in year 1, Q2 species showed modest increases in abundance (Table 1b and Fig. 2II b). Similarly, and in contrast to the most common

species, Q1 species demonstrated an overall increase in abundance with either variable or fixed species composition (Table 1a, b and Fig. 2I, II a). Of these least abundant species, 24 were found to be increasing (17 significantly) and 12 were decreasing (8 significantly, Table 1c).

Biomass

When calculated in terms of biomass the patterns largely reflected those for abundance (Table 2, Fig. 3), although while both were declining this was steeper when considered in terms of abundance rather than biomass. This can be partially explained by the fact that the most abundant birds tended to be smaller (there is a negative correlation between body mass and abundance, $r_s = -0.4077$, $P < 0.001$, Fig. S7). Hence, reductions in abundance in lighter birds were not reflected in terms of biomass. Moreover, when biomass for the most common Q4 species was calculated allowing for a variable species composition, we actually found only a modest decrease in biomass (Fig. 3I d). This is largely due to the most common (Q4) species in year 1 of the study (mean body mass = 51.93 g SD = 92.22) being replaced by heavier species (mean body mass = 65.84.6 g SD = 110.44) by the end of the study (Fig. S8). The common wood pigeon *Columba palumbus*, has shown a particularly dramatic increase in biomass since 1980.

DISCUSSION

European birds are declining at an alarming rate, and much of this decline has been attributed to decreases in the number of farmland birds caused by agricultural intensification (Donald *et al.* 2001). In addition, there have been a number of well-publicised declines of very common European birds such as the House Sparrow (De Laet & Summers-Smith 2007) and Common Starling (Smith *et al.* 2012). At the same time a number of the rare species have shown dramatic increases in recent years, probably due to the impacts of direct conservation action (Gregory *et al.* 2003; Holling *et al.* 2011). It has, however, remained unclear as to whether being common in itself is a factor affecting population trajectory. This work demonstrates for the first time how more common birds are generally declining faster than less abundant species while accounting for other factors which have been postulated as being responsible for avian population declines. This is particularly worrying as by definition the commonest birds are the most numerous and hence declines in these species have a much greater impact in terms of the ecosystem function and services which they provide. Our results are based on the outcomes of many thousands of individual surveys of breeding birds throughout Europe, each with associated variation and uncertainty, and hence we emphasise the point that our results are abundance and biomass estimates. However, that the data used has undergone considerable verification and quality control and our conclusions remain unaffected by high levels of added random variation which gives us confidence in the patterns we describe.

In addition to changes in avian abundance, we also provide evidence for a shift in the body mass distribution

within European birds, with a general trend for smaller birds to decline faster than larger birds and for larger birds to be increasing in abundance, which is likely to be the main reason why avian biomass has not declined as rapidly as has abundance. These changes in body mass distribution will also likely have impacts in terms of the ecosystem services provided by birds as the levels of many of these services are linked to consumption rates (e.g. pest control, scavenging services), which are driven by metabolic rates, which are in turn a function of body mass. As the mean power-law scaling exponent of field metabolic rate and body mass relationship has been estimated at 0.64 for birds (Hudson *et al.* 2013), a reduction in abundance of lower body mass species will lead to a disproportionate loss in ecosystem services even if this loss is, to a certain extent offset by increases in abundance of species with greater body mass. Our results confirm trends for a number of species of farmland bird species, many of which are common and have shown steep declines in a number of European countries in recent years (Chamberlain *et al.* 2000; Fox 2004; Wretenberg *et al.* 2006). A proportion of the patterns we present may be attributed to changes previously described such as the declines in farmland bird species and the associated declines in granivorous birds (Moorcroft *et al.* 2002), indeed Q4 contains a greater proportion of farmland granivores than other quartiles, although there are more insectivores and birds utilising habitats other than farmland within this quartile. We did not, however, find any significant interactions between feeding guild and time or habitat and time.

While conservation policy aims to identify declines in as wide a range of species as possible, including the most common species, it is almost inevitable, given limited resources, that conservation action has a long history of focusing on rarity and this approach has had some notable successes (Male & Bean 2005; Donald *et al.* 2007; Hoffman *et al.* 2010). Being common, however, does not provide immunity from future decline and possible extinction. Indeed the literature provides numerous examples of once common species that have been driven to extinction, or have ceased to be common, in relatively short periods (Gaston & Fuller 2007; Lindenmayer *et al.* 2011). In this study, we have demonstrated that the vast majority of the decline in European birds is explained by considerable losses in number of relatively few common bird species. Conversely, less abundant species are generally increasing in number. While our results do not contain data on species considered especially rare in Europe (< 1500 breeding pairs; Holling 2011), those for Q1 reflect the population trends that have been reported regionally for such species, with a UK rare species indicator, e.g. demonstrating a 260% increase between 1973 and 1998 (Gregory *et al.* 2003), with much of that increase being due to targeted conservation action.

One possible clue to the declines in the most abundant species is that, almost by definition, common species are widespread and their numbers are linked to the deterioration of the quality of the environment on a landscape scale (Gaston & Fuller 2007). Conservation management tends to be targeted locally to increase the abundance of rare species,

often through the establishment and maintenance of protected areas. Such management plans, however, offer little protection for more common and widespread species (Hoffman *et al.* 2010). While protected areas are vital to conserving rare and endangered species, we suggest an increasing proportion of conservation funding and effort be afforded to wider scale environmental improvement programs, such as effective agri-environment and urban green space schemes.

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AUTHORSHIP

RI, RG & KJG designed the study. JPD, RG & PV collected and collated the data. RI, KJG, JPD & IS performed the analysis. RI wrote the manuscript and all authors contributed to subsequent revisions.

REFERENCES

Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004). *IUCN Red List of Threatened Species. A global Species Assessment*. IUCN (World Conservation Union), Gland, Switzerland.

Barton, K. (2011) Model selection and model averaging based on information criteria (AICc and alike). R package, version 1.9.5. Available at: <http://cran.r-project.org/web/packages/MuMIn/index.html>. Last accessed 21 February 2014.

Bates, D., Bolker, B., Maechler, M. & Walker, S. (2013) lme4: linear mixed-effect models using Eigen and S4. R package, version 1.0-4. Available at: <http://cran.r-project.org/web/packages/lme4/index.html>. Last accessed 21 February 2014.

BirdLife International (2004). *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife Conservation Series no. 12. BirdLife International, Cambridge, UK.

BirdLife International (2012). Species factsheets: *Oenanthe isabellina* & *Oenanthe leucura*. Available at: <http://www.birdlife.org>. Last accessed 21 February 2014.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, Berlin.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A. *et al.* (2010). Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.

Caughley, G. & Gunn, A. (1995). *Conservation Biology in Theory and Practice*. Blackwell Science, Oxford.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubbs, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.*, 37, 771–788.

De Laet, J. & Summers-Smith, J.D. (2007). The status of the urban house sparrow *Passer domesticus* in north-western Europe: a review. *J. Ornithol.*, 148(Suppl 2), S275–S278.

Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. Biol. Sci.*, 268, 25–29.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D. & Waliczky, Z. (2007). International conservation policy delivers benefits for birds in Europe. *Science*, 317, 810–813.

Dunning, J.B. Jr (2007). *CRC Handbook of Avian Body Masses*, 2nd edn. Taylor & Francis, Boca Raton.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. *et al.* (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.*, 3, 479–486.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000). Analysis of population trends for farmland birds using generalized additive models. *Ecology*, 81, 1970–1984.

Fox, A.D. (2004). Has Danish agriculture maintained farmland bird populations? *J. Appl. Ecol.*, 41, 427–439.

Gangoso, L., Agudo, R., Anadon, J.D., de la Riva, M., Suleyman, A.S., Porter, R. *et al.* (2013). Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem service providers. *Conserv. Lett.*, 6, 172–179.

Gaston, K.J. (1994). *Rarity*. Chapman and Hall, London.

Gaston, K.J. (2008). Biodiversity and extinction: the importance of being common. *Prog. Phys. Geogr.*, 32, 73–79.

Gaston, K.J. (2010). Valuing common species. *Science*, 327, 154–155.

Gaston, K.J. (2011). Common ecology. *Bioscience*, 61, 354–362.

Gaston, K.J. & Fuller, R.A. (2007). Commonness, population depletion and conservation biology. *Trends Ecol. Evol.*, 23, 14–19.

Geider, R.J., Delucia, E.H., Falkowski, P.G., Finzi, A.C., Grime, J.P., Grace, J. *et al.* (2001). Primary productivity of planet Earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Glob. Change Biol.*, 7, 849–882.

Gelman, A., Su, Y.S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J. *et al.* (2013). Arm: data analysis using regression and multi-level/hierarchical models. R package, version 1.6-09. Available at: <http://cran.r-project.org/web/packages/arm>. Last accessed 21 February 2014.

Gregory, R.D. & van Strien, A. (2010). Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithol. Sci.*, 9, 3–22.

Gregory, R.D., Noble, D., Field, R., Marchant, J., Raven, M. & Gibbons, D.W. (2003). Using birds as indicators of biodiversity. *Ornis Hungar.*, 12–13, 12–24.

Gregory, R.D., van Strien, A., Vorisek, P., Gmelig, A.W., Noble, D.G., Foppen, R.P.B. *et al.* (2005). Developing indicators for European birds. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 360, 269–288.

- Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate filter and founder effects. *J. Ecol.*, 86, 902–910.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.*, 24, 699–711.
- Handbook of the Birds of the World Alive (2013). Available at: <http://www.hbw.com/>. Last accessed 21 February 2014.
- Henderson, P.A. & Magurran, A.E. (2010). Linking species abundance distributions in numerical abundance and biomass through simple assumptions about community structure. *Proc. Biol. Sci.*, 277, 1561–1570.
- Hoffman, M. *et al.* (2010). The impact of conservation on the status of the world's vertebrates. *Science*, 330, 1503–1509.
- Holling, M. & Rare Breeding Birds Panel (2011). Rare breeding birds in the United Kingdom 2009. *Br. Birds*, 104, 476–537.
- Hudson, L.N., Isaac, N.J.B. & Reuman, D.C. (2013). The relationship between body mass and field metabolic rate among individual birds and mammals. *J. Anim. Ecol.*, 82, 1009–1020.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2013) lmerTest: Tests for random and fixed effects for linear mixed effect models. R package, version 2.0-3. Available at <http://cran.r-project.org/web/packages/lmerTest/index.html>. Last accessed 21 February 2014.
- Lindenmayer, D.B., Wood, J.T., McBurney, L., MacGregor, C., Youngentob, K. & Banks, S.C. (2011). How to make a common species rare: a case against conservation complacency. *Biol. Conserv.*, 144, 1663–1672.
- Male, T.D. & Bean, M.J. (2005). Measuring progress in US endangered species conservation. *Ecol. Lett.*, 8, 986–992.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Kassa Benecha, H., *et al.* (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995–1015.
- Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. (2002). The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J. Appl. Ecol.*, 39, 535–547.
- Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effect models. *Methods Ecol. Evol.*, 4, 133–142.
- R Core Team (2012). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at: <http://www.R-project.org/>. Last accessed 21 February 2014.
- Richards, S.A. (2008). Dealing with overdispersed count data in applied ecology. *J. Appl. Ecol.*, 45, 218–227.
- Satterthwaite, F.E. (1946). An approximate distribution of estimates of variance components. *Biometrics*, 2, 110–114.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.*, 1, 103–113.
- Sekercioglu, C.H., Daily, G. & Ehrlich, P.R. (2004). Ecosystem consequences of bird declines. *Proc. Natl Acad. Sci. USA*, 99, 263–267.
- Smith, H.G., Ryegard, A. & Svensson, S. (2012). Is the large-scale decline of the starling related to local changes in demography? *Ecography*, 35, 741–748.
- Snow, D.W. & Perrins, C.M. (1998). *The Birds of the Western Palearctic*, Concise edn. Oxford University Press, Oxford.
- Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F. *et al.* (2011). The need to quantify ecosystem services provided by birds. *Auk*, 128, 1–14.
- Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008). Ecosystem services provided by birds. *Ann. N. Y. Acad. Sci.*, 1134, 25–60.
- Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. & Pärt, T. (2006). Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *J. Appl. Ecol.*, 43, 1110–1120.

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