

Avian assemblage structure and domestic cat densities in urban environments

Victoria Sims¹, Karl L. Evans^{1*}, Stuart E. Newson², Jamie A. Tratalos^{1†} and Kevin J. Gaston¹

¹Biodiversity and Macroecology Group,
Department of Animal and Plant Sciences,
University of Sheffield, Sheffield S10 2TN, UK,
²British Trust for Ornithology, the Nunnery,
Thetford IP24 2 PU, UK

ABSTRACT

While there is intense debate regarding the impact of domestic cat populations on wildlife, its resolution is hindered by the lack of quite basic information. Domestic cats are generalist and obligate predators that receive supplementary food, and their population density reflects that of humans more than the density of their prey. In such a predator–prey system there is the potential for cat populations to have negative impacts on avian assemblages, which may be indicated by negative correlations between cat density and avian species richness and density. Here we report on the nature of such correlations across urban areas in Britain both for groups of species classified regarding their vulnerability to cat predation and individual species. Taking the availability of green space into account, we find negative relationships between cat densities and the number of bird species breeding in urban 1 km × 1 km squares. These relationships are particularly strong among groups of species that are vulnerable to cat predation. We find positive correlations between cat and avian densities; these have low explanatory power and shallow slopes among the species groups that are particularly vulnerable to cat predation. Evidence that the densities of individual species that are vulnerable to cat predation are negatively correlated with cat densities is equivocal, with at least half the species showing no marked pattern, and the remainder exhibiting contrasting patterns. Our results appear not to be confounded by the density of nest-predating corvids (carrion crow, magpie, and jay), as the density of these species was not strongly negatively correlated with avian species richness or density. The general lack of marked negative correlations between cat and avian densities at our focal spatial scale may be a consequence of consistently high cat densities in our study areas (minimum density is 132 cats per square kilometre), and thus uniformly high impacts of cat populations on urban avian assemblages.

Keywords

Domestic cats, birds, corvids, species richness, population density, predation, urban.

*Correspondence: Karl L. Evans, Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.
E-mail: karl.evans@sheffield.ac.uk
†Present address: British Antarctic Survey, High Cross, Madingley Road, Cambridge, UK.

INTRODUCTION

Without doubt the domestic cat *Felis catus* has contributed to the recent extinction and endangerment of a number of avian species, particularly following its introduction to remote oceanic islands (Lowe *et al.*, 2000; Kawakami & Higuchi, 2002; Nogales *et al.*, 2004). In contrast, in areas where the domestic cat has been present for much longer periods, such as Britain, there is intense debate regarding its impact on wild bird populations. Among the general public, large domestic cat populations combined with frequent observations of cats stalking and/or killing wildlife has contributed to a widespread belief that domestic cats kill large numbers of birds, and may have contributed to the marked

population declines that have occurred in recent decades (Baillie *et al.*, 2006). This perception is supported by research suggesting that cats may be responsible for one third of the mortality occurring in some local bird populations (Churcher & Lawton, 1987) and estimates, derived from scaling up local studies to the national level, that cats kill 25–29 million birds per annum in Britain (Woods *et al.*, 2003). On the other hand, there is no conclusive empirical evidence that domestic cats have a markedly adverse impact on avian populations in areas other than somewhat isolated oceanic islands (Mead, 1982; Liberg, 1984; Fitzgerald & Turner, 1988; Fitzgerald, 1988, 1990; Jarvis, 1990; Barratt, 1997, 1998; Woods *et al.*, 2003). Understanding the relationships between domestic cats and bird populations is,

however, severely constrained by the lack of even quite basic information.

A common initial step when investigating the impact of predators on prey populations is to document, either temporally or spatially, relationships between the numbers of prey and their predators (Thomson *et al.*, 1998; Siriwardena, 2006). Such studies have generally revealed negative correlations between wild felids and their prey: examples include populations of lion *Panthera leo* and wildebeest *Connochaetes taurinus* (Tambling & duToit, 2005), tiger *Panthera tigris* and various ungulate species (Seidensticker & McDougal, 1993), and species of *Lynx* and their *Lepus* prey (O'Donoghue *et al.*, 1998; Kauhala & Helle, 2000). These negative correlations arise because wild felids are generalists, and thus when their preferred prey species decline, individuals can maintain their hunting efficiency by switching to other prey species with the consequence that felid population densities are maintained.

Domestic cats are generalist obligate predators, which appear to hunt opportunistically, and receive regular supplementary food and other care from humans (Pearre & Maass, 1998). Domestic cat densities and those of their prey may thus be decoupled. This decoupling has two important consequences. First, domestic cat densities may reflect human population density and the predisposition of humans towards keeping cats as pets. Thus cat densities are likely to be highest in the places with the most people, i.e. cities and other urbanized areas. Second, the nature of this predator–prey system is one in which negative correlations between predator and prey densities could arise (Newton, 1998). If domestic cats behaved in a similar manner to wild felids one might expect that avian and domestic cat population densities would be negatively correlated, at least for species that are vulnerable to cat predation. Here, we investigate the nature of the relationship between domestic cat densities and the structure of avian assemblages in urban areas. We use Britain as a case study due to its highly urbanized nature, and the particularly high density of some urban cat populations in this region. We consider the relationships between cat densities and both avian species richness and population densities, and take the potentially confounding effects of the availability of green space into account. Our initial hypothesis was that cats were adversely impacting urban bird population, and thus negative correlations between cat density and avian species richness and/or density would arise. We assumed that small-bodied and potential prey species were more vulnerable to cat predation, and thus predicted that the species richness and density of these groups would exhibit the strongest negative relationships with cat densities.

METHODS

Avian data

Avian species richness and density were obtained from the BTO/JNCC/RSPB Breeding Bird Survey (BBS) for 2000 at the resolution of 1 km × 1 km squares (see Raven *et al.*, 2005 for full details). BBS squares are selected from a random stratified sample according

to the availability of volunteer observers in each of 83 recording regions (roughly counties or groups of counties) across Britain. Avian data are collected twice per annum (early April to mid-May, and mid-May to late June). Birds are recorded within 200-m sections along two 1-km transects in one of three distance bands (0 to < 25 m, 25–100 m, > 100 m) within each 1 km × 1 km square. Flying birds are excluded unless they are actively using resources in the square. Juvenile and immature birds are also not counted, as the main aim of the survey is to measure trends in the numbers of breeding adult birds. Habitat within each 200-m transect section is recorded according to a four-level hierarchical coding system that documents the main habitat, such as farmland or human settlement, together with finer level habitat features such as gardens, parks, and manmade surfaces (Crick, 1992).

Species richness was calculated as the observed number of species. Previous analyses of these data have demonstrated that using species richness estimators, such as the jack-knife family of estimators, does not generate systematically different spatial patterns in species richness (Evans *et al.* in press).

Distance sampling software (DISTANCE, version 4.1 Release 2; Buckland *et al.*, 2001; Thomas *et al.*, 2004) was used to calculate the density of each species within each 1 km × 1 km square (c. 2000 squares). The decline in detectability with distance from the transect line was modelled, and the heterogeneity in detectability between species, habitats, and regions was taken into account. Detectability functions for each species with 40 or more observations were calculated. For other species the detectability function for a commoner surrogate species, which was as similar as possible to the rare species in its conspicuousness and habitat type, was used. Detectability functions were constructed using nine main habitat types (broad-leaved woodland, coniferous woodland, mixed woodland, scrub, seminatural grassland, heath and bog, farmland, human sites, and waterbodies, based on Crick, 1992) and 11 regions (nine English Government Office Regions, Wales, and Scotland) as factors. Half-normal and hazard-rate key functions were fitted, and the detectability function that provided the best fit to the data as judged by Akaike Information Criteria (AIC) values was selected. Once this best fitting detectability function had been chosen for a species it was applied to the encounters from surveyed squares to produce an estimate of the number of individuals of that species within each square.

From the 110 squares in which all of the ten 200-m transect sections were identified as urban, 30 were chosen at random to include in this study ($n = 30$; see Table S1 in Supplementary Material). All the squares could not be used due to the time constraints imposed by obtaining data on cat densities. For each of these 30 squares we calculated the species richness and avian density for five groups of species: (1) all species, (2) small-bodied species, i.e. = 150 g, (3) large-bodied species, i.e. > 150 g, (4) potential, and (5) non-potential prey species (see Table S2 in Supplementary Material). Body mass data were obtained from the compilation in Gaston & Blackburn (2000). Potential prey species were identified as species which, as either adults or fledglings, are vulnerable to cat predation due to spending a large amount of

time on the ground, in low vegetation or at bird feeding stations, in combination with being relatively small and/or not aggressive. All of the species that we classify as being potential prey have been recorded as being predated by domestic cats in Britain; we did not take nest type into account as data suggest that this does not determine vulnerability to cat predation (Churcher & Lawton, 1987; Woods *et al.*, 2003; Baker *et al.*, 2005).

Cat density data

Cat density data were obtained by conducting telephone and door-to-door surveys with households within each of the 30 urban BBS squares between November 2004 and November 2005; these types of surveys have been found to yield higher response rates than alternatives such as postal surveys (White *et al.*, 2005). Each household was asked how many cats they owned. Although these data were collected a few years after the bird survey data were collected, we consider that there will be a strong correlation between domestic cat density in 2000 and that in 2004/5. The primary reason for this is that the predominant factor influencing the size of domestic cat populations is housing density (e.g. in our data $r = 0.83$; $P < 0.0001$), and due to a marked lack of investment in house building, housing density exhibited very little change within urban areas in the UK during this period (Barker, 2004). In addition, any temporal changes in domestic cat density are highly unlikely to alter the observed spatial variation in cat density, which varies by more than a factor of 10.

We conducted a boot-strap analysis in the statistical package R to determine the minimum number of households that needed to be sampled to estimate cat density with sufficient accuracy. First, we constructed four hypothetical cat populations by randomly allocating cats to houses with (1) 200 cats to 1000 houses, (2) 900 cats to 1000 houses, (3) 200 cats to 4000 houses, and (4) 1500 cats to 4000 houses. This range of scenarios was designed to span that of potential situations in urban areas of Britain based on knowledge of cat densities in areas of high and low housing density (1138 cats in a $1 \text{ km} \times 1 \text{ km}$ square with 3251 houses; and 257 cats in a $1 \text{ km} \times 1 \text{ km}$ square with 1427 houses; V.S., unpublished data). Second, we randomly sampled houses from these four distributions and calculated cat densities. This process was repeated 100 times, and the analysis showed that, with any of the simulated cat distributions, improvements in estimates of cat density were marginal ($< 1\%$) once 50 houses were sampled. In each square we thus obtained data from 50 households in each of our 30 squares, giving a total of 1500 households. Sampling more households per square would have reduced the number of squares that we could include in our survey, and thus the power of our analyses.

Telephone surveys were conducted in 26 squares using phone numbers that were obtained haphazardly using local phone books. We first obtained the names of all roads, within each focal $1 \text{ km} \times 1 \text{ km}$ square, from a local street map. We then identified names and phone numbers for 200 households on these streets by searching a local phone book starting from a haphazardly located page. The selection of phone numbers was

not randomised as this would have required finding precise addresses for each of the households in each square (approximately 57,000 in total) and then selecting addresses at random from this list, and then finding phone numbers. Such a selection process would have taken much longer than that which we selected, which took 12 weeks of full-time work, for one person, to implement. Moreover, it is difficult to identify potential mechanisms that may bias our estimates of cat densities due to our selection of phone numbers using a haphazard technique rather than a truly random one. Door-to-door surveys were conducted in four $1 \text{ km} \times 1 \text{ km}$ squares that were located relatively close to our residential addresses as these were quicker than phone surveys. In these squares door-to-door enquiries were conducted in randomly chosen streets. Cat densities did not differ between squares where phone and door-to-door surveys were conducted (mean values of \log_{10} cat density $\pm 1 \text{ SE}$ are, respectively, 2.57 ± 0.07 and 2.66 ± 0.06 for door-to-door and phone surveys).

Calls and visits were made between 18 : 00 and 20 : 00 h during weekdays, and between 12 : 00 and 16 : 00 on Sundays. These times were selected as a pilot study indicated that they maximized response rates. If no answer was obtained then the respondent was re-contacted the following day. Response rates ranged from 33% to 66% (mean 47%), but there was no relationship between response rate and \log_{10} cat density ($r = -0.008$; $P = 0.97$) suggesting that non-respondents did not differ markedly from respondents in the number of cats they owned.

We calculated the number of cats per household and then scaled this up to the $1 \text{ km} \times 1 \text{ km}$ square using data on the number of households. The latter were obtained from the 2001 census (Boyle & Dorling, 2004) using the following weighted approach. For each census output area sharing at least part of its location with one of the squares, the number of households for the output area was obtained, and its value multiplied by the proportion of the output area lying within the BBS square. The values obtained by this process were summed for each grid square to obtain an estimate of the number of households in each square.

We did not distinguish between cats that were confined indoors and those that had outside access. Indoor cats are very rare in Britain. A detailed door to door survey in Sheffield, the fifth largest urban area in England, showed that 97% of domestic cats went outside (V. S., unpublished data). Equivalent high quality data are not available at a national level, but it has been suggested that 90% of British domestic cats are outside cats (Hartwell, 2006). Moreover, spatial variation in the percentage of outdoor cats will be very low as there are no British laws or voluntary guidelines promoting keeping cats indoors. In contrast, the Royal Society for the Prevention of Cruelty to Animals (the largest and most influential animal welfare organization in the UK) advises cat owners to ensure that domestic cats have outdoor access (see www.rspca.org.uk). Feral cats also comprise less than 10% of the total cat population in Britain, and are usually rapidly assimilated into the domestic cat population (UFAW, 1981; Harris *et al.*, 1995; Bradshaw *et al.*, 1999; Turner & Bateson, 2000).

Green-space data

These were obtained using Ordnance Survey MasterMap topographical data from the period summer 2004 to summer 2005 (Murray & Shiell, 2003). We defined green space as every parcel of land classified as a natural surface or garden; this included municipal parks, gardens, cemeteries, vegetated areas of school playing fields, woodland, vegetated road verges, scattered trees, and other patches of vegetation.

Analyses

We constructed multiple regression models in SAS version 8.2 using the species richness and density of each of our five species groups (all species, small-bodied species, large-bodied species, potential and non-potential prey species) as response variables. We used generalized linear models; species richness data were consistently normally distributed (Anderson–Darling test $P > 0.05$), but avian density data were \log_{10} transformed to meet statistical assumptions. We used cat density, \log_{10} transformed in order to reduce the skew in its distribution, and the area of green space (km^2) as predictors. We also used the square terms of both predictor variables in order to detect simple nonlinear relationships. Our models were thus of the form $y = \log_{10}\text{catdensity} + \log_{10}\text{catdensity}^2 + \text{green-space} + \text{green-space}^2$. Our analyses are not influenced by collinearity between log-transformed cat density and the amount of green space, as the tolerance factor for these variables was 0.73 which is much greater than the threshold value below which this becomes a concern (Quinn & Keough, 2002).

We also modelled the densities of individual species using the same predictor variables as described above. The densities of individual species were not normally distributed, and could not consistently be transformed to a normal distribution using an identical transformation. We thus modelled these data using PROC GLIMMIX with a Poisson error distribution and a log link, while taking overdispersion into account. R^2 values cannot be calculated from Poisson error models, and we thus measure the explanatory power of models of the density of individual species as the change in deviance in the fitted model relative to that in a null model that lacks predictors (D^2). It is not practical to model spatial variation in the density of a species that only occurs in a small number of squares. We thus chose to only model the densities of species that occurred in at least eight squares; the choice of threshold value is somewhat arbitrary, but means that a species was present in twice as many squares as the maximum number of predictor variables.

Birds predominantly obtain their resources from within areas of green space (albeit with some exceptions such as those that nest in buildings, such as house sparrows *Passer domesticus*). An alternative analytical approach is thus to calculate avian densities in terms of the available amount of green space, rather than the area of the square *per se*, and to regress this density against cat density. This alternative method generated qualitatively identical results to the method described above, and thus we only present results based on avian densities calculated across the entire $1 \text{ km} \times 1 \text{ km}$ square.

As is increasingly recommended, we used an information theoretic approach to model selection (Johnson & Omland, 2004; Whittingham *et al.*, 2006). All possible models, given the predictor variables, were constructed and that with the most parsimonious fit, i.e. the smallest AIC, is selected as the most parsimonious model. We calculated the Akaike weight of each model which is the probability that it provides the most parsimonious fit to the data. When inferring predicted values and the nature of modelled relationships we conducted model averaging across all models, weighting the predictions from each by its Akaike weight.

Spatially structured data such as that which we use here may be influenced by spatial autocorrelation that invalidates the assumption of independent errors and may render classical tests of association misleading (Cressie, 1991; Legendre *et al.*, 2002). Techniques are available that measure the magnitude of spatial autocorrelation and take it into account, but our sample size is at the threshold at which such techniques are considered appropriate (Littell *et al.*, 1996). However, we assessed the form and significance of spatial autocorrelation remaining in the residuals from the best fitting model for each response variable using SAM version 1 (Rangel *et al.*, 2005). In all cases there was no evidence of significant residual spatial autocorrelation, suggesting that the latter did not unduly bias the results of the independent error models. Other studies of urban avian assemblages have also

Table 1 Spatial variation in urban avian assemblages, cat populations, and the availability of green space. Means are used as a measure of central tendency, unless data are not normally distributed, in which case medians are used (indicated by *). Note that even when squares contained a large amount of green space this consisted of gardens, parks etc. located within an urban matrix.

Variable	Central measure	Min	Max
Total species richness	18.2	9	28
Small-bodied species richness	12.5	5	21
Large-bodied species richness	5.0	2	10
Potential prey species richness	13.0	6	20
Non-potential prey species richness	5.3	1	11
Total avian density (km^{-2})	1021.3*	506.0	2923.6
Density small-bodied species (km^{-2})	759.9*	271.0	2366.3
Density large-bodied species (km^{-2})	237.6*	69.1	885.0
Density potential prey species (km^{-2})	917.8*	428.2	2744.3
Density non-potential prey species (km^{-2})	146.8*	16.2	524.6
Ratio avian to cat density – all species	2.9*	0.5	8.5
Ratio avian to cat density – small-bodied species	2.1*	0.2	7.0
Ratio avian to cat density – large-bodied species	0.5*	0.1	1.8
Ratio avian to cat density – potential prey species	2.5*	0.4	7.4
Ratio avian to cat density – non-potential prey species	0.3*	0.02	1.5
Cat density (km^{-2})	417.3*	131.8	1579.2
% green space	64.4%*	37.2%	87.8%

Table 2 Multiple regression models of avian species richness and density in relation to cat density, while taking green space into account. Model selection followed an information theoretical approach. The model weight indicates the probability that the model provides the most parsimonious fit to the data out of all possible models (of those constructed). We present the 95% confidence set of models, i.e. those whose cumulative model weights are 0.95, or where this set includes more than three models we present the three best fitting models. Model averaged parameter estimates are given in the first line for each model, along with model averaged partial r^2 values. Positive and negative effects are indicated respectively by + and –.

Response	Log ₁₀ cat density	Log ₁₀ cat density ²	Green space	Green space ²	Model weight	Model r^2	Weighted partial r^2 cat density	Weighted partial r^2 green space
Total spp. Richness	+3.37	–1.61	+45.45	–36.78	0.95	21.8	15.6	2.9
Small-bodied species richness	+1.82	–1.63	+25.62	–22.66	0.93	24.6	20.0	1.5
"	–		+	–	0.05	24.4		
Large-bodied species richness	+9.00	–1.95	+17.73	–14.98	0.87	8.7	4.2	2.0
"	–		+	–	0.08	7.6		
Potential prey species richness	+7.36	–2.51	+24.46	–25.11	0.92	25.4	22.2	4.4
"	–		+	–	0.06	24.9		
Non-potential prey species richness	+1.7	–0.58	+16.72	–10.61	0.89	9.82	2.1	2.9
"		–	+	–	0.06	9.78		
Log ₁₀ total species density	+0.46	–0.06	+4.44	–3.39	0.30	21.9	4.9	15.4
"			+	–	0.30	14.1		
"	+		+	–	0.28	21.1		
Log ₁₀ small-bodied species density			+	–	0.47	33.3	1.1	31.2
"	+0.47	–0.08	+6.60	–4.81	0.27	36.1		
"	+		+	–	0.21	34.7		
Log ₁₀ large-bodied species density	+0.35	–0.007	+1.88	–2.11	0.38	28.8	9.5	7.4
"	+		–	–	0.28	28.8		
"			+	–		18.0		
Log ₁₀ potential prey species density	+0.41	–0.05	+3.74	–2.78	0.31	18.7	6.6	11.6
"	+		–	–	0.30	18.4		
"			+	–	0.22	9.4		
Log ₁₀ non-potential prey species density	+1.06	–0.22	+7.83	–6.23	0.44	15.2	0.8	12.3
"			+	–	0.29	13.5		
"	–		+	–	0.19	13.8		

found little evidence for spatial autocorrelation, and that which does occur is at lag distances that are much shorter, typically less than 2 km, than the distances between the sites that we consider here (R.A. Fuller *et al.*, unpublished data).

RESULTS

There was marked spatial variation in both cat densities and the structure of avian assemblages (Table 1). The former varied by an order of magnitude (from 132 to 1580 cats km^{–2}); avian densities varied slightly less (from 506 to 2924 birds km^{–2}), and avian species richness varied from nine to 28. The ratio of individual birds to cats varied from 0.5 to 8.5.

Avian species richness

For each species group the most parsimonious model had a high model weight and contained both log-transformed cat density, green space, and the square terms of both these variables (Table 2). Averaging parameter estimates across all models by their parameter weights indicated that the number of species in each group peaked at intermediate values of green space.

However, the explanatory power of green space was consistently low, with weighted partial r^2 values never exceeding 2%.

Model averaging across all models revealed that the number of species in each of our five groups was negatively related to log-transformed cat density (Fig. 1a–e); the explanatory power of this relationship varied markedly with a weighted partial r^2 value of 2% and 4%, respectively, for non-potential prey and large-bodied species, but 16%, 20%, and 22% for total, small-bodied, and potential prey species richness, respectively. The slopes of these relationships were also lower for large-bodied species and non-potential prey than in the other three groups (Fig. 1). Formal comparison of the slopes of these relationships is complicated by the retention of both linear and square terms in the most parsimonious models. For comparative purposes it is, however, useful to contrast the slopes of linear regressions of the predicted values obtained from model averaging against log-transformed cat density. So doing yields 95% confidence intervals for the slopes of these relationships of –1.7 and –1.2 for large-bodied species and equivalent values of –1.5 and –1.4 for non-potential prey species, –7.9 and –7.1 for total richness, –7.1 and –6.7 for small-bodied species, and –6.4 and –5.7 for potential prey species.

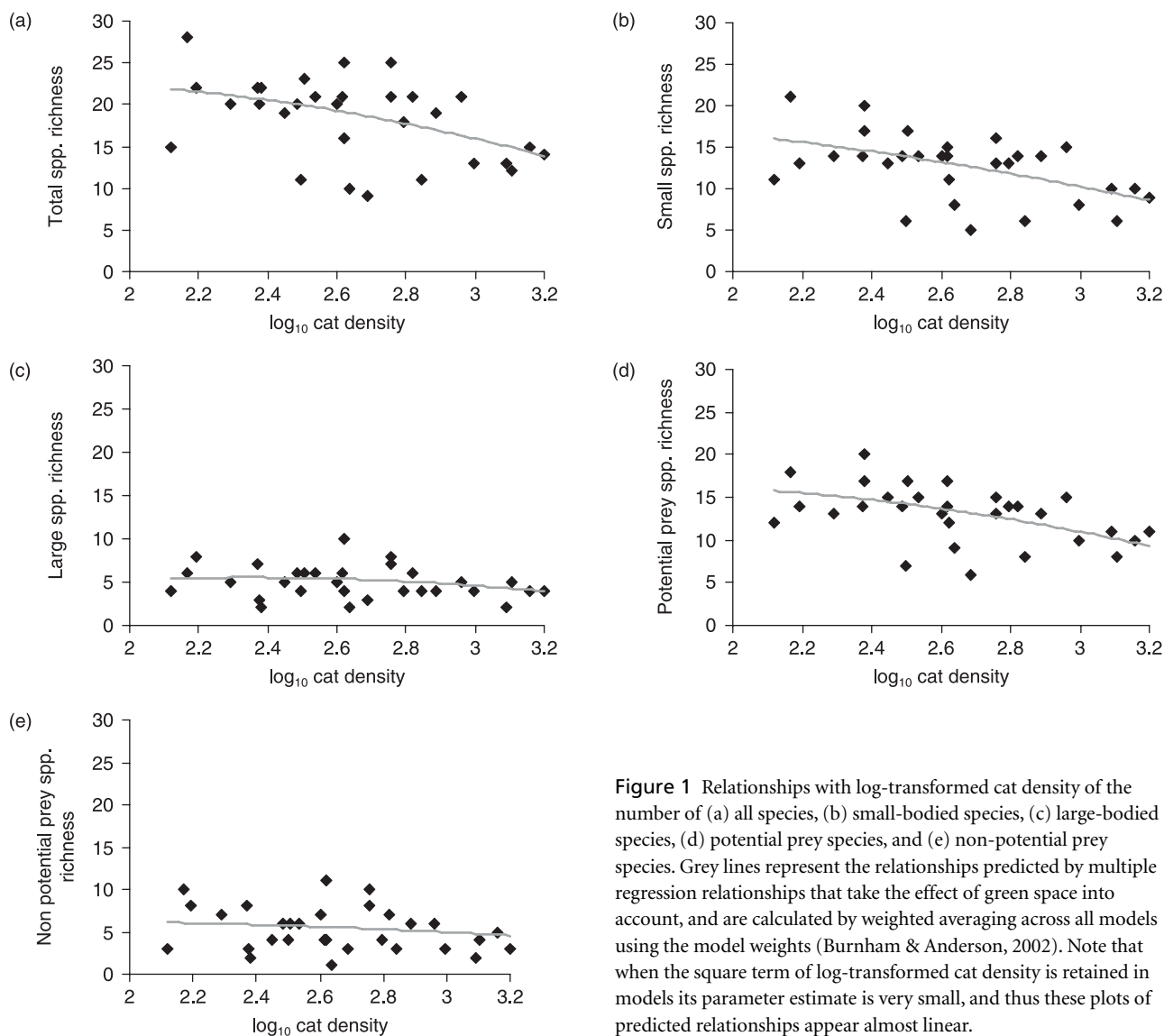


Figure 1 Relationships with log-transformed cat density of the number of (a) all species, (b) small-bodied species, (c) large-bodied species, (d) potential prey species, and (e) non-potential prey species. Grey lines represent the relationships predicted by multiple regression relationships that take the effect of green space into account, and are calculated by weighted averaging across all models using the model weights (Burnham & Anderson, 2002). Note that when the square term of log-transformed cat density is retained in models its parameter estimate is very small, and thus these plots of predicted relationships appear almost linear.

Summed avian density

For each of the species groups there were a number of competing models with similar weights (Table 2). Both green space and its square term were consistently retained in these competing models, and model averaging of parameter estimates across all models revealed that avian densities peaked at intermediate values of green space. The weighted partial r^2 values for green space were 15%, 30%, 6%, 12%, and 11% for the densities of all, small-bodied, large-bodied, potential, and non-potential prey species, respectively.

Model averaging indicated that avian densities were positively related to cat densities in all species groups except non-potential prey species (Fig. 2a–e). The slopes of the positive relationships were consistently less than one, but were steeper for large-bodied species. Regressing the predicted values obtained from model averaging against log-transformed cat density yields 95% confidence intervals for the slopes of these relationships of 0.313

and 0.314 for large-bodied species, and equivalent values for small-bodied of 0.04 and 0.06, for potential prey species of 0.01 and 0.02, and for non-potential prey species of -0.09 and -0.04 . Explanatory power also varied between groups. Weighting the partial r^2 values for the effects of cat density on avian densities by the Akaike weights gives weighted mean values of 5% for all species, 10% for large-bodied species, 1% for small-bodied species, and 5% for potential prey species. While the density of non-potential prey species was negatively correlated with cat density, both the slope of the relationship and the explanatory power ($r^2 = 0.8\%$) were very low.

Density of individual species

Twenty-one bird species occurred in a sufficient number of squares to model spatial variation in their density. For the majority of species there was not a single best fitting model, rather there was a number of competing models with similar model weights

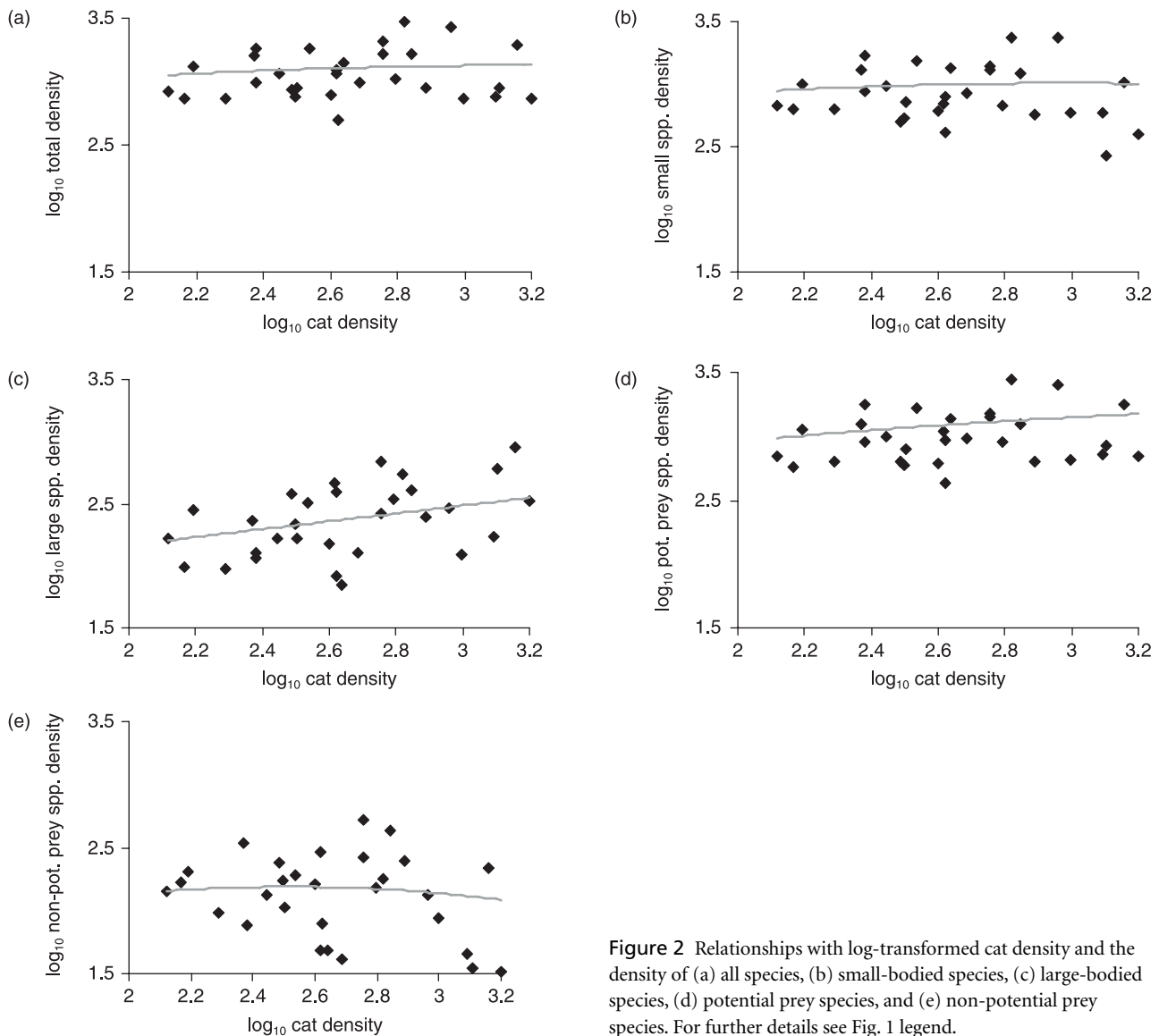


Figure 2 Relationships with log-transformed cat density and the density of (a) all species, (b) small-bodied species, (c) large-bodied species, (d) potential prey species, and (e) non-potential prey species. For further details see Fig. 1 legend.

(Table 3). The explanatory power of these models, measured by the change in deviance relative to a null model (i.e. D^2), varied markedly from 5% to 54% in the blue tit *Parus caeruleus* and starling *Sturnus vulgaris*, respectively.

Model averaging indicates that eight species had partial D^2 values, for the effects of green space, which were greater than 10%. In four of these species avian densities peaked at intermediate values of green space (carrion crow *Corvus corone*, mallard *Anas platyrhynchos*, pied wagtail *Motacilla alba*, woodpigeon *Columba palumbus*); and in four species densities increased with green space along a positive decelerating curve (collared dove *Streptopelia turtur*, house sparrow *Passer domesticus*, magpie *Pica pica*, and starling).

In nine species the weighted partial change in deviance (D^2) for the effects of cat density was greater than 10%. In four of these species avian densities were negatively related to cat densities, and in each case these species were small bodied: blackcap *Sylvia atricapilla* (17%, Fig. 2a), pied wagtail (16%, Fig. 2f), robin

Erithacus rubecula (14%, Fig. 2g), and song thrush *Turdus philomelos* (12%, Fig. 2h). The densities of five species were positively related to cat densities; three species were large bodied: carrion crow (12%, Fig. 2b), collared dove (14%, Fig. 2c), and feral pigeon *Columba livia* (20%, Fig. 2d); and two were small bodied: house sparrow (13%, Fig. 2e) and starling (16%, Fig. 2i).

DISCUSSION

There is marked spatial variation in both avian species richness and density in our focal urban areas, which highlights the fact that the latter should not be viewed as homogenous (Jokimäki & Kaisarilahti-Jokimäki, 2003). A general pattern does, however, emerge of lower avian species richness and higher population density in these urban areas compared to equivalent data from rural areas (Tratalos *et al.*, 2007), which is typical of urban avian assemblages (Blair, 1996, 2001; Clergeau *et al.*, 2001; Marzluff, 2001; Shochat, 2004). While cat densities vary by an order of

Table 3 Multiple regression models of the density of individual bird species in response to cat density, while taking green space into account. Models are constructed for all species that occurred in at least eight of the 30 1 km × 1 km squares, i.e. occupancy ≥ 8. Model selection followed an information theoretical approach; the model weight indicates the probability that the model provides the most parsimonious fit to the data. If the weight of the best fitting model is < 0.95 we present the two best fitting models. Explanatory power is indicated by the percentage of the null model deviance explained by the focal model, i.e. D^2 . We also present partial D^2 values for the effects of both cat density and green space calculated using model averaging, i.e. using the model weights to weight partial D^2 values, across all models.

Species	Occupancy	Log ₁₀ cat density	Log ₁₀ cat density ²	Green space	Green space ²	Model weight	Model D^2	Weighted partial D^2 cat density	Weighted partial D^2 green space
Blackbird	30	+6.04	-1.15	+		0.520	11.6	2.8	4.2
"	"	+5.79	-1.11	+	-	0.393	11.8		
Blackcap	10	+41.36	-8.30	+	-	0.635	18.9	16.6	2.6
"	"	+42.31	-8.45		-	0.206	17.6		
Blue tit	29	-2.18	+0.44	+	-	0.580	5.5	0.4	3.8
"	"		+0.03	+	-	0.196	5.2		
Carrion crow	23	+1.35		+	-	0.477	23.9	12.3	12.4
"	"		+0.25	+	-	0.291	23.7		
Chaffinch	22		-0.14	+	-	0.414	12.6	2.6	4.7
"	"	-0.74		+	-	0.284	12.6		
Collared dove	28	+23.45	-4.14	+	-	> 0.999	26.2	14.1	9.6
Dunnock	22	+0.65		+	-	0.435	8.1	2.3	7.0
"	"		+0.12	+	-	0.384	8.1		
Feral pigeon	19	-6.24	+1.59	+	-	> 0.999	48.7	19.6	3.8
Great tit	26	+4.25	-0.96	+	-	0.785	11.0	5.4	2.3
"	"		-0.14	+	-	0.156	10.3		
Greenfinch	20	+8.52	-1.57	+	-	> 0.999	6.9	1.0	4.0
House sparrow	30	+6.20	-0.94	+	-	> 0.999	33.7	13.4	23.4
Long-tailed tit	10	+3.49	-0.70	+	-	> 0.999	4.1	0.3	4.0
Magpie	25		+0.05	+	-	0.357	24.1	0.4	23.0
"	"	+0.27		+	-	0.323	24.1		
Mallard	8	+21.22	-4.12	+	-	> 0.999	15.3	3.9	11.8
Mistle thrush	13			+	-	0.342	11.1	0.4	9.5
"	"	-0.44		+	-	0.271	11.7		
Pied wagtail	8		-0.48	+	-	0.419	25.8	15.7	11.6
"	"	+8.43	-2.14	+	-	0.338	26.4		
Robin	29	+18.98	-3.72	+	-	0.631	15.5	13.8	1.5
"	"	+19.59	-3.83		-	0.259	15.1		
Song thrush	19	+20.11	-4.05			0.379	15.1	12.3	0.3
"	"	+19.37	-3.89		-	0.266	15.5		
Starling	28	-3.27	+0.86	+	-	> 0.999	53.4	15.9	48.9
Woodpigeon	26	+7.12	-1.26	+	-	> 0.999	15.9	2.5	12.4
Wren	26	+17.18	-3.32		-	0.351	9.3	8.8	0.3
"	"	+17.22	-3.32	-		0.278	9.2		

magnitude, the range of values lies within those previously reported for other urban areas (Liberg *et al.*, 2000; Lepczyk *et al.*, 2004; Baker *et al.*, 2005). The ratio of birds to cats also varies by an order of magnitude. We are not aware of any other studies that report comparable data, although it is notable that the values we find are much lower than reported ratios of prey abundance relative to their wild felid predators (Schaller, 1972; Sunquist & Sunquist, 1989; Viljoen, 1993; Tambling & duToit, 2005).

The aim of this analysis was not to conduct a detailed investigation of how urban avian assemblages responded to green space; however, two points regarding the latter are worth noting. First, in our study the availability of green space has a much stronger effect on avian densities than on species richness. This

pattern probably arises because species richness exhibits greater sensitivity to additional factors, such as habitat type, diversity, and modification, than does avian density (Clergeau *et al.*, 2001; Chace & Walsh, 2006; but see Jokimäki, 1999). Second, the densities of each of our four species groups peaked at intermediate values of green space. The decline in avian densities at higher values of green space may arise because the latter areas are dominated by large open expanses of green space, such as sports fields, which have a simple habitat structure that supports relatively few individuals. The densities of four species responded to green space along a positive decelerating curve (collared dove, house sparrow, magpie, and starling), and these species are arguably more generalist than the equal number of species whose

densities exhibit a unimodal response to green space (carrion crow, mallard, pied wagtail, woodpigeon). Such generalist species are perhaps more likely to have their habitat requirements met in relatively simple landscapes, and the degree of specialization may explain the nature of species response to the availability of green space.

Confounding factors, such as housing density, may influence the nature of relationships between cat density and the structure of urban avian assemblages. There was no marked correlation between the proportion of households that owned cats and housing density ($r = 0.18$; $P = 0.34$), and thus housing density is very strongly correlated with cat densities ($r = 0.83$; $P < 0.0001$). Moreover, across the range of housing densities included in this study, housing density correlates negatively with avian species richness, and positively with avian density (Tratalos *et al.*, 2007). Therefore, even though we take the availability of green space into account spatial variation in housing density may contribute to the patterns we observe. Thus, while we found negative relationships between domestic cat densities and avian species richness we cannot conclude that these relationships are causal. It is interesting, however, that these relationships were stronger in species that are particularly vulnerable to cat predation, i.e. small-bodied species and those identified as potential prey species. Our results are compatible with the only other previously published study on this issue which found that domestic cat densities were negatively correlated with the number of specialist scrub breeding bird species in habitat fragments surrounded by suburban development (Crooks & Soulé, 1999).

Avian and cat densities were positively correlated in all species groups, except non-potential prey species in which there was a very marginally negative relationship. For small-bodied and potential prey species the slopes and explanatory power of these relationships were almost negligible and contrasted with the more marked positive relationship exhibited by large-bodied species. Consideration of the relationships between the densities of individual species and cats generated equivocal results. Cat density explained less than 10% of the deviance in avian density in approximately half of the species we considered. The remainder were almost equally split into those that exhibited broadly positive and negative relationships, with the former group being dominated by large-bodied species and the latter by small-bodied species. These results suggest that large-bodied species have a tendency to exhibit positive relationships between avian and cat densities, but provide little evidence for a correlation between cat densities and those of birds that are vulnerable to cat predation. It is perhaps particularly noteworthy that cat densities correlate positively with those of the house sparrow, as this is typically the avian species found to be most commonly taken by cats in Britain and has previously been identified as potentially vulnerable to the impact of cat predation (Churcher & Lawton, 1987; Howes, 2002; Woods *et al.*, 2003; Baker *et al.*, 2005; but see Mead, 1982).

Positive correlations between avian and cat densities may arise if areas of high cat density are those where humans provide more supplementary food for birds, and if doing so increases avian populations.

Table 4 Results of bivariate relationships between the density of nest predating corvids (Carrion crow, magpie, and jay) and the structure of urban avian assemblages. When modelling species richness and summed densities, we used general linear models and measure explanatory power using r^2 values. When modelling the densities of individual species we used Poisson models and the percentage of the null model deviance explained by the fitted model (D^2) to measure explanatory power.

Response	Slope \pm 1 SE	P value	Model r^2 / D^2
Total species richness	1.18 \pm 1.91	0.54	1.3%
Small-bodied species richness	-0.75 \pm 1.56	0.63	0.8%
Large-bodied species richness	1.46 \pm 0.67	0.04	14.4%
Potential prey species richness	-0.97 \pm 1.29	0.46	2.0%
Non-potential prey species richness	2.15 \pm 0.92	0.03	16.3%
Log ₁₀ total avian density (km ⁻²)	0.12 \pm 0.07	0.08	10.4%
Log ₁₀ density small-bodied species (km ⁻²)	0.12 \pm 0.08	0.16	6.9%
Log ₁₀ density large-bodied species (km ⁻²)	0.16 \pm 0.11	0.15	7.3%
Log ₁₀ density potential prey species (km ⁻²)	0.10 \pm 0.08	0.20	5.6%
Log ₁₀ density non-potential prey species (km ⁻²)	0.41 \pm 0.12	0.002	29.3%
Blackbird density	-0.30 \pm 0.20	0.14	6.7%
Blackcap density	-0.23 \pm 0.62	0.71	0.6%
Blue tit density	0.11 \pm 0.31	0.71	0.5%
Chaffinch density	-0.29 \pm 0.45	0.51	1.6%
Collared dove density	0.19 \pm 0.54	0.72	0.6%
Dunnock density	0.32 \pm 0.52	0.53	1.7%
Feral pigeon density	0.33 \pm 0.69	0.63	1.1%
Great tit density	0.54 \pm 0.37	0.15	7.0%
Greenfinch density	-0.40 \pm 0.59	0.50	2.1%
House sparrow density	0.61 \pm 0.38	0.11	9.7%
Long-tailed tit density	-0.14 \pm 0.62	0.82	0.2%
Mallard density	0.55 \pm 0.87	0.52	1.9%
Mistle thrush density	0.33 \pm 0.63	0.59	1.1%
Pied wagtail density	-0.86 \pm 0.59	0.14	7.8%
Robin density	0.53 \pm 0.40	0.18	7.0%
Song thrush density	-0.43 \pm 0.36	0.24	3.9%
Starling density	0.59 \pm 0.37	0.11	9.4%
Woodpigeon density	1.37 \pm 0.42	0.001	29.6%
Wren density	0.01 \pm 0.37	0.98	< 0.1%

Households included in this survey were also asked if they fed birds, but there was no significant correlation between feeding birds and cat ownership (Spearman rank correlation: $r_s = -0.023$, $P = 0.372$, $n = 150$); concurring with a similar investigation in North America (Lepczyk *et al.*, 2004a). Provision of supplementary food may, however, still be higher in areas of high cat density due to a greater number of households in such areas. It remains an open question whether supplementary feeding increases avian species richness and abundance at spatial scales larger than an individual garden, and empirical investigations are rare (Beebee, 2001; Cannon *et al.*, 2005). In Sheffield, the fifth largest urban area in England, bird feeder density is positively correlated with the breeding density of some species that take supplementary

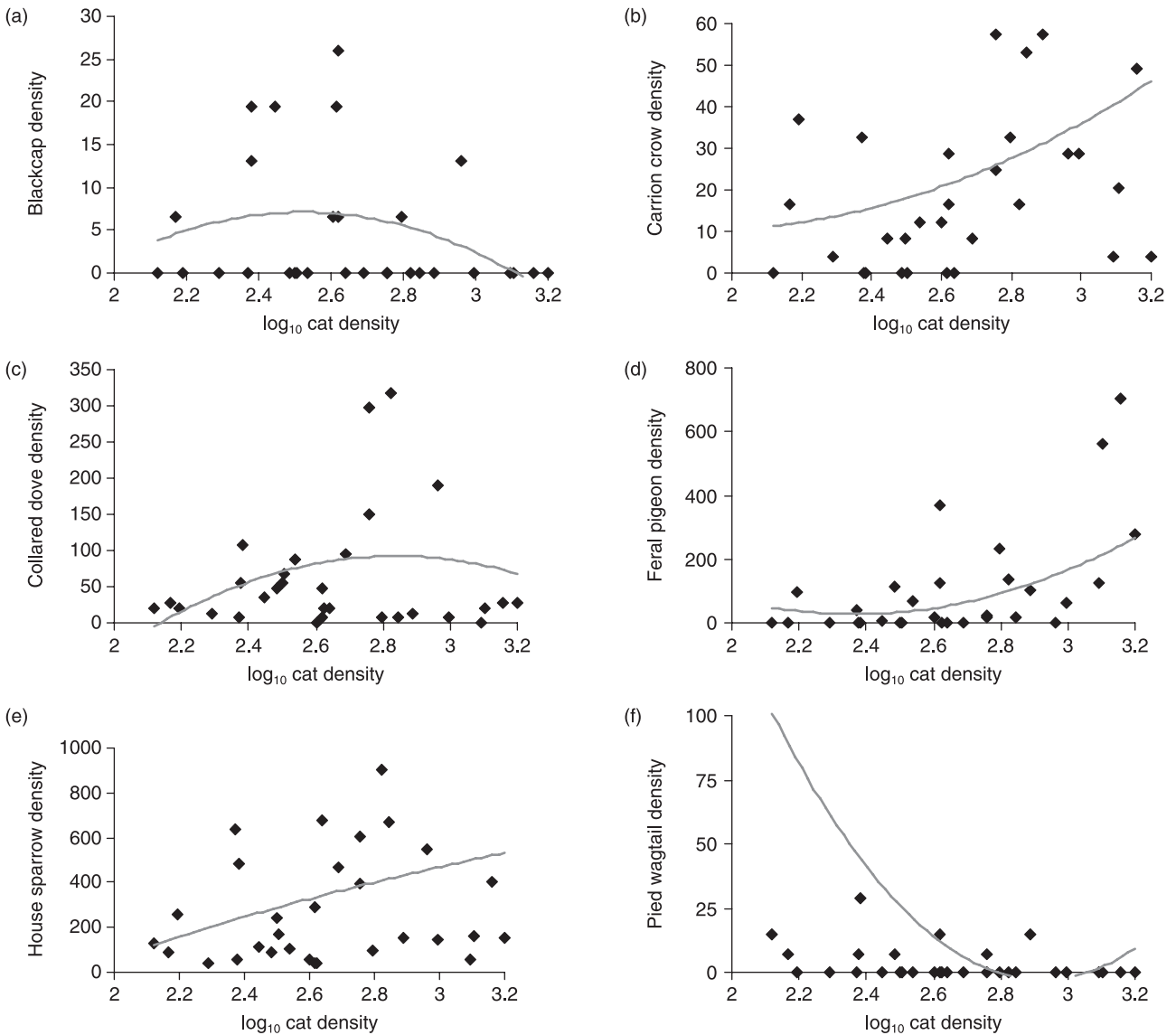


Figure 3 Relationships with log-transformed cat density and the densities of (a) blackcap, (b) carrion crow, (c) collared dove, (d) feral pigeon, (e) house sparrow, (f) pied wagtail, (g) robin, (h) song thrush, and (i) starling. Data are presented for all species that occurred in eight or more squares, and in which cat density explained 10% or more of the deviance in a null model, i.e. one that lacks predictors. Black diamonds represent the raw data and grey lines indicate the predicted relationship from multiple regression relationships that take the effect of green space into account, and are calculated by weighted averaging across all models using the model weights (Burnham & Anderson, 2002).

food (blackbird *Turdus merula*, house sparrow, and starling) but not others (blue tit, great tit *Parus major*, and woodpigeon; Fuller *et al.*, in press). Similar interspecific variation in the form of the correlation between the number of feeding stations and avian density has been described for winter assemblages (Jokimäki & Kaisarilahti-Jokimäki, 2003). It thus seems unlikely that covariation between cat density and the provision of supplementary food for birds is likely to drive generally the positive correlations between cat and avian densities, although it may do so for some particular species.

The lack of negative relationships between avian and cat densities may arise if the structure of urban avian assemblages were negatively influenced by other predators. Carrion crows,

magpies, and jays all frequently predate nests, and rates of nest predation have been found to correlate positively with corvid abundance in some areas, albeit inconsistently (Jokimäki *et al.*, 2005). Moreover, the densities of carrion crows and magpies are typically highest in urban areas (Antonov & Atanasova, 2003; Tratalos *et al.*, 2007). The summed estimated densities of nest-predating corvids in our focal squares, carrion crow, magpie, and jay, ranged from 0 to 150, mean 48.1, but corvid density was not strongly negatively correlated with avian species richness or density in any of our focal groups or individual species (Table 4). Indeed, other studies have found no evidence that corvids reduce the size of avian populations in Britain (Gooch *et al.*, 1991; Thomson *et al.*, 1998; Siriwardena, 2006).

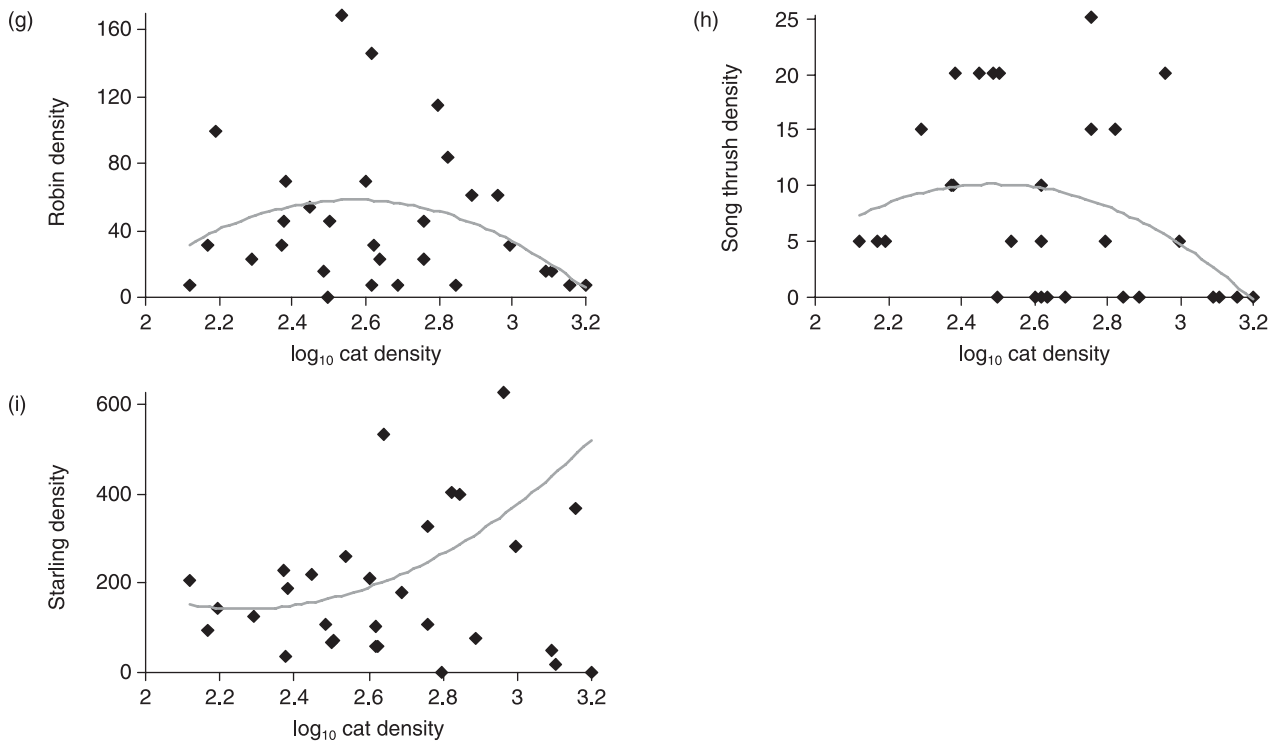


Figure 3 Continued

If domestic cat populations adversely impacted their prey populations then, as in some wild felid populations, one may expect negative correlations to arise between domestic cat densities and avian densities. Other patterns are, however, possible. Cat densities may be sufficiently large across our study area that their impact on avian population densities is uniformly large, thus generating no marked negative correlation between cat and avian densities (Fig. 3). Indeed, while domestic cat densities vary by an order of magnitude across our study sites they are consistently high, with the lowest value being 132 cats km⁻². Moreover, at most there were nine adult birds per cat, while in one plot there were two cats for every adult bird. These ratios are sufficiently low that even if individual cats only rarely preyed on birds, the total predation rate in a region may be sufficiently high to adversely impact bird populations. Moreover, the uniformly high cat densities may result in consistently high predation rates and insufficient spatial variation in predation to generate a pattern in the relationship between domestic cat and avian densities. This is supported by the observation that across a rural to urban gradient there was little variation in cat predation rates on birds despite a threefold variation in cat density (Lepczyk *et al.*, 2004b). Therefore, domestic cat impacts on bird populations may be uniformly high in urban areas, and a negative relationship between avian and cat densities may only arise when assessed over both high and low values of the latter. More is likely to be gained from further study if an experimental design could be adopted that compared urban biotas in areas with and without cats, but creating and maintaining such experimental areas would be very difficult to achieve.

ACKNOWLEDGEMENTS

We thank the numerous volunteer ornithologists for collecting the avian data, and the British Trust for Ornithology for making them available. MasterMap topographical data were kindly supplied by Ordnance Survey, by licence through the CityForm Consortium. R.A. Fuller, J.J.D. Greenwood, J. Jokimäki, O. Petchey, B. Sims, J. Thwaites and an anonymous referee provided discussion and assistance. K.J.G. holds a Royal Society-Wolfson Research Merit Award. This work was funded by the Natural Environment Research Council.

REFERENCES

- Antonov, A. & Atanasova, D. (2003) Small-scale differences in the breeding ecology of urban and rural magpies *Pica pica*. *Ornis Fennica*, **80**, 21–30.
- Baillie, S.R., Marchant, J.H., Crick, H.Q.P., Noble, D.G., Balmer, D.E., Coombes, R.H., Downie, I.S., Freeman, S.N., Joys, A.C., Leech, D.I., Raven, M.J., Robinson, R.A. & Thewlis, R.M. (2006) *Breeding birds in the wider countryside: their conservation status 2005*. British Trust for Ornithology (BTO) Research Report No. 435. BTO, Thetford, UK. (Available at <http://www.bto.org/birdtrends>).
- Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, **35**, 302–312.
- Barker, K. (2004) *Barker review of housing supply. Delivering stability: securing our future housing needs*. (Available at www.barkerreview.org.uk).

- Barratt, D.G. (1997) Predation by house cats, *Felis catus*, in Canberra, Australia. I. Prey composition and preference. *Wildlife Research*, **24**, 263–277.
- Barratt, D.G. (1998) Predation by house cats in Canberra, Australia. II. Factors affecting the amount of prey caught and estimates on the impact on wildlife. *Wildlife Research*, **25**, 475–487.
- Beebee, T.J. (2001) British wildlife and human numbers: the ultimate conservation issue? *British Wildlife*, **13**, 1–8.
- Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506–519.
- Blair, R.B. (2001) Creating a homogeneous avifauna. *Avian ecology and conservation in an urbanising world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 459–486. Kluwer Academic Publishers, London.
- Boyle, P. & Dorling, D. (2004) Guest editorial: the 2001 UK census: remarkable resource or bygone legacy of the ‘pencil and paper era’? *Area*, **36**, 101–110.
- Bradshaw, J.W.S., Horsfield, G.F., Allen, J.A. & Robinson, I.H. (1999) Feral cats: their role in the population dynamics of *Felis catus*. *Applied Animal Behaviour Science*, **65**, 273–283.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Cannon, A.R., Chamberlain, D.E., Toms, M.P., Hatchwell, B.J. & Gaston, K.J. (2005) Trends in the use of private gardens by wild birds in Great Britain 1995–2002. *Journal of Applied Ecology*, **42**, 659–671.
- Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46–49.
- Churcher, P.B. & Lawton, J.H. (1987) Predation by domestic cats in an English village. *Journal of Zoology*, **212**, 439–455.
- Clergeau, P., Jokimäki, J. & Savard, J.P. (2001) Are urban bird communities influenced by the bird density of adjacent landscapes? *Journal of Applied Ecology*, **38**, 1122–1134.
- Cressie, N. (1991) *Statistics for spatial data*. John Wiley & Sons, New York.
- Crick, H.Q.P. (1992) A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land management and human activity. *Bird Study*, **39**, 1–12.
- Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.
- Evans, K.L., Newson, S.E., Storch, D., Greenwood, J.J.D. & Gaston, K.J. (in press) Spatial scale, abundance and the species–energy relationship in British birds. *Journal of Animal Ecology*.
- Fitzgerald, B.M. (1988) Diet of domestic cats and their impact on prey populations. *The domestic cat: the biology of its behaviour* (ed. by D.C. Turner and P. Bateson), pp. 151–176. Cambridge University Press, Cambridge, UK.
- Fitzgerald, B.M. (1990) Is cat control needed to protect urban wildlife? *Environmental Conservation*, **17**, 168–169.
- Fitzgerald, B.M. & Turner, D.C. (1988) Hunting behaviour of domestic cats and their impact on prey populations. *The domestic cat: the biology of its behaviour* (ed. by D.C. Turner and P. Bateson), pp. 151–176. Cambridge University Press, Cambridge, UK.
- Fuller, R.A., Irvine, K.A., Davies, Z.G., Armsworth, P.R. & Gaston, K.J. (in press) Interactions between people and birds in urban landscapes. *Studies in Avian Biology*.
- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and process in macroecology*. Blackwell Science, Oxford, UK.
- Gooch, S., Baillie, S.R. & Birkhead, T.R. (1991) Magpie *Pica pica* and songbird populations – retrospective investigation of trends in population-density and breeding success. *Journal of Applied Ecology*, **28**, 1068–1086.
- Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Joint Nature Conservation Committee, Peterborough, UK.
- Hartwell, S. (2006) *Cat keeping in Britain and America*. Available at <http://www.messybeast.com/catsusuk.htm>.
- Howes, C.A. (2002) Red in tooth and claw: 2. Studies on the natural history of the domestic cat *Felis catus* in Yorkshire. *Naturalist*, **127**, 101–130.
- Jarvis, P. (1990) Urban cats as pests and pets. *Environmental Conservation*, **17**, 169–171.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **201**, 1–8.
- Jokimäki, J. (1999) Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. *Urban Ecosystem*, **3**, 21–34.
- Jokimäki, J., Kaisanlahti-Jokimäki, M.L., Sorace, A., Fernandez-Juricic, E., Rodriguez-Prieto, I. & Jimenez, M.D. (2005) Evaluation of the ‘safe nesting zone’ hypothesis across an urban gradient: a multi-scale study. *Ecography*, **28**, 59–70.
- Jokimäki, J. & Kaisanlahti-Jokimäki, M.L. (2003) Spatial similarity of urban bird communities: a multiscale approach. *Journal of Biogeography*, **30**, 1183–1193.
- Kauhala, K. & Helle, P. (2000) The interactions of predator and hare populations in Finland – a study based on wildlife monitoring counts. *Annales Zoologici Fennici*, **37**, 151–160.
- Kawakami, K. & Higuchi, H. (2002) Bird predation by domestic cats on Hahajima Island, Bonin Islands, Japan. *Ornithological Science*, **1**, 143–144.
- Legendre, P., Dale, M.T., Fortin, M., Gurevitch, J., Hohn, M. & Myers, D. (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, **25**, 601–615.
- Lepczyk, C.A., Mertig, A.G. & Liu, J.G. (2004a) Assessing landowner activities related to birds across rural-to-urban landscapes. *Environmental Management*, **33**, 110–125.
- Lepczyk, C.A., Mertig, A.G. & Liu, J.G. (2004b) Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation*, **115**, 191–201.
- Liberg, O. (1984) Food habits and prey impact by feral and house-based domestic cats in a rural area in southern Sweden. *Journal of Mammalogy*, **65**, 424–432.
- Liberg, O., Sandell, M., Pontier, D. & Natoli, E. (2000) Density,

- spatial organisation and reproductive tactics in the domestic cat and other felids. *The domestic cat: the biology of its behaviour* (ed. by D.C. Turner and P. Bateson), pp. 120–145. Cambridge University Press, Cambridge, UK.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS system for mixed models*. SAS Institute, Cary, North Carolina.
- Lowe, S., Browne, M., Boudjelas, S. & de Poorter, M. (2000) *100 of the world's worst invasive alien species: a selection from the global invasive species database*. Invasive Species Specialist Group, IUCN. Available at: www.issg.org/booklet.pdf.
- Marzluff, J.M. (2001) Worldwide urbanization and its effects on birds. *Avian ecology and conservation in an urbanising world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 19–47. Kluwer Academic Publishers, London.
- Mead, C.J. (1982) Ringed birds killed by cats. *Mammal Review*, **12**, 183–186.
- Murray, K.J. & Shiell, D. (2003) A new geographic information framework for Great Britain. *Photogrammetric Engineering and Remote Sensing*, **69**, 1175–1182.
- Newton, I. (1998) *Population limitation in birds*. Academic Press, London.
- Nogales, M., Martin, A., Tershy, B.R., Donlan, J., Veitch, D., Puerta, N., Wood, B. & Alonso, J. (2004) A review of feral cat eradication on islands. *Conservation Biology*, **18**, 310–319.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.
- Pearre, S. & Maass, R. (1998) Trends in the prey size-based trophic niches of feral and house cats (*Felis catus*). *Mammal Review*, **28**, 125–139.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2005) SAM v. 1.0 Spatial analysis in macroecology (software and user's guide) – <http://www.ecoevol.ufg.br/sam>.
- Raven, M.J., Noble, D.G. & Baillie, S.R. (2005) *The breeding bird survey 2004. BTO research report 403*. British Trust for Ornithology, Thetford, UK.
- Schaller, G.B. (1972) *The Serengeti lion: a study of predator–prey relations*. Wildlife Behaviour and Ecology Series. University of Chicago Press, Chicago, Illinois.
- Seidensticker, J. & McDougal, C. (1993) Tiger predatory behaviour, ecology and conservation. *Mammals as predators: the proceedings of a Zoological Society of London and the Mammal Society symposium, London, 22–23 November 1991* (ed. by N. Dunstone and M.L. Gorman), pp. 105–125. Clarendon Press, Oxford.
- Shochat, E. (2004) Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos*, **106**, 622–626.
- Siriwardena, G.M. (2006) Avian nest predation, competition and the decline of British marsh tits *Parus palustris*. *Ibis*, **148**, 255–265.
- Sunquist, M.E. & Sunquist, F.C. (1989) Ecological constraints on predation by large felids. *Carnivore behaviour, ecology and evolution* (ed. by J.L. Gittleman), pp. 283–302. Cornell University Press, Ithaca, New York.
- Tambling, C.J. & duToit, J.T. (2005) Modelling wildebeest population dynamics: implications of a predation and harvesting in a closed system. *Journal of Applied Ecology*, **42**, 431–441.
- Thomas, L., Laake, J.L., Derry, J.F., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Strindberg, S., Hedley, S.L., Burt, M.L., Marques, F., Pollard, J.H. & Fewster, R.M. (2004) *Distance 4. 1*. Research Unit for Wildlife Population Assessment, University of St. Andrews, Fife, Scotland.
- Thomson, D.L., Green, R.E., Gregory, R.D. & Baillie, S.R. (1998) The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **265**, 2057–2062.
- Tratalos, J., Fuller, R.A., Evans, K.L., Davies, R.G., Newson, S.E., Greenwood, J.J.D. & Gaston, K.J. (2007) Bird densities are associated with household densities. *Global Change Biology*, **13**, 1685–1695.
- Turner, D.C. & Bateson, P. (2000) *The domestic cat: the biology of its behaviour*, 2nd edn. Cambridge University Press, Cambridge, UK.
- Universities Fund for Animal Welfare (UFAW) (1981) *The ecology and control of feral cats*. UFAW, Potters Bar, Herts, UK.
- Viljoen, P.C. (1993) The effects of changes in prey availability on lion predation in a large natural ecosystem in northern Botswana. *Mammals as predators: symposium of the Zoological Society of London*, No. 65 (ed. by N. Dunstone and M.L. Gorman), pp. 193–213. Zoological Society of London, London, UK.
- White, P.C.L., Jennings, N.V., Renwick, A.R. & Barker, N.H.L. (2005) Questionnaires in ecology: a review of past use and recommendations for best practice. *Journal of Applied Ecology*, **42**, 421–430.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75**, 1182–1189.
- Woods, M., McDonald, R.A. & Harris, S. (2003) Predation of wildlife by domestic cats (*Felis catus*) in Great Britain. *Mammal Review*, **33**, 174–188.

Editor: David Richardson

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 List of the thirty 1 km × 1 km squares used in this study, their location, and the survey method used to conduct questionnaires.

Table S2 Species lists for each of the three species groups used in analyses.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00444.x>
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.