

Urban bird declines and the fear of cats

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Abstract

The role of domestic cats *Felis catus* in the troubling, on-going decline of many urban bird populations in the UK is controversial. Debate, in the UK and elsewhere, has centred on the level of avian mortality directly imposed by cats, and on whether this is principally compensatory (the 'doomed surplus' hypothesis) or additive (the 'hapless survivor' hypothesis). However, it is well established that predators also have indirect, sub-lethal effects on their prey where life-history responses to predation risk affect birth and death rates. Here, using a simple model combining cat predation on birds with a sub-lethal (fear) effect of cat density on bird fecundity, we show that these sub-lethal effects may be substantial for urban songbirds. When cat densities are as high as has been recorded in the UK, and even when predation mortality is low (e.g. <1%), a small reduction in fecundity due to sub-lethal effects (e.g. <1 offspring year⁻¹ cat⁻¹) can result in marked decreases in bird abundances (up to 95%). Thus, low predation rates in urban areas do not necessarily equate with a correspondingly low impact of cats on birds. Sub-lethal effects may depress bird populations to such an extent that low predation rates simply reflect low prey numbers.

Introduction

The widespread and on-going decline of rural and urban bird populations is a critical conservation issue (Gering & Blair, 1999; Marzluff, Bowman & Denny, 2001; McKinney, 2002; Crick *et al.*, 2003; Thorington & Bowman, 2003; DEFRA, 2004b; Baker *et al.*, 2005; Pauchard *et al.*, 2006). In the UK, despite recent improving trends in farmland and rural bird population sizes (Crick *et al.*, 2003; DEFRA, 2004b), urban bird populations show few signs of stabilizing or increasing. Species such as the starling *Sturnus vulgaris* and house sparrow *Passer domesticus* have declined by up to 60% in urban areas of the UK over the past 30 years (Crick *et al.*, 2002, 2003). This has occurred despite suggestions that these populations should benefit from urban habitat characteristics that include low predator diversity, high food availability (often explicitly provided by people) and abundant nest sites (again, often provided by people, e.g. Marzluff *et al.*, 2001; McKinney, 2002). Current hypotheses about urban bird population declines, and their lack of recovery, reflect changes in such habitat characteristics. Specifically, many of the hypotheses link low offspring survival to a loss of nesting sites, reductions in invertebrate food, Allee effects and predation by domestic cats *Felis catus* (DEFRA, 2004a).

The effects of increases in the abundances of predators, including domestic cats, corvids and Sparrowhawks *Accipiter nisus*, on rural and, particularly, urban bird populations have generated substantial debate over the past 30 years (May, 1988; Fitzgerald, 1990; Jarvis, 1990; Gooch, Baillie &

Birkhead, 1991; Newton, Dale & Rothery, 1997; Thomson *et al.*, 1998; Crooks & Soule, 1999; Hole *et al.*, 2002; Lepczyk, Mertig & Liu, 2004; MacLeod *et al.*, 2006). The possible significance of predation by domestic cats has generated the most polarized debate, centred on the level of avian mortality directly imposed by cats, and on whether this is principally compensatory (the 'doomed surplus' hypothesis) or additive [the 'hapless survivor' hypothesis; (Churcher & Lawton, 1987; May, 1988; Gil-Sanchez, Valenzuela & Sanchez, 1999; Marzluff *et al.*, 2001; Woods, McDonald & Harris, 2003; DEFRA, 2004b; Kays & DeWan, 2004)]. Resolution of this debate has proven difficult because robust quantitative data on mortality rates and functional responses, the traditional measure of the effect of predation, have proven difficult to obtain and remain rather scarce.

The absolute levels of mortality exerted by domestic cats may not, however, be the most important issue. Predators influence prey populations not only by eating prey individuals but also by altering prey behaviours, including foraging patterns and use of different habitats (Lima, 1987, 1998). Empirical research on a wide range of species, including birds, demonstrates that behavioural responses to predation risk can have profound population-level effects by altering traits such as adult and juvenile survival, clutch size or clutch number (Lima, 1987, 1998). Moreover, it is emerging that the consequences of these effects at the population level may be larger than those of predation mortality (Preisser, Bolnick & Benard, 2005). Such empirical evidence has motivated a few avian-specific models

examining aspects of these sub-lethal effects of predators on bird population size and dynamics (Ruxton & Lima, 1997; Kokko & Ruxton, 2000). Here, we build on these insights to ask whether domestic cats may be capable of exerting strong influences on bird populations by altering prey-reproductive performance. In particular, we take into account the fact that the domestic cat is a supplementally fed, generalist predator occurring at high densities, which does not depend on prey abundance, or indeed the consumption of any natural prey.

This hypothesis is motivated particularly by current trends in cat ownership and thus density. The Pet Food Manufacturers' Association in the UK estimates that in 2003, there were ~9.2 million domestic cats in the UK, an ~13% annual increase over 40 years (Fig. 1, based on a linear regression of cat ownership through time: $F = 257.1$, d.f. = 1,24, $P < 0.001$, $R^2 = 91\%$, PFMA, 2003). Approximately 90% of the UK human population is suburban/urban (ODPM, 2001), and ~16 637 km² (6.7%) of the UK land surface comprises built-up areas and gardens (from a full count of cover based on a 25-m grid, Fuller *et al.*, 2002). Assuming that per capita levels of cat-ownership are approximately constant across rural and suburban/urban landscapes, the mean density of domestic cats in the UK is thus ~500 individuals km⁻² (allowing for a doubling of rural or urban cat ownership, relative to the other habitat, would lead to estimates of 440–525 individuals km⁻², respectively); some urban areas exceed this cat density by a factor of at least two (based on 1 km² plots; V. Sims, pers. comm.).

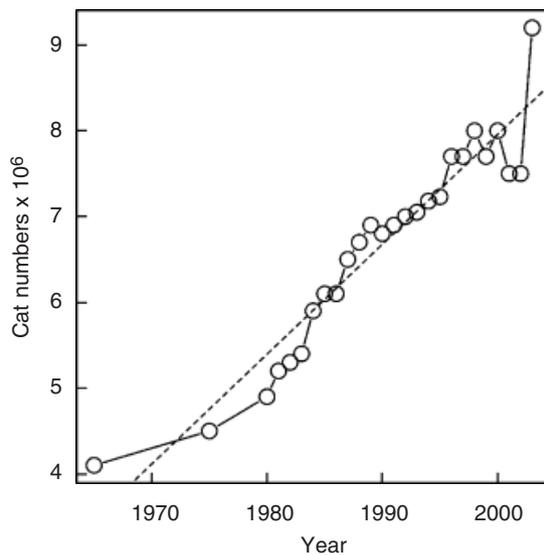


Figure 1 Cat *Felis catus* numbers have increased substantially over time. These data are drawn from the Pet Food Manufacturing Association (PFMA, 2003) and document the estimates of cat ownership in the UK, based on pet food sales. Combined with data on the proportion of the UK population in urban areas (see text), these data suggest a substantial increase in the density of cats in urban areas.

This density of meso-predators is unparalleled in natural systems and is two to three orders of magnitude higher than the density of similar-sized, and closely related species of wild cats (Nowell & Jackson, 1996). In contrast, density estimates of common urban songbird species in the UK range from an average of <20 to more than 300 individuals km⁻² (Dunnock *Prunella modularis* = 15, Blackbird *Turdus merula* = 104, Starling *S. vulgaris* = 223, House Sparrow *P. domesticus* = 345 individuals km⁻², Newson *et al.*, 2005). Thus, on a per-species basis, urban cat predator:avian prey ratios range from ~35:1 to 1.5:1. Here, we use a simple model to articulate the hypothesis that cat density *per se* may detrimentally impact avian productivity, leading both to low-population sizes and low-predation rates.

Model

A model in which domestic cats may both eat birds and reduce the fecundity of survivors by a per-predator sub-lethal (fear) rate, and in which cat density does not respond to bird abundance, takes the form

$$\frac{dB}{dt} = (b_0 - \gamma(C) - hB)B - dB - \alpha BC$$

where B is the density of the bird species, C is the cat density, b_0 is the maximum number of bird offspring, h is the strength of intra-specific density dependence, d is the intrinsic, density-independent death rate, α is the attack rate by cats on birds, αB is a Type I functional response (Case, 2000) and $\gamma(C)$ is the function describing the predator-induced reduction in bird productivity (the sub-lethal effect). There are no published reports of cat functional responses on birds, so we have used a conservative and simple representation. We specified $\gamma(C)$ as a decreasing linear function of predator density such that $\gamma(C) = \omega C$, where ω is the per-predator effect on bird fecundity. Our results are qualitatively insensitive to this functional form, relying only on the existence of a negative relationship.

We first examined properties of the analytic equilibrium predicted by the model. We then examined quantitatively the effect of six possible levels of sub-lethal reductions in fecundity (0, 1, 2, 3, 6 and 9%) at three hypothetical levels of mortality (0, 1 and 5%) on predicted equilibrium densities of bird populations. These plausible but theoretical values are used because, as noted above, there are no published data on predation rates or on the sub-lethal effects of cats on songbirds.

We present the effects of the sub-lethal impact of cat predators by comparing the per cent change in predicted equilibrium density between models with no sub-lethal effect with the equilibrium at increasing levels of sub-lethal effects. By comparing per cent change, the model presentation is insensitive to specific model parameters. Thus, any positive parameters chosen for b_0 , d and h will lead to the same conclusions, as long as the resulting carrying capacity is positive. For simplicity, we use estimates of birth, death and

Table 1 Values used in analysis of the effect of cat *Felis catus* density on the per cent change in carrying capacity

	Intrinsic birth rate (b_0)	Intrinsic death rate (d)	Density dependence (h)
Value	21	1	0.066

The qualitative and quantitative details of the analysis are insensitive to the values of these parameters, as long as they result in a positive carrying capacity. In our simulations, the intrinsic birth rate was set based clutch size and clutch number data on house sparrows *Passer domesticus* from DEFRA (Crick *et al.*, 2002; DEFRA, 2004a). Intrinsic death rate was set at one and density dependence was calculated by assuming a carrying capacity, $(b_0-d)/h$, of ~ 300 birds at a 0 cat density (see text for equilibrium solution to model that allows calculation).

density dependence based on house sparrow data published in recent proceedings by DEFRA, UK (Table 1; Crick *et al.*, 2002; DEFRA, 2004a). The model is examined over a predator density ranging from zero, through UK average of 500 km^{-2} , to 1500 km^{-2} , the highest reported urban cat density in the UK.

Results

When the effect of cat density is to reduce linearly the birth rate of birds, the equilibrium bird density = $(b_0-d-C\alpha-C\omega)/h$. Thus, the population will be constant with no lethal ($\alpha = 0$) and sub-lethal ($\omega = 0$) effects, and declines with either, or both additively (Fig. 2a). Predators in this model can drive prey to extinction when $C > (b_0-d)/(\omega + \alpha)$. Thus, for a given level of predation, increasing the per predator effect of fear on prey fecundity (ω) further lowers the right-hand side of this inequality, making it easier to satisfy at a given predator population.

A systematic, numerical assessment of the proportional reduction of bird carrying capacity under combined lethal and sub-lethal effects leads to four main results. First, for a given level of predation mortality (α), increasing either cat density (C) or the per-predator, sub-lethal reduction in fecundity (ω), leads to declines in bird abundance from equilibrium (Fig. 2a–c). At low levels of predation mortality (Fig. 1a and b), the impact of sub-lethal effects can be substantial. In these cases, sub-lethal effects result in major reductions in population size, relative to equilibrium, as the predator density increases.

Second, even when predation mortality is zero (Fig. 2a), small reductions in fecundity due to fear can result in a substantial decrease in bird abundance. These reductions can be very large if cat densities are as high as the recorded $1000 \text{ individuals km}^{-2}$ (Fig. 2a). For example, empirical estimates of house sparrow production range from 16 to 20 offspring per annum (assuming four to five eggs over four clutches per annum) (Crick *et al.*, 2002, 2003; DEFRA, 2004a). Assuming the national average cat density ($500 \text{ individuals km}^{-2}$), a 2% decrease in fecundity (see Fig. 2) equates to a reduction in productivity of, on average, less than one bird offspring by each cat every 2 years.

Third, predation mortality clearly mediates the consequences of sub-lethal effects (Fig. 2). At the UK average cat density of $500 \text{ individuals km}^{-2}$, a range of 1–3% sub-lethal decrease in fecundity can result in substantial reductions of population size from carrying capacity when mortality itself

is low (e.g. 75–25% of carrying capacity when predation rates are zero; Fig. 3). As our model assumes that lethal and sub-lethal limits to population size are additive, increasing mortality rates from predation further lowers the expected population size (Fig. 3).

Finally, rural rates of predation by cats may be of the order 15–30% [from digitized data in Churcher & Lawton, 1987; the upper estimate is mean (annual catch cat^{-1} per density of birds), and the lower one is the intercept estimate from intercept-only regression per mean density of birds]. Current research continues to reinforce that urban predation rates are likely to be less than or equal to rural ones (V. Sims, pers. comm., and see Haskell, Knupp & Schneider, 2001; Shochat, 2004). Our model suggests that urban predation rates must be very low, assuming linear density dependence, additive effects of mortality and sub-lethal effects and a constant predation rate (Type I functional response). Based on these assumptions, current empirical estimates of domestic cat and bird densities could only co-occur if predation rates do not exceed 5% (Figs 2 and 3).

There is some uncertainty regarding estimates of urban area and therefore our assumption of a UK average of 500 cats km^{-2} . We note, however, that none of these conclusions would be altered even if cat densities were half of the estimate we use (i.e. 250 rather than 500 cats km^{-2}). Even at these lower densities, cat-generated sub-lethal reduction in fecundity or survival has the potential to reduce bird population sizes drastically (Figs 2 and 3).

Discussion

The decline of farmland and urban birds remains an important issue in British and European conservation (Marzluff *et al.*, 2001; Benton *et al.*, 2002; Crick *et al.*, 2002, 2003; Hole *et al.*, 2002; Benton, Vickery & Wilson, 2003; Vickery *et al.*, 2004; MacLeod *et al.*, 2006). Predation, by avian and mammalian predators, remains a central, hypothetical explanation of the decline, complementing suggestions that changes in habitat availability and food may also be important (Crick *et al.*, 2002; Hole *et al.*, 2002; MacLeod *et al.*, 2006). In the 12 years since May (1988) speculated on the impact of cats on urban birds, the number of cats estimated in the UK has increased from 6.7 to 9.2 million (Fig. 1), while detailed data on the effects of cats on urban birds have been slow to develop (e.g. mortality rates and functional responses). Current predation theory and empirical research on birds (e.g. Lima, 1987; Lima, 1998) highlight, however,

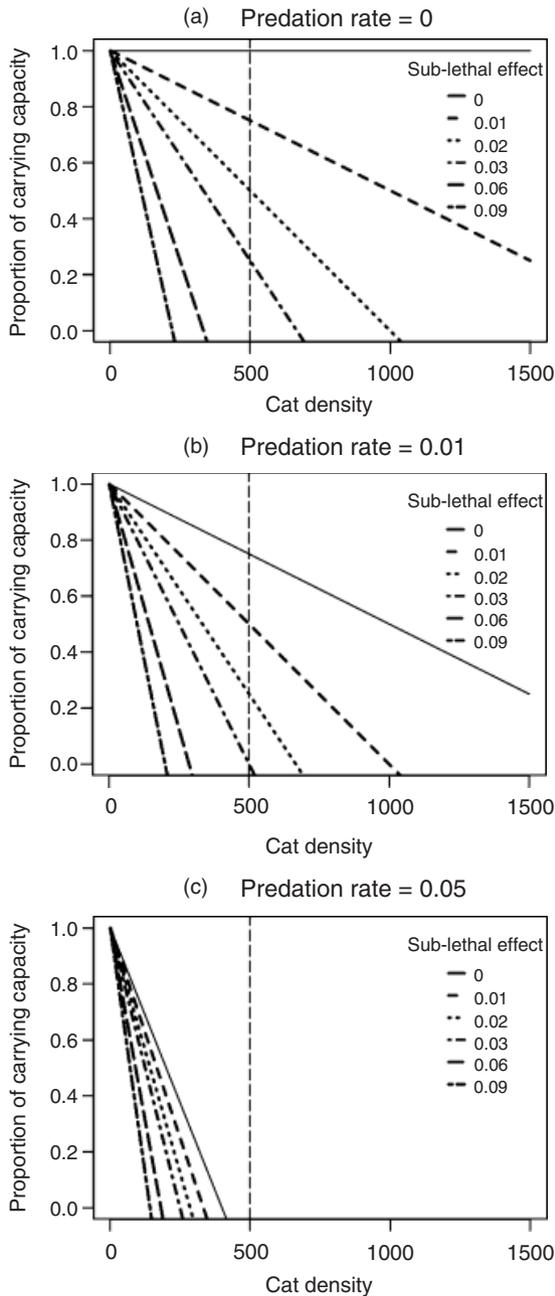


Figure 2 Proportional reduction from equilibrium prey density as the predator density increases. The panels show the effects of increasing the magnitude of sub-lethal effects (dashed lines) over a range of cat *Felis catus* densities under three predation scenarios: (a) no predation mortality (only sub-lethal effects); (b) 1%; (c) 5% direct mortality. The dashed vertical lines reference UK current estimates of suburban/urban cat density across the UK (500 individuals km⁻²). Solid black lines present bird equilibrium densities without sub-lethal effects. The presentation of the model as per cent change from equilibrium is only sensitive to the model structure. Any positive parameters chosen for b_0 , d and h will lead to the same conclusions, as long as the resulting carrying capacity is positive (see text for details).

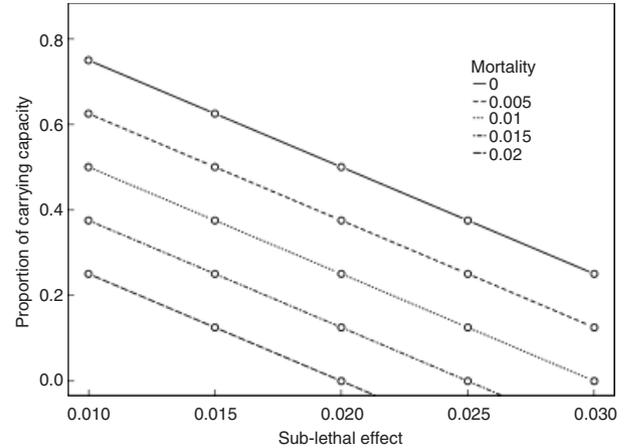


Figure 3 Effects of predation rate and sub-lethal effects on prey equilibrium density. The plotted contours mark, for the UK, average cat *Felis catus* density of 500 individuals km⁻², the percentage reduction in equilibrium density that arises from a combination of fear effect (percentage reduction in bird fecundity) and predation mortality. Each contour represents a different level of predation mortality (0, 0.5, 1, 1.5, 2%) as a function of the sub-lethal effect gradient on the x-axis (1–3%). As in Fig. 1, the presentation of the model as per cent change from equilibrium is only sensitive to the model structure and not to specific parameter values (see text for details).

that the absolute levels of mortality exerted by domestic cats may not be the most important issue. Our model represents one of the first explorations of the sub-lethal predator hypothesis that urban predator abundance can limit substantially the population of urban birds by reducing a life-history trait such as fecundity. Furthermore, it indicates that sub-lethal effects may depress bird populations to such an extent that low-predation rates simply reflect low-prey numbers.

The addition of this hypothesis to the pool of competing explanations for the decline of urban birds underlines the need for detailed data on the lethal and sub-lethal effects of predators, amidst variation in life history and productivity generated by nest site availability and food (e.g MacLeod *et al.*, 2006). However, it does not necessarily affect the nature of suggestions for protecting urban birds. The Royal Society for the Protection of Birds (RSPB, 2005), British Trust for Ornithology (BTO, 2005) and independent research (Ruxton, Thomas & Wright, 2002) have suggested a number of approaches to reduce the mortality inflicted on wild bird populations by domestic cats. These include restricting the outdoor activity of cats either spatially or temporally, fitting bells that make them more conspicuous to potential prey and providing food for birds in places and with regularity that limits their need to forage in areas where they are at a greater risk of predation by cats. Our model suggests that low suspected predation rates in urban areas need not reflect a correspondingly low impact of cats on birds. Indeed, cat density *per se* may detrimentally impact avian productivity, leading both to low population sizes and low predation rates. If this is so, the recommended measures

to reduce cat–bird contact (although not necessarily those that increase the conspicuousness of cats) are also likely to reduce the sub-lethal effects of cats, which may be just as important as predation in their impact on urban bird populations. Clearly, there is a pressing need to collect detailed data on the sub-lethal effects of cats on bird reproductive success. However, our model emphasizes that given the uniquely high densities of urban cats, there are significant effects on bird populations even with very weak sub-lethal effects.

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