# Ecological traps and behavioural adjustments of urban songbirds to fine-scale spatial variation in predator activity

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## Abstract

The influence of predators on bird populations is controversial and poorly understood, especially in urban areas where predator densities can be particularly high. We assessed if fine-scale spatial variation in predator activity and proximity have direct and indirect effects on urban songbird distributions and breeding success, by testing the hypotheses that (1) songbirds that are sensitive to nest predation select territories with reduced activity of nest predators; (2) blackbird *Turdus merula*, a species that experiences high nest predation rates, lays smaller clutches in territories located in areas with higher numbers of nest predators as predicted by Skutch's hypothesis; (3) songbirds that are sensitive to nest predation have higher nest predation rates in areas with greater predator activity. We tested these hypotheses using two sites in urban Sheffield, UK, and focus on nest predatory corvids and grey squirrels *Sciurus carolinensis*. We found no evidence that songbirds that are most sensitive to nest predation adjust their territory location in response to fine-scale spatial variation in predator distributions. It thus seems unlikely that urban predators are indirectly regulating urban bird population size by restricting habitat availability. Blackbirds did not vary their clutch size in response to predator distributions. These findings generate the potential for an ecological trap in which prey species fail to avoid areas with the highest concentrations of nest predators, or to exhibit behavioural adjustments to reduce the risk of nest predation at such sites. We find some evidence for such ecological traps as, while fine-scale variation in grey squirrel occurrence and activity were not associated with nest predation rates, nests located in closer proximity to corvids and in areas with higher indices of corvid activity experienced slightly higher nest predation rates.

## Introduction

Urban bird populations are exposed to high densities of nest predators including corvids (Sims *et al.*, 2008), the influence of which is controversial and poorly understood. In rural environments indices of corvid activity and abundance have typically been associated with higher avian nest failure rates (Angelstam, 1986; Andrén, 1992; Huhta, Mappes & Jokimaki, 1996; Sieving & Willson, 1998, 1999; Paradis *et al.*, 2000; Luginbuhl *et al.*, 2001; Baláž *et al.*, 2007). Fewer studies have assessed such associations in urban environments (but see Groom, 1993; Marzluff *et al.*, 2007). Moreover, a positive association between predator abundance and nest failure rates is not, by itself, sufficient evidence that predators influence prey population densities as many species have the capacity to initiate additional nesting attempts following predation (Newton, 1998). Evidence that corvids influence the annual productivity of avian prey

species or their population densities is much more limited (Gooch, Baillie & Birkhead, 1991; Thomson *et al.*, 1998; but see Tomiałojć, 2011). Indeed, an experimental removal study found no evidence that magpies limited the breeding success of urban songbirds (Chiron & Julliard, 2007). This limited impact could arise because of redundancy in the suite of predator species, with any reduction in corvid nest predation being counterbalanced by increased predation from other species. Indeed, a number of mammal species frequently predate birds' nests (Schaefer, 2004; Weidinger, 2009; Weidinger & Kočvara, 2010). The grey squirrel *Sciurus carolinensis*, a non-native species in the UK, is one such nest predator (Møller, 1983) and is widespread in urban areas (Bonnington, Gaston & Evans, 2014a). There is much concern about its potential impact on avian assemblages (Hewson *et al.*, 2004; Bonnington, Gaston & Evans, 2014b). A study, conducted at a large spatial scale across rural areas in the UK, found that nest failure rates of a small

number of songbirds are greater in areas with larger grey squirrel populations (Newson *et al.*, 2010*a*), and that the population size of these species is probably reduced, albeit slightly, by grey squirrels (Newson *et al.*, 2010*b*).

Some of the impact that predators can have on the size of their prey populations may arise through indirect effects that alter prey behaviour; these effects may even be greater than those arising from direct mortality (Cresswell, 2008, 2011). Birds frequently reduce the rate at which they feed offspring to minimize the likelihood of visually orientated predators' detecting nests, leading to reductions in clutch size or offspring quality (Skutch, 1949; Ghalambor & Martin, 2000; Bonnington, Gaston & Evans, 2013). Predation risk may also influence the fine-scale distributions of prey, which may avoid areas in which there is a high risk of predation, even if these sites meet all other requirements, leading to a reduction in carrying capacity and population size (Pulliam & Danielson, 1991). Some observational studies and experimental manipulations of perceived predator density within non-urban environments demonstrate that birds tend to avoid potential territories occupied by avian predators (including corvids; Roos & Pärt, 2004; Morosinotto, Thomson & Korpimäki, 2010; Trnka, Peterková & Grujbárová, 2011), and mammalian predators (including members of the squirrel family; Morton, 2005; Emmering & Schmidt, 2011; Eichholz *et al.*, 2012). However, this effect of predators on territory selection by prey species is not universal with the magnitude of association varying between species and sites (Marzluff *et al.*, 2007; Morosinotto *et al.*, 2010). Furthermore, at fine spatial scales, habitat characteristics can explain much more of the variation in songbird distributions than predator distributions (Møller, 1988; Chiron & Julliard, 2007).

We are not aware of any studies, in urban areas, assessing associations between songbird territory locations and fine-scale predator distributions and their consequences for avian demographic traits. Our overall objective here is to assess the impacts of nest predators on urban bird assemblages, by testing the hypotheses that (1) songbirds select territories with reduced predator activity in order to reduce nest predation rates; (2) nest predation rates are positively associated with increased use of a locality by nest predators; (3) blackbirds *Turdus merula* (a common urban species with high rates of nest predation) lay smaller clutches in territories with higher numbers of nest predators.

## Materials and methods

During the 2011 bird breeding season (March to August), fieldwork was conducted in Beauchief estate (53°19′43.N, 1°30′06.W) and Loxley and Wadsley Common Local Nature Reserve (LNR) (53°24′43.N, 1°31′51.W), within the urban area of Sheffield, UK. The two sites consist of a mosaic of habitats, including grassland, woodland and scrub. To ensure consistency in results, the same single observer conducted all surveys reported in this study (C. Bonnington).

## Territory mapping

Each site was surveyed nine times during the bird nesting season to establish territory locations following the Common Birds Census (CBC) methodology (Marchant, 1983). Surveys were conducted during periods of high bird activity, but avoiding the dawn chorus peak in activity, that is, before 09:00 h ($n = 7$ at each site) or in the late afternoon/evening, that is, starting after 15:30 h ($n = 2$ at each site). Survey duration was consistent at each site, with surveys taking 3–3.5 h at Beauchief estate (*c.* 150 ha), and 2–2.5 h at Loxley and Wadsley Common LNR (*c.* 50 ha). All surveys were conducted during dry and calm conditions (wind speeds of 3 or less on the Beaufort scale). All birds detected and their activity (nest building, territorial activity, etc.) were recorded onto base maps from which territory maps were compiled for each species.

## Predator distributions

Each site contained three species of nest-predating corvids: magpie, carrion crow and jay *Garrulus glandarius*. Jackdaws *Corvus monedula* occurred at the sites in small numbers, but this corvid feeds predominantly on invertebrates, fruit, seeds and carrion and only occasionally eats small vertebrates and eggs (Lockie, 1955; Robinson, 2005). Furthermore, indices of corvid abundance (see below) that were constructed with and without including jackdaws were strongly correlated (Pearson's correlation: $R = 0.87$, d.f. = 221, $P < 0.0001$), and we thus only used those that excluded jackdaws. The distributions of the three nest predatory corvids were determined from the CBC territory mapping with the magpie being the most abundant species (9 and 7 territories, respectively, in Beauchief estate and Loxley and Wadsley Common LNR), followed by carrion crow (6 and 4 territories) and jay (6 and 4 territories). Grey squirrels were frequently detected during the CBC territory mapping (mean of $17.4 \pm 1.56$ SE sightings per visit at Beauchief estate, and $4.2 \pm 0.62$ at Loxley and Wadsley Common LNR). Mustelids were observed on just two occasions. Domestic and feral cats *Felis catus* were never observed at the study sites. These data were used to construct indices of avian and mammalian predator activity across the study sites at two spatial scales, $50 \times 50$ m and $100 \times 100$ m grid cells. There were 156 and 67 $100 \times 100$ m grid cells respectively in Beauchief estate and Loxley and Wadsley Common LNR (624 and 268 $50 \times 50$ m grid cells). Cells that contained the site boundary were included only if the entire area of the cell could be observed. Cells were then added as an overlay to maps of the study site using Hawth's Tools v. 3.27 (Beyer, 2004), in ArcMap 9.3 (ESRI Corporation, Redlands, CA, USA). For each cell, we constructed the following two indices of predator activity: (1) the total number of grey squirrels observed pooled across the site visits; (2) the total number of nest-predating corvids observed pooled across the site visits. Direct counts of corvids provide a good indication of corvid foraging locations and hence an appropriate estimate of the relative prob-

ability of corvid nest predation, and we thus use these rather than alternative measures, such as corvid nest counts, which are likely to be less informative as corvids frequently forage considerable distances from the nest (Charles, 1972). There was considerable spatial variation, within both survey sites, in our indices of predator activity (Supporting Information Fig. S1). At both spatial scales, corvids and grey squirrels were not observed in some grid cells, but there was less variation in the relative abundance in the number of predators at the $50 \times 50$ m spatial grain across both survey sites (Supporting Information Table S1), and preliminary analyses indicated that conclusions were consistent regardless of the choice of spatial grain. We thus only report analyses conducted at the $100 \times 100$ m spatial grain. We also calculated additional indices based on proximity to predators calculated as the distance from the cell boundary to the nearest corvid and squirrel observation (the distance to the nearest corvid and squirrel observation was scored as zero in cells in which the focal predator was observed). We also calculated the distance from the active nest to the nearest corvid and squirrel record.

## Canopy cover

To take the effects of habitat type into account when assessing how predator distributions influenced the location of prey species' territories the percentage canopy cover within each cell was recorded using aerial photographs of the study sites obtained via Google Earth. Cover was recorded to the nearest 5%, except in cells with less than 5% cover where it was recorded to the nearest 2%. These images were taken during the summer of 2008, and were checked against the onsite habitats during the CBC surveys, to validate the measure of canopy cover.

## Nest predation survey

Nest searching was conducted at each site, from March to August 2011, using a combination of cold searching and parental behavioural cues. Search effort was constant across the sites and season, and was not biased towards particular species [166 nests were found for 17 species, of which 64 (39%) were predated; Supporting Information Table S2]. Nest contents and nest height (m) were recorded, and nests were checked every three days to determine changes in their contents and fate (predated, fledged or abandoned). Offspring were considered to have fledged if they were old enough to do so and the nest was empty with no signs of damage, or if newly fledged young were seen in close proximity. Nests were recorded as predated if contents were missing and offspring were too young to fledge, or egg shell fragments or chick remains were present in or close to the nest, or the nest was damaged.

## Statistical analyses

Analyses were conducted in R i386 2.15.1 (R Development Core Team, 2012) unless stated otherwise. Nest predation is typically the main cause of nest failure in songbirds (Thompson, 2007). Species were classified as most sensitive to nest predation (24 species, typically open or dome nesting ones; Supporting Information Table S2) if their daily failure rates were greater than 1% nest/day as calculated from the British Trust for Ornithology's nest record card scheme (Baillie *et al.*, 2013), and least sensitive to nest predation if their daily failure rates were lower than this (12 species, typically cavity nesters and aggressive large bodied species; Supporting Information Table S2). There was a clear gap in the distributions of daily nest predation rates between the two groups of species (most sensitive species: 1.10 to 4.27%; least sensitive species: 0.08 to 0.74%).

To test the hypothesis that predator distributions influence territory selection by breeding urban songbirds, we modelled the number of territories as a function of the corvid and squirrel activity indices, distance to the nearest corvid observation and distance to the nearest squirrel observation, canopy cover, the interactions between canopy cover and all predator predictors, and site (as a random factor). Separate regressions were constructed for species that are most sensitive and least sensitive to nest predation. We constructed generalized linear mixed models using the lme4 package (Bates, Maechler & Bolker, 2013), and used an information theoretic approach to model selection. We constructed all possible models given the suite of predictor variables using the MuMIn package (Bartoń, 2012). Model averaging was conducted across the top 95% confidence model set. We use $D^2$ as a measure of explanatory capacity; $D^2 = (\text{ND} - \text{RD})/\text{ND}$ where ND is the null deviance and RD is the residual deviance, which cannot be explained by the model, thus 'ND–RD' is the explained deviance. $D^2$ thus varies from zero to one, and equals one when there is no residual deviance and the deviance can be explained completely by the model. We calculated the partial $D^2$ for all predictors retained in the top 95% confidence model set. For each of these retained predictors, model averaged parameter estimates and unconditional standard errors were calculated based on averaging across the 95% confidence set. The tolerance values of all predictors were consistently above the threshold (0.10; minimum 0.53 for squirrel relative abundance in the models of territory number) below which correlations between predictor variables induces major problems in multiple regression analyses (Dormann *et al.*, 2013).

The hypothesis that nest predation rates were associated with predator distributions was tested using generalized linear mixed models with a logistic-exposure link function, following the approach of Shaffer (2004). This approach includes, within the link function, the number of exposure days as a 'nuisance' variable, which ensures that the tests for associations between nest predation rates and the variables always takes into account the fact that nests vary in their exposure time (see Shaffer, 2004). These models were constructed using the packages lme4 (Bates *et al.*, 2014) and MASS (Venables & Ripley, 2002) in R i386 3.1.2 (R Development Core Team, 2014). Abandoned nests were omitted from analyses as it was impossible to ascertain if

abandonment was related to predator activity or other factors. Separate models were constructed at the incubation and chick stage. Nest fate (incubation stage: predated or eggs hatched; chick stage: predated or fledged) was modelled as a function of corvid distance (m, minimum distance of the nest to the nearest corvid recorded during the CBC surveys), corvid activity index, squirrel distance, squirrel activity index, nest height (m), date (day 1 = 28 March; this is the date in which nest fate was determined, that is, eggs hatch, chicks fledge or predation occurs), and site (random factor, included in all models). Preliminary analyses indicated that there was no evidence of non-linear effects so only linear terms were included in the models; these were constructed separately for the species that were most sensitive to nest predation and those that were least sensitive. Modelling was not possible for the least sensitive at the incubation stage because of an insufficient sample size. The tolerance values of all predictors were above 0.10 (minimum of 0.45 for squirrel distance at chick stage for least sensitive species) demonstrating that they were acceptable for multiple regression analysis (Dormann *et al.*, 2013).

Finally, we tested the hypothesis that songbirds adjusted their clutch size in relation to predation risk (Skutch, 1949) using the blackbird as a case study as this was the only sensitive species with sufficient sample size ($n = 37$ nests). Blackbird clutch size was modelled, using a generalized linear mixed model using the lme4 package (Bates *et al.*, 2013), as a function of corvid activity index, corvid proximity, squirrel activity index, squirrel proximity, days into nesting season (with square term) and site (random factor). The tolerance values of all predictors met the recommendations of Dormann *et al.* (2013).

We used the spdep package to test response variables for spatial autocorrelation following the methodology of Dormann *et al.* (2007), by comparing full models constructed with and without taking spatial autocorrelation into account. The results indicated that spatial autocorrelation had limited influence on parameter estimates and explanatory power (Supporting Information Tables S3–S7). We thus only report the results from non-spatial models.

## Results

### Avian territories and predators

The generalized linear mixed models explained 6 and 13% of the variation in the territory number of the most sensitive and least sensitive species, respectively (Table 1). For the most sensitive species, territory number had a limited positive association with corvid and squirrel activity indices (partial $D^2 = 0.02$ and 0.01, respectively). Territory number of the most sensitive species had a negligible positive association with canopy cover (partial $D^2 = 0.01$) and negligible negative association with squirrel distance (partial $D^2 < 0.001$; Table 2). For the least sensitive species, territory number had a limited positive association with canopy cover and squirrel relative abundance (partial $D^2 = 0.04$ and 0.02,

**Table 1** Multiple regression models of the number of avian territories (of species that were most and least sensitive to nest predation) as a function of predator activity indices and distance while taking canopy cover into account

| Avian response variable | Model averaged $D^2$ | Corvid activity index | | Corvid distance | | Squirrel activity index | | Squirrel distance | | Canopy cover | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Partial $D^2$ | Mean ± SE | Partial $D^2$ | Mean ± SE | Partial $D^2$ | Mean ± SE | Partial $D^2$ | Mean ± SE | Partial $D^2$ | Mean ± SE |
| Territory number of avian species most sensitive to nest predation | 0.060 | 0.019 | 0.561 ± 0.109 | n/a | n/a | 0.014 | 0.875 ± 0.263 | <0.001 | −0.003 ± 0.0006 | 0.005 | 0.019 ± 0.018 |
| Territory number of avian species least sensitive to nest predation | 0.126 | 0.003 | 0.057 ± 0.065 | <0.001 | −0.001 ± 0.001 | 0.023 | 0.423 ± 0.128 | 0.005 | −0.002 ± 0.003 | 0.036 | 0.025 ± 0.004 |

Site was treated as a random factor. An information theoretic approach to model selection was adopted and data reported are model averaged values (with unconditional standard errors) for predictors retained in the 95% confidence set of models (no interactions were retained in this set). n/a represents predictors that were not retained in the 95% confidence set for the focal analysis

**Table 2** Generalized linear mixed models (log-exp link function) of nest fate (of species that were most sensitive to nest predation) as a function of predator abundance and distance, nest height and days into nesting season

| Response variable | Model averaged $D^2$ | Corvid activity index Partial $D^2$ | Corvid activity index Mean ± SE | Corvid distance Partial $D^2$ | Corvid distance Mean ± SE | Squirrel activity index Partial $D^2$ | Squirrel activity index Mean ± SE | Squirrel distance Partial $D^2$ | Squirrel distance Mean ± SE | Nest height Partial $D^2$ | Nest height Mean ± SE | Date Partial $D^2$ | Date Mean ± SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nest fate for avian species most sensitive to nest predation (incubation stage) | 0.075 | 0.048 | 0.215 ± 0.109 | < 0.001 | −0.0001 ± 0.002 | 0.004 | 0.052 ± 0.095 | 0.007 | −0.002 ± 0.003 | 0.008 | 0.119 ± 0.179 | < 0.001 | −0.001 ± 0.003 |
| Nest fate for avian species most sensitive to nest predation (chick stage) | 0.117 | < 0.001 | −0.004 ± 0.015 | 0.100 | −0.022 ± 0.011 | 0.001 | −0.004 ± 0.028 | 0.012 | −0.003 ± 0.005 | < 0.001 | 0.001 ± 0.012 | 0.002 | −0.001 ± 0.003 |

Site was treated as a random factor, and is present in all models. An information theoretic approach to model selection was adopted and data reported are model averaged values (with unconditional standard errors) for predictors retained in the 95% confidence set of models. The null model explained nest fate of least sensitive species, better than all recorded predictors, at the chick stage. Equivalent models of nest fate for the least sensitive species at the incubation stage could not be conducted because of an insufficient sample size.

respectively), negligible positive association with corvid relative abundance (partial $D^2 < 0.005$), and negligible negative association with squirrel and corvid distance (partial $D^2 = 0.01$ and < 0.001, respectively; Table 1). No interaction between canopy cover and any of the predator predictors was retained in the top 95% confidence set of models for either analysis.

## Nest fate and predators

The generalized linear mixed models with logistic-exposure link function, explained 8 and 12% of the variation in the nest fate of the most sensitive species at the incubation and chick stages, respectively (Table 2). At the incubation stage, the strongest predictor of nest predation rates of the most sensitive species was corvid activity index (partial $D^2 = 0.05$), with the relationship being positive (Table 2). At the chick stage, nest predation rates of the most sensitive species were negatively associated with corvid distance, that is, higher predation rates at nests closer to corvids (partial $D^2 = 0.10$). All other predictor variables, including the squirrel activity index and squirrel distance, had negligible associations with the nest fate of the most sensitive species (Table 2).

When modelling nest fate at the chick stage, of species that were least sensitive to nest predation, the null model, that is, one that lacked any predictor variables, had a lower AICc than any of the models which contained predictors. The sample size at the incubation stage for these species was insufficient to model nest fate.

## Blackbird clutch size and predators

The null model explained the clutch size (mean $3.16 \pm 0.11$, $n = 37$) of blackbirds better than all recorded predictors, including those relating to the abundance and proximity of nest-predating corvids and grey squirrels.

## Discussion

### Avian territories and the distribution of nest predators

We found no evidence that predator distributions influence territory selection by urban breeding birds. In fact, even when taking canopy cover into account, corvid relative abundance had a limited positive association with the number of breeding territories of the most sensitive bird species. This is likely partly to be a consequence of predators and prey favouring similar habitat types and of canopy cover, in isolation, being an insufficient measure of habitat quality. Although some studies have reported bird species selecting breeding territories based on the distribution of their predators (e.g. Roos & Pärt, 2004; Emmering & Schmidt, 2011; Tomiałojć, 2011), such associations are species and spatially dependent (Marzluff et al., 2007) or are

limited in comparison with other factors, such as habitat type (Chiron & Julliard, 2007).

## Nest predation rates and the distribution of nest predators

We found negligible evidence that grey squirrel relative abundance or the proximity of squirrels from the nest were associated with nest predation rates, with squirrel indices typically explaining less than 1% of the variation in nest predation rate. Mammals are documented as being important nest predators (e.g. Rodewald & Yahner, 2001; Grégoire *et al.*, 2003; Marzluff *et al.*, 2007; Weidinger, 2009). Grey squirrels are nest predators, although much of the evidence is anecdotal and equivocal (see Hewson *et al.*, 2004). Only recently have associations between the nest failure of open-nesting species and the abundance of grey squirrels been subject to empirical analyses; this work found higher failure rates were associated with higher squirrel densities in rural areas at much larger spatial grains ($1 \times 1$ km cells) than those used here (Newson *et al.*, 2010*a*). It is unclear if this contrast with our study is driven by the focus on different habitat types or spatial grain, but in combination the results suggest that typically grey squirrel predation is currently having limited impact on songbird reproductive success in the UK. This does not preclude the potential for direct impacts on other rare and more sensitive songbirds, not included in the studies, or of indirect effects caused by squirrels (see Bonnington *et al.*, 2013 for an assessment of these).

In contrast to the effects of grey squirrels, we did find some evidence that sensitive species experienced higher nest predation rates in areas with greater corvid activity at the incubation stage. In addition, predation during the chick stage was negatively associated with distance from the nearest location with corvid activity. The explanatory capacity of all these relationships was, however, rather modest and these results thus provide only limited support to other studies which have documented positive associations between corvid abundance and nest predation rates at larger spatial scales (Andrén, 1992; Paradis *et al.*, 2000; Luginbuhl *et al.*, 2001; White *et al.*, 2008). We suspect that the limited associations between predator activity and nest predation rates at fine spatial scales arise in part because in our focal urban areas there are no nesting locations that are used sufficiently infrequently by nest predators to have a large effect on nest predation rates. It is also plausible that in locations with higher predator activity, parental birds partially compensate for the higher risk of nest predation by placing their nests in more concealed locations, although evidence for such adaptive placement within the natural range of magnitude of concealment is limited (Remes, 2005; Latif, Heath & Rotenberry, 2012). Alternatively, there may be considerable intra-specific variation within populations of generalist opportunistic nest predators, such as corvids and grey squirrels, in their propensity for nest predation (Weidinger & Kočvara, 2010), which would reduce the association between indices of predator activity and predation

risk. Nest predation by the squirrel *Tamiasciurus hudsonicus*, for example, seems to be a learnt behaviour, the frequency of which varies with prior experience (Pelech, Smith & Boutin, 2010).

## Blackbird clutch size and the distribution of nest predators

Contrary to conventional theory (Skutch, 1949), we found no evidence that blackbirds (the most commonly recorded sensitive songbird within the study sites) adjusted their clutch size in response to predator distributions even though blackbird clutch size is responsive to other forms of environmental variation (Evans *et al.*, 2005). The lack of adjustment in clutch size could make the nest more vulnerable to predation as increased provisioning rates could increase the chance of visually orientated predators locating the nest (Skutch, 1949), and by increasing the duration over which nests are exposed to predators (songbirds typically lay one egg per day; Martin & Geupel, 1993). While the lack of behavioural adjustment may be expected to increase nest predation rates, creating an ecological trap (see Schlaepfer, Runge & Sherman, 2002; Millspaugh *et al.*, 2006), we find no evidence for this as spatial variation in predator distributions only has a limited influence on nest predation rates.

## Conclusions

We find no evidence that the songbirds that are sensitive to nest predation adjust their territory location in response to fine-scale spatial variation in predator distributions. Urban predators are thus unlikely to be indirectly regulating urban bird population size by restricting habitat availability. Similarly, blackbirds (which have high nest predation rates) did not vary their clutch size in response to predator distributions. Given that corvid distributions are positively associated with the nest failure rate of the most sensitive songbirds to nest predation, there is potential for the creation of an ecological trap, where birds fail appropriately to respond to predation risk. Presently the association between grey squirrels and songbird nest failure is negligible, while the equivalent association between corvids and songbird nest failure is stronger but remains limited. We do, however, recommend future monitoring, particularly as the distribution and population size of grey squirrels are predicted to rapidly increase across Europe (Bertolino *et al.*, 2008).

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# Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Grid choropleth maps showing the predator activity indices at (a) Loxley and Wadsley Common Local Nature Reserve, and (b) Beauchief estate. The predator activity indices are the total number of nest-predating corvids and grey squirrels pooled across the site visits. Each square is $100 \times 100$ m.

**Table S1.** The variation in predator activity indices at both survey sites at the lower, and higher, spatial grains. The values are average predator number per grid cell (+SE), and the values in brackets are the range in predator number within the grid cell. Because of the lack of variation in predator activity indices at the lower spatial grain ($50 \times 50$ m), all analyses are conducted using predator indices at the greater spatial grain ($100 \times 100$ m).

**Table S2.** Bird species recorded at the survey sites, and their classification as most sensitive, or least sensitive, to nest predation. Predation is the main cause of nest failure and species were considered most sensitive to nest predation if their daily nest failure rates were greater than 1% nest/day as calculated from the BTO's nest record card scheme (Baillie *et al.*, 2013). Using this methodology, cavity nesters and aggressive large bodied species were typically classified as least sensitive to predation while other species were classified as being most sensitive to predation. The value in parentheses after the number of nests represents the number of

abandoned nests for that particular species that were excluded from analysis.

**Table S3.** The results of the generalized linear mixed model (log-exp link function) analyses, constructed for nest fate at the incubation stage for most sensitive species, modelled against all predictors only (termed full model), and all predictors and the autocovariate term (termed ac model), for Beauchief estate (BC) and BC and Loxley and Wadsley Common LNR (LWC) pooled. Analyses could not be conducted for LWC alone, as the sample size was too limited. The autocovariate model was constructed in the spdep package (R i386 3.1.2, 2014) using an autocovariate term and following the methodology proposed by Dormann *et al.* (2007). Parameter estimates (mean ± SE) and the explanatory power (in parentheses) of the predictors related to predators were relatively consistent between the respective models. Similar comparisons were not made for least sensitive species at the incubation stage, as the sample size was too limited to run the full models. The explanatory power was not given for nest height at BC likely because of issues of model over-specification.

**Table S4.** The results of the generalized linear mixed model (log-exp link function) analyses, constructed for nest fate at the chick stage for most sensitive species, modelled against all predictors only (termed full model), and all predictors and the autocovariate term (termed ac model), for Beauchief estate (BC), and BC and Loxley and Wadlsey Common LNR (LWC) pooled. Analyses could not be conducted for LWC alone, as the sample size was too limited. The autocovariate model was constructed in the spdep package (R i386 3.1.2, 2014) using an autocovariate term and following the methodology proposed by Dormann *et al.* (2007). Parameter estimates (mean ± SE) and the explanatory power (in parentheses) of the predictors relating to predators were relatively consistent between the respective models. Similar comparisons were not made for least sensitive species at the chick stage, as the null model performed better than all predictors.

**Table S5.** The results of the analyses, constructed for territory number of most sensitive species, modelled against all predictors only (termed full model), and all predictors and the autocovariate term (termed ac model), for each site (Loxley and Wadsley Common LNR; LWC and Beauchief estate; BC) separately and for the sites combined. The autocovariate model was constructed in the spdep package (R v. 2.15.1, 2012) using an autocovariate term and following the methodology proposed by Dormann *et al.* (2007). Parameter estimates (mean ± SE) and the explanatory power (in parentheses) of the predictors related to predators were relatively consistent between the respective models. Generalized linear mixed model analyses were used for the sites combined, and the explanatory power presented is model and partial $D^2$; and generalized linear model analyses were used for the sites separately, and the explanatory power presented is model and partial $R^2$.

**Table S6.** The results of the analyses, constructed for territory number of least sensitive species, modelled against all predictors only (termed full model), and all predictors and

the autocovariate term (termed ac model), for each site (Loxley and Wadsley Common LNR; LWC and Beauchief estate; BC) separately and for the sites combined. The autocovariate model was constructed in the spdep package (R v. 2.15.1, 2012) using an autocovariate term and following the methodology proposed by Dormann *et al.* (2007). Parameter estimates (mean ± SE) and the explanatory power (in parentheses) of the predictors related to predators were relatively consistent between the respective models. Generalized linear mixed model analyses were used for the sites combined, and the explanatory power presented is model and partial $D^2$; and generalized linear model analyses were used for the sites separately, and the explanatory power presented is model and partial $R^2$.

**Table S7.** The results of the generalized linear mixed model analyses, constructed for blackbird clutch size, modelled against all predictors only (termed full model), and all predictors and the autocovariate term (termed ac model), for the sites combined. The autocovariate model was constructed in the spdep package (R v. 2.15.1, 2012) using an autocovariate term and following the methodology proposed by Dormann *et al.* (2007). Parameter estimates (mean ± SE) and the explanatory power (in parentheses) of the predictors related to predators were relatively consistent between the respective models. Equivalent analyses were not possible for the sites individually because of low sample sizes.