Brain size and resource specialization predict long-term population trends in British birds

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Large-scale population declines have been documented across many faunal assemblages. However, there is much variation in population trends for individual species, and few indications of which specific ecological and behavioural characteristics are associated with such trends. We used the British Common Birds Census (1968–1995) to identify specific traits associated with long-term abundance trends in UK farmland birds. Two factors, resource specialization and relative brain size, were significantly associated with population trend, such that species using atypical resources and with relatively small brains were most likely to have experienced overall declines. Further analyses of specific brain components indicated that the relative size of the telencephalon, the part of the brain associated with problem solving and complex behaviours, and the brain stem might be better predictors of population trend than overall brain size. These results suggest that flexibility in resource use and behaviour are the most important characteristics for determining a species' ability to cope with large-scale habitat changes.

Keywords: British Common Birds Census; brain architecture; niche position; behavioural flexibility; farmland birds

1. INTRODUCTION

Many faunal assemblages across the globe are showing serious declines in the populations of their constituent species (Loh *et al.* 2005; IUCN: www.redlist.org). However, within these assemblages there is much interspecific variation in the direction and magnitude of population trends. Identifying characteristics that cause some species to be intrinsically vulnerable to declines could help focus and prioritize the development of conservation management strategies. Identifying shared ecological or life-history traits that are the ultimate causes of population declines has been described as 'one of the most important challenges for contemporary ecologists' and 'as of vital importance in the quest to stop biodiversity loss' (Kotiaho *et al.* 2005).

Most previous studies that have addressed this challenge have considered the effects of variation in life history, ecological and/or behavioural traits on extinction risk (Gaston & Blackburn 1995; Bennett & Owens 1997; Owens & Bennett 2000; Purvis *et al.* 2000; Harcourt *et al.* 2002; Norris & Harper 2004; Kotiaho *et al.* 2005). Fewer studies have tested explicitly which traits correlate with population decline (but see, e.g. Jennings *et al.* 1999; Davies *et al.* 2004). Here, we use data for British farmland birds to determine whether specific intrinsic factors are related to well-documented, long-term population changes in these species.

Farming is now one of the most severe threats faced by the world's birds (Green *et al.* 2005). Changing agricultural practices threaten biodiversity in both the developed and developing world, both through loss of natural habitat to farming and through continued modification of the farmland habitat (Green *et al.* 2005). In northwest Europe, agricultural intensification in the last four decades of the twentieth century (Chamberlain *et al.* 2000; Shrubb 2003) has coincided with dramatic declines in geographic range and abundance of populations of many bird species (Tucker & Heath 1994; Fuller *et al.* 1995; Berthold *et al.* 1998; Siriwardena *et al.* 1998; Donald *et al.* 2001). A wealth of evidence now links the declines of many species to specific aspects of agricultural intensification (Aebischer *et al.* 2000a; Boatman *et al.* 2002; Vickery *et al.* 2004a). However, previous attempts to relate the population trends of European birds to intrinsic factors have not been very productive (e.g. Fuller *et al.* 1995; Siriwardena *et al.* 1998), with only a qualitative definition of specialization being correlated with declines.

What intrinsic characteristics are likely to insulate farmland birds against the deleterious effects of agricultural intensification? A key factor is likely to be a species' ability to switch resource use, or seek out novel resources, as a response to environmental change. Species that use a variety of resources are able to occupy more habitat types than species with narrow resource requirements. It follows that if individuals are able to switch resources as a response to changes in the relative availability of resources in their environment, they will be less affected by large-scale habitat alteration. Measures of niche space, such as niche

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Table 1. Parameters used in predicting long-term population trends of UK farmland birds.

parameter	description
body size	natural log average male and female body size
annual productivity	number of clutches per year multiplied by average clutch size
migration strategy	categorical variable of resident and long-distance migrant
niche position	indication of how 'typical' resource use is compared to other community members. Natural logged.
niche breadth	measure of diversity of habitat types occupied. Natural logged.
relative brain size	residuals of log–log body–brain RMA regression, including a grade shift (see Electronic Appendix, part B)
relative telencephalon size	residuals of log–log body–telencephalon RMA regression, including a grade shift
relative brain stem size	residuals of log–log body–brain stem RMA regression
relative cerebellum size	residuals of log–log body–cerebellum RMA regression
relative optical lobe size	residuals of log–log body–optical lobe RMA regression

breadth (variety of resources used) and niche position (how typical the resources used are, relative to resource use by the community as a whole) are, therefore, likely to be important (Gregory & Gaston 2000). In addition, behavioural flexibility, especially in terms of the ability to seek out novel resources, can help species cope with environmental change. Recent papers have shown that several measures of behavioural flexibility, including invasion success (Sol & Lefebvre 2000; Sol et al. 2002, 2005) and feeding innovation rate (Lefebvre et al. 2004), are correlated with brain size and architecture in birds. Thus, brain size may be a good surrogate for the capacity to respond behaviourally to environmental change.

Migratory status may also influence vulnerability to population declines. Migrant birds may be subject to additional pressures and constraints on their wintering grounds, and have been shown to be more susceptible to population decline in both North America (Sauer et al. 1996) and Europe (Berthold et al. 1998). Furthermore, while climate change may, in all species, cause a mismatch between the timing of breeding and the period when food availability is most suitable for breeding, migrants may be particularly susceptible to these effects as their departure from their wintering grounds is influenced by conditions away from the breeding grounds (Dunn 2004; Visser et al. 2004; Gordo et al. 2005). Finally, studies of extinction risk have often found correlations with measures of fecundity and body size (Owens & Bennett 2000; Purvis et al. 2000), which may influence the ability of species to resist or recover from population declines.

In this paper, we investigate the relationships between avian population trends in the British farmland environment and body size, niche breadth and position, fecundity, migration strategy and cognitive capacity. The British bird fauna is perhaps the best known in the world, and so represents an ideal assemblage in which to examine the impact of species' characteristics on vulnerability to long-term population declines in the face of agricultural intensification, one of the most widespread and pervasive threats to global biodiversity.

2. MATERIAL AND METHODS

(a) Data

Population trends from 1968 to 1995 were taken from farmland plots of the UK Common Birds Census (CBC; Marchant et al. 1990), for forty common UK bird species (see Electronic Appendix, part A for list of species). The CBC was developed to monitor wide-scale annual population trends in abundant bird species. The set of species chosen were all those species common enough to be recorded in sufficient UK farmland CBC plots to allow the calculation of a farmland CBC abundance index for all the years (Siriwardena et al. 1998). The list is, therefore, neither an exclusive nor an exhaustive list of farmland species (some species are too rare to provide an index) and includes some species which are more characteristic of other habitats, but which nevertheless were recorded regularly in farmland CBC plots. Although population trends are available for these species for more recent years, through the new Breeding Bird Survey (Eaton et al. 2004), we used the CBC index for this period as it was coincident with the main period of multivariate intensification of agriculture (Chamberlain et al. 2000; Shrubb 2003). Additionally, this restricts the data used to the period during which farmland bird populations declined and before any populations started to recover following recent (conservation-driven) changes in management. Population change was derived by setting initial populations to an index of one and calculating the overall proportion change from this initial index (such that a decline between 1968 and 1995 of 75% would equal an index of 0.25). Two stocked species (*Phasianus colchicus* and *Alectoris rufa*) were excluded from this analysis, as their populations, in part, are artificially maintained.

The independent variables are summarized in table 1. The data for these predictor variables came from the following sources except where noted (Cramp & Simmons 1977–1983; Cramp 1985–1992; Cramp & Perrins 1993–1994). Body size was estimated by taking the mean of reported male and female body mass in the UK. Annual productivity was calculated by multiplying the mean number of broods per year by the mean clutch size. Brain size data were taken from Mlikovsky (1989a–c, 1990). Brain–body residuals values (which we refer to as 'relative brain size') were calculated using the following equation of estimated brain mass as a function of body mass, from Armstrong & Bergeron (1985): $E = 0.138 \times S^{0.58}$, where S is the body size for each species (see Electronic Appendix, part B for more details).

Variation in resource use was described using two measures, niche breadth and niche position, derived from Gregory & Gaston (2000). In their analyses, canonical correspondence analysis (CCA) was used to relate 34 climatic and habitat characteristics (independent variables) to estimates of individual species' abundance from BBS surveys (dependent variables) across 1830 1 km² square plots.

The CCA analysis reduced the habitat characteristics to four main environmental axes. Individual species show a Gaussian (bell-shaped) distribution of tolerance across the environmental gradient described by each axis. The standard deviation of this distribution is an estimate of tolerance or niche breadth along a given environmental axis (ter Braak 1990). For example, in Gregory & Gaston (2000), the first environmental axis describes a gradient from warm, sunny habitats towards wet, upland, moorland habitats. A tolerant species, or one with a wide niche breadth, will occur on plots across the entire gradient and will have high values for niche breadth on this axis. An overall estimate of niche breadth can be calculated by the root mean squared standard deviations across all four axes.

Their second estimate, niche position, was calculated as the mean distance between individual species' scores along each axis (an estimate of the centre of the distribution for each species along an axis) and the weighted mean of all species (the centroid) across all four environmental axes. Niche position, in contrast to niche breadth, gives a value for how typical the resource use of a particular species is relative to all other species and the resources available. This value increases as species use resources that are increasingly atypical of that specific community. As niche position correlates with both abundance and range size (Gregory & Gaston 2000), we compared population change with range size data (Sharrock 1976) from the start of the period to ensure that any relationship between niche position and trend was not an artefact of distribution. As there are no reliable population abundance data that predate the onset of the declines, it was not possible to test directly whether abundance is associated with population trends; however, range size and abundance are typically highly positively correlated across British bird species (e.g. Gaston *et al.* 2000).

(i) *Statistical analyses*
Related species cannot be assumed to be independent data points, and so the method of phylogenetic generalized least squares (PGLS) was used to test for phylogenetic non-independence in our data (Grafen 1989; Martins 1999; Garland & Ives 2000). PGLS explicitly incorporates the expected covariance among species into a statistical model fit by generalized least squares. The correlation between error terms is thus altered to reflect the degree of phylogenetic relatedness amongst the species to which they relate (see Electronic Appendix, part C for a thorough justification of the PGLS approach). The PGLS approach was implemented in R (Ihaka & Gentleman 1996) using the Analysis of Phylogenetics and Evolution (APE) package (Paradis *et al.* 2004) and code written by R. P. Duncan. PGLS requires a hypothesis about the phylogenetic relatedness of the species analysed. We assumed that the species in our dataset were related according to the phylogeny of Sibley & Ahlquist (1990), with generic relationships as described in Sibley & Monroe (1990). Since we did not know all the branch lengths in the phylogeny, we repeated the analysis with two different assumptions about branch length models. In the first, all branches in the model were set equal. In the second, branch lengths were set to be proportional to the number of taxa below each node in the phylogeny. Branch lengths were calculated using TREEEDIT v.1.0a10.

Separate univariate analyses were performed to test the effect of each predictor variable on population change. We then used stepwise simplification to identify minimum

adequate models (MAMs) from all possible predictors, such that only predictors that were significant ($p < 0.05$) were included in the MAMs. To minimize the likelihood of selecting a sub-optimal model, we used both forward and backwards stepwise selection. The effects of individual predictors were assessed using an F statistic.

To explore further an apparent relationship between relative brain size and population trend, we analysed separately four component parts of the brain: telencephalon, cerebellum, optical lobes and brain stem (after Portmann 1947). Brain component–body residuals were calculated using a reduced major axis (RMA) regression of log brain component mass against body size (see Electronic Appendix, part B). Telencephalon residuals were taken directly from Burish *et al.* (2004) to ensure comparability between studies. We also calculated telencephalon residuals in the same manner as the other brain components, but this had no qualitative impact on the results.

3. RESULTS
For all analyses, the best-fit evolutionary model was one with $\lambda = 0$, regardless of the branch length assumption. Thus, there is no evidence of phylogenetic autocorrelation in these data, and consequently the statistics we report below are from tests performed across species.

Univariate analyses revealed two significant predictors of population change: relative brain size and niche position (table 2). Relatively large-brained species on average declined less than relatively smaller-brained species, while species using resources typical of their community had lower rates of decline than those species that used atypical resources. The latter relationship is not an artefact of the initial distribution of the species, as there was no significant relationship between population change and geographic range ($r^2 = 0.02$, $F_{1,38} = 0.94$, $p = 0.34$). Stepwise model selection resulted in a model with only niche position and relative brain size as significant predictors (table 2). There was a negative relationship between niche position and niche breadth (Pearson's $r = -0.69$, $n = 40$, $p < 0.001$). However, there were no other significant correlations between the independent variables.

Population change was significantly positively associated with the relative size of two brain components, the telencephalon and the brain stem (table 3). Although the telencephalon explained more variation in univariate analyses, both brain components explained similar variation in population decline when incorporated into models with niche position (table 4), and far more variation than the models using total brain size and niche position (adjusted r^2: 43% and 44%, versus 25%; tables 2 and 4). There was no clear support for one model over the other when an AIC-based information theoretic approach was used for model comparisons (table 4), and telencephalon and brain stem sizes are highly correlated ($r^2 = 0.699$, $p < 0.001$). A stepwise linear regression model retained only telencephalon and niche position ($F_{2,23} = 9.77$, $p = 0.001$) while excluding brain stem ($t = 1.50$, $p = 0.15$). The remaining brain components, the cerebellum and the optical lobe, explained little of the variation in population trend.

Table 2. Results of univariate and multiple regression analyses to predict population change for all available species.

univariate tests

continuous variables		slope	r^2	F	p
life history	body size	0.02	0.01	$F_{1,38}=0.32$	0.58
	annual productivity	−0.02	0.03	$F_{1,38}=1.19$	0.28
resource use	niche breadth	0.01	0.04	$F_{1,38}=1.44$	0.24
	niche position	−0.31	0.19	$F_{1,38}=8.66$	0.006
relative brain size		1.15	0.13	$F_{1,37}=5.57$	0.024

categorical variables		mean	s.e.	F	p
migration strategy	migrant	0.84	0.11	$F_{2,37}=0.73$	0.40
	resident	1.03	0.06		

multiple regression model

				model			
predictors	d.f.	F	p	d.f.	F	p	adjusted r^2
niche position	1,36	7.94	0.008	2,36	7.28	0.002	0.25
brain size	1,36	4.24	0.047				

4. DISCUSSION

Two previous papers have attempted to identify factors associated with recent population trends of UK farmland birds. Fuller *et al.* (1995) were unable to identify any factors that distinguished declining from non-declining species. Siriwardena *et al.* (1998) found no evidence that diet, nesting habitat, migration strategy or taxonomic grouping were associated with a species' long-term population trend. The only factor significantly associated with population declines was whether a species was broadly categorized as a farmland generalist or specialist, with specialists declining more. However, the behavioural and life history categories used in these two analyses were generally qualitative in nature. Here, we used quantitative life history and behavioural variables.

As in the analysis by Siriwardena *et al.* (1998), long-term population change in British farmland birds was associated with a measure of specialization. In this analysis, niche position, which is a quantitative measure of how atypical the habitat use is by a particular species, was found to be a strong predictor of long-term population trend. These results are consistent with agricultural intensification as the cause of population declines, as intensification is associated with a loss of habitat diversity and simplification of farming systems (Benton *et al.* 2003). It is conceivable that rarity itself, rather than specialization, makes species more vulnerable to declines. However, were this the case, geographic range should be associated with decline rate, yet it was not. An obvious conservation response given these results would be to ensure that the habitats and resources needed by the 'atypical' species are given priority in management plans. In fact, this is already embodied in agri-environment strategy in England, where geographically targeted 'higher tier' schemes provide resources for the rarest species (Aebischer *et al.* 2000*b*), while lower tier schemes deliver for the declining but still more widespread species (Vickery *et al.* 2004*b*).

Table 3. Univariate analyses of population changes against relative size of four brain components.

continuous variables	slope	r^2	$F_{1,23}$	p
telencephalon	1.44	0.35	12.58	0.002
brain stem	1.83	0.28	5.84	0.02
cerebellum	0.93	0.11	2.59	0.12
optical lobes	0.61	0.04	0.90	0.35

Niche position has been shown to be a significant predictor of abundance and distribution of British birds (Gregory & Gaston 2000) and here the influence is extended to population trend. One potential shortcoming of the niche variables is that they were calculated from data collected in 1996 (Gregory & Gaston 2000), which is after the main period of population decline. The niche variables do not document spatial and temporal variability in habitat and resource use, yet it is very unlikely that there is a constant 'equilibrium niche'. Many species are territorial in the breeding season and occupy territories despotically, in order of habitat quality, so it is possible that niche breadth, for example, will narrow as population density declines (Fretwell & Lucas 1970; O'Connor 1987). It is, therefore, possible that any correlation with niche breadth is a consequence rather than a cause of population declines. However, niche breadth was not a significant predictor of population declines. Moreover, it is unlikely that the correlations between niche position and population change suffer from this problem, as niche breath and position are not correlated (Gregory & Gaston 2000). Nevertheless, spatial and temporal analyses of the intraspecific variability of niche breath and position might prove revealing in understanding patterns of distribution, abundance and population trends.

The lack of relationship between niche breadth and population trend could be an artefact of the way that the

Table 4. Results of brain component models. All models were run with predictors for a subset of 24 species, for which estimates of all four brain components were available. Hurvich and Tsai's Information Criteria for small sample sizes are used to determine the relative support for each model.

model	predictors	d.f.	F	p	model d.f.	F	p	adjusted r^2	AIC$_c$	ΔAIC$_c$	weight
1	Ln niche position	1,21	8.25	0.009	2,21	9.86	0.001	0.44	0.88	0	0.54
	brain stem	1,21	12.02	0.004							
2	Ln niche position	1,21	5.03	0.014	2,21	9.10	<0.001	0.43	1.39	0.42	0.44
	telencephalon	1,21	13.81	0.002							
3	Ln niche position	1,21	3.15	0.09	2,21	2.99	0.07	0.15	9.75	8.78	0.01
	cerebellum	1,21	0.89	0.36							
4	Ln niche position	1,21	4.19	0.053	2,21	2.65	0.09	0.13	10.31	9.34	0.01
	optical lobe	1,21	0.32	0.56							

variable was estimated. Gregory & Gaston's (2000) niche breadth measures the use of habitats by species across landscapes, rather than the specific use of food or other resources at a finer scale. An analysis that incorporates finer microhabitat and resource use of individual species may provide better measures of niche breadth. Nevertheless, similar criticisms could be made of niche position, and yet this variable does correlate with population changes in farmland birds.

The relationship between population change and brain size is intriguing and this is the first time, to our knowledge, that such a relationship has been found. Relative brain size has been associated with a number of life history traits, including low annual productivity and altricial development (Bennett & Harvey 1985). In this study, explicit tests for life history variables were non-significant, indicating that relative brain size itself is an important factor in predicting bird population trends, rather than having an indirect relationship via life history. An obvious benefit of a larger brain is through increased cognitive skills. A recent study of invasion success in birds showed that species with larger brains were more likely to establish non-native populations, that large-brained species also have higher documented rates of behavioural innovation, and that innovation rate also correlates with establishment success (Sol *et al.* 2005). Sol *et al.* concluded that large brains appear primarily to help birds respond to novel conditions by enhancing their cognitive skills rather than by other mechanisms. Similarly, species with larger brains may be better able to cope with the rapidly changing nature of resources on farmland, and to respond to the availability of opportunities in other habitats, such as food provided at feeders by humans (Cannon 1999).

Support for the role of cognitive ability comes from the relationships we report between population change and brain component size. The relationship between decline rates and telencephalon and brain stem sizes were stronger than for total brain size. Although the functional importance of different brain components is poorly understood, the telencephalon is generally thought to be functionally equivalent to the mammalian neocortex, in that these regions appear to be important in problem solving and complex social behaviour (Reader 2003). The significance of telencephalon size is thus consistent with an influence of cognitive ability on population change in farmland birds. In contrast, the role of the brain stem is

puzzling, as this region of the brain is generally assumed primarily important for control of vital functions such as heartbeat and metabolism. As brain stem was dropped from stepwise models, we suggest that the strong relationship between population change and brain stem size might be most probably the result of the tight correlation between brain stem and telencephalon size. Clearly, further research is required on the possible influence of brain architecture on behavioural and ecological characteristics.

In summary, our results suggest that the farmland birds whose populations have suffered most under agricultural intensification are those with more specialized resource and habitat use and lesser cognitive abilities. As this is the first study of its type, to our knowledge, to examine the association between cognitive capacity and population trends, it remains to be seen whether these conclusions apply to other taxa. In particular, the influence of cognitive abilities seems unlikely to generalize beyond the 'higher' vertebrates. Nevertheless, our study shows that it is possible to identify characteristics that might make some species particularly vulnerable to habitat changes, and hence whether or not the same characteristics are important for all taxa, it is an approach that could be applied to other groups. While the urgent need for robust long-term monitoring is undiminished (Balmford *et al.* 2005; Gregory *et al.* 2005; Loh *et al.* 2005), this study suggests a potential short cut that might in some cases help to identify priority cases at an earlier stage.

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