

Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations?

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Even though they are fed daily by their owners, free-ranging pet cats *Felis catus* may kill wild birds and, given their high densities (typically > 200 cats/km²), it has been postulated that cat predation could be a significant negative factor affecting the dynamics of urban bird populations. In this study, we: (1) used questionnaire surveys in 10 sites within the city of Bristol, UK, to estimate cat density; (2) estimated the number of birds killed annually in five sites by asking cat owners to record prey animals returned home; and then (3) compared the number of birds killed with breeding density and productivity to estimate the potential impact of cat predation. In addition, we (4) compared the condition of those birds killed by cats versus those killed in collisions, e.g. window strikes. Mean (\pm sd) cat density was 348 ± 86 cats/km² ($n = 10$ sites); considering the eight species most commonly taken by cats, the mean ratios of adult birds/cats and juvenile birds/cats across the five sites were 1.17 ± 0.23 and 3.07 ± 0.74 , respectively. Approximately 60% of the cats studied for up to 1 year at each site never returned any prey home; despite this, the estimated number of birds killed was large relative to their breeding density and productivity in many sites. Across species, cat-killed birds were in significantly poorer condition than those killed following collisions; this is consistent with the notion that cat predation represents a compensatory rather than additive form of mortality. Interpretation of these results is, however, complicated by patterns of body mass regulation in passerines. The predation rates estimated in this study would suggest that cats were likely to have been a major cause of mortality for some species of birds. The effect of cat predation in urban landscapes therefore warrants further investigation. The potential limitations of the current study are discussed, along with suggestions for resolving them.

Keywords: fluctuating asymmetry, garden birds, hyperpredation, introduced species, urban biodiversity.

The accidental or deliberate introduction of species into areas beyond their natural geographical range by humans is widely recognized as one of the major processes adversely affecting global biodiversity (Atkinson 1996, Mack *et al.* 2000, Clavero & Garcia-Berthou 2005) and predatory non-native mammals have notably caused the extinction, extirpation and decline of a wide range of vertebrate species (Fitzgerald 1988, Kinnear *et al.* 1988, 1998, 2002, Roy 2001, Keitt *et al.* 2002, Nogales *et al.* 2004, Davey *et al.*

2006, Wayne *et al.* 2006). Domestic cats *Felis catus* exhibit varying degrees of dependence on humans from truly feral animals, such as on islands, that are totally non-reliant on people for food and shelter, to semi-feral individuals that are fed to some degree by humans (Centonze & Levy 2002, Levy *et al.* 2003), through to companion animals (also known as house cats and inside/outside cats) that are provided with food daily and which co-habit with their owners. The size of a truly feral population is therefore dependent on the abundance and availability of natural prey species and, consequently, most documented impacts on native prey species involve feral cat populations (Meffe & Carroll 1997).

Conversely, the density of companion animal populations is wholly independent of natural prey

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availability, and pet cats can be found at very high densities where humans are also very numerous, such as in urban areas (Matheson 1944, Baker *et al.* 2005, Gaston *et al.* 2005, Sims *et al.* 2008). Given their high density and that they are typically allowed to roam freely within their neighbourhood where they may catch and kill prey (Mead 1982, Liberg 1984, Churcher & Lawton 1987, Dunn & Tessaglia 1994, Barratt 1997, 1998, Robertson 1998, Howes 2002, Gillies & Clout 2003, Lepczyk *et al.* 2003, Woods *et al.* 2003, Baker *et al.* 2005), it has been postulated that cats could have a significant negative effect on prey populations in urban areas, even if individual cats kill few prey (May 1988). Populations of companion animals also pose particular management problems (Proulx 1988, Fitzgerald 1990, Lilith *et al.* 2006), as their close association with humans can limit the application of conventional approaches commonly used to tackle conflicts with introduced species, in particular culling. Conversely, it does allow alternative solutions to be implemented that would not otherwise be possible, e.g. the fitting of anti-predation devices (Ruxton *et al.* 2002, Nelson *et al.* 2005), the use of chemical and ultrasonic deterrents (Nelson *et al.* 2006), curfews and the banning of ownership of cats within sensitive areas (Lilith *et al.* 2006).

Currently, however, there are few data available on: the numbers of different species killed by cats; how predation rates vary with cat and prey density; the age, sex or physical condition of animals killed; and how the number of birds predated compares with the density of breeding birds and young (Wegglar & Leu 2001). All of these factors may affect the degree to which predation by cats is important within the dynamics of prey populations. For example, cats may selectively predate juvenile animals and/or those in poor physical condition (Møller & Erritzoe 2000, Dierschke 2003), although these classes may be expected to have high natural mortality rates in the absence of cats, such that cat predation could wholly or partially compensate for natural mortality rather than being additive to it.

Therefore, in this study we quantified (1) cat density and (2) the numbers of different species of birds killed by cats in selected areas within the city of Bristol, UK, by asking cat owners to record prey returned home to them by their pet(s). We then (3) compared these figures with estimates of breeding density and productivity at each site to consider whether the number killed could potentially affect prey population dynamics. We also (4) compared the physical

condition of those birds killed by cats with that of birds killed by (assumed) stochastic mortality events; these data were used to assess whether cats were killing poorer quality individuals in order to estimate whether cat predation was likely to be additive or compensatory to natural mortality.

METHODS

Data were collected for 10 sites within the city of Bristol, UK. Nine 1-km² squares were surveyed in 2005 (OS grid references: ST5277, ST5768, ST5772, ST5876, ST5878, ST5974, ST6076, ST6174 and ST6272). These sites were chosen at the outset to reflect a range of densities of bird species commonly taken by cats (R. Bland pers. comm.). In addition, data were included from a 4.2-km² area in the north-west of the city surveyed in 2002, already detailed by Baker *et al.* (2005). This pilot study was centred on OS grid reference ST5676, although the data presented in the current manuscript refer to the whole study area.

Cat density

A questionnaire was delivered to every household on each of the 10 study sites requesting information on the number of pet cats present and whether owners would be willing to participate further in the study by recording prey animals returned home by their pet(s). Such surveys are potentially susceptible to reporting biases, e.g. owners whose cats were killing lots of birds may have been unwilling to provide information if they believed the study was to be used to criticise cat ownership in urban areas. Therefore, we adopted a two-tier sampling protocol. Every householder was initially asked to leave their completed questionnaire on their doorstep on a given day for collection (hereafter termed 'original' questionnaires). A sample of non-respondents was then contacted door-to-door and asked to complete the form in a face-to-face interview ('follow-up' questionnaires). Cat density (D) was then estimated as: $D = C_O + C_F + [(T_H - H_O - H_F) \times P_F \times M]$, where C_O is the absolute number of cats owned by those householders who completed the questionnaire during the first phase, C_F is the absolute number of cats owned by those householders who completed the questionnaire during the follow-up phase, T_H is the total number of households within the 1-km² survey site, H_O and H_F are the numbers of householders that replied during the first and second phases, respectively, P_F is the proportion of householders in

the follow-up phase that owned cats (non-respondents in the follow-up phase were assumed not to own any cats) and M is the average number of cats per household. M was taken as 1.43 for the pilot study area (Baker *et al.* 2005) and 1.56 for the nine 1-km² sites surveyed in 2005. The latter was the average number of cats per household based upon the responses of all cat-owners across all nine sites.

Predation rates

The numbers of animals killed annually were estimated for the pilot study area and four 1-km² sites (ST5277, ST5772, ST5876 and ST5974). Householders were asked to contact us each time a prey animal was killed so we could collect it for identification and necropsy where appropriate (see below); where prey were not collected and where we were not confident that the householder was able to identify the prey species accurately, animals were recorded as 'unidentified'. Householders on the pilot study site were asked to record the number of prey killed across four 3-month seasons within the period December 2002 to August 2004 (Baker *et al.* 2005); householders on the four other sites were asked to record the number of prey returned for a continuous 12-month period from August 2005 to July 2006 inclusive.

The number of prey animals returned was used to estimate the minimum (M_{MIN}) and maximum (M_{MAX}) number of animals killed at each site. Due to high levels of participant drop-out at each of the four sites surveyed from August 2005 to July 2006, it was necessary to estimate the number of prey animals that would have been returned if all householders had participated for the whole duration of the study. The minimum number of prey animals that would have been returned over the 12-month period at each of these sites was calculated as: $P_{\text{MIN}} = P \times (C_{\text{SURVEY}} \times 365) / N_{\text{SURVEY}}$, where P is the observed number of prey animals returned home, C_{SURVEY} is the total number of cats in the prey survey and N_{SURVEY} is the total number of cat-days that the animals were followed during the study period. The maximum number of prey animals that would have been returned was calculated as: $P_{\text{MAX}} = P \times (C_{\text{KILLED}} \times 365) / N_{\text{KILLED}}$, where C_{KILLED} is the number of cats in the prey survey that returned ≥ 1 prey and N_{KILLED} is the total number of cat-days that the animals that returned ≥ 1 prey were followed during the study period. Minimum and maximum numbers killed on each survey site

were then estimated as: $M_{\text{MIN}} = P_{\text{MIN}} / C_{\text{SURVEY}} \times 3.3 \times D$ and $M_{\text{MAX}} = P_{\text{MAX}} / C_{\text{KILLED}} \times 3.3 \times D$, where D is total cat density at each site and 3.3 is a conversion factor to account for the fact that only 30% of prey killed are returned home (after Kays & DeWan 2004). The minimum and maximum number of prey killed in each 3-month survey period on the pilot study area were calculated without having to correct for participant drop-out, and summed to estimate numbers killed annually (Baker *et al.* 2005).

The minimum (K_{MIN}), intermediate (K_{INT}) and maximum (K_{MAX}) numbers of individuals of each species killed in each survey square were estimated as: $K_{\text{MIN}} = M_{\text{MIN}} \times (S_{\text{I}}/P)$, $K_{\text{INT}} = M_{\text{MIN}} \times (S_{\text{R}}/P)$ and $K_{\text{MAX}} = M_{\text{MAX}} \times (S_{\text{R}}/P)$, where S_{I} is the number of individuals of a given species that were positively identified and S_{R} is the number of individuals of a given species estimated to have been returned home after redistributing unidentified prey items amongst positively identified prey groups, assuming that they exactly mirrored the distribution of the identified prey. For example, if the cats in a given square had returned 18 dead birds consisting of 10 individuals of Species A, five individuals of Species B and three unidentified individuals, we would have used counts of 10 and 12, respectively, to represent S_{I} and S_{R} for Species A and counts of 5 and 6, respectively, to represent S_{I} and S_{R} for Species B. In redistributing unidentified prey, all unidentified mammals were assumed to be small rodents or insectivores (i.e. mice, voles and shrews) and all unidentified birds were assumed to be passerines.

Breeding bird density and productivity

Breeding bird density in selected 1-km squares has been measured annually in the city of Bristol for a number of years (e.g. Bland 2001) following the methodology of the British Trust for Ornithology's (BTO) Breeding Bird Survey (Gregory & Baillie 1998, Freeman *et al.* 2007). In each survey, two 1-km transects were walked early in the morning twice each year, first between 1 April and 15 May and then again before the end of June, with a minimum intervening period of 4 weeks. Surveyors were able to recognize species by sight and song. Counts for the number of birds in the nine 1-km squares centred on the pilot study and in each of the four sites used for estimating predation rates were obtained from R. Bland and J. Tully (pers. comm.). Bird density was estimated using DISTANCE (Buckland *et al.* 2001);

as this is a modified approach to the method employed for estimating density and productivity in our original analysis (Baker *et al.* 2005), we have recalculated the predation rates and impacts for the pilot study area in this paper. Surveyors recorded the number of individuals of each species within 100 m of a central transect line. Counts were then converted to densities using species-specific detection probabilities derived from a sample of 1-km squares in urban areas surveyed by the BTO (S. Newson pers. comm.). For all species, adult sex ratio was assumed to be 1 : 1.

Productivity was estimated by multiplying the number of breeding pairs, the number of broods raised per pair per annum and average brood size at fledging. Where possible, these data were obtained from studies of each species in suburban or urban habitats. Failing this, data were obtained from a national scheme that records nesting success across a broad range of habitats (www.bto.org); this will over-estimate species' productivity and under-estimate the impact of cat predation if the productivity of that species is typically lower in suburban and urban habitats. Productivity per breeding pair for the eight most common species predated by cats during the study is outlined in Table 1. The minimum (K_{MIN}), intermediate (K_{INT}) and maximum (K_{MAX}) number of birds killed in each survey square was divided by the density of breeding adults (A) and/or juveniles (J) to derive an estimate of the minimum (I_{MIN}), intermediate (I_{INT}) and maximum (I_{MAX}) potential impact of cat predation for each bird species at each site as follows: $I_{\text{MIN}} = K_{\text{MIN}}/(A + J)$, $I_{\text{INT}} = K_{\text{INT}}/J$ and $I_{\text{MAX}} = K_{\text{MAX}}/A$. A value > 1 indicates that the number of birds killed by cats exceeded the total pre-breeding density of adult

birds (I_{MAX}), the total density of fledged young (I_{INT}) or the combined density of adults and juveniles (I_{MIN}), respectively.

Physical condition of birds killed by cats

The physical condition of passerines killed by cats was compared with that of birds of the same species killed by a collision accident, e.g. with a window or car within the city of Bristol (i.e. in addition to those sites outlined above) between July 2005 and July 2006. The latter are considered 'random' causes of mortality and are more representative of the potential prey population as a whole (Møller & Erritzoe 2000). Only carcasses that were not damaged were included in analyses. Age (adult or juvenile: Svensson 1994), season of death, body mass to the nearest 1 g, wing length (mm), fat reserves measured on scale of 0–5, cross-sectional shape of pectoral muscle mass on a three-point scale (Gosler 1991, Gosler *et al.* 1998), primary and secondary moult score (Ginn & Melville 2000), and degree of asymmetry of the tarsometatarsus and 8th and 9th primary feathers were recorded for each individual. All measurements were taken blind with respect to the source of mortality.

Asymmetry was recorded as the signed difference between the measurements of the right and left sides ($R - L$). The possible effect of measurement error on asymmetry estimates (Palmer & Strobeck 1986) was quantified using 10 birds (five randomly chosen from each source of mortality) using a mixed-model ANOVA with individual, side (left or right) and repeats (five repeated measurements per side per bird) as factors. Asymmetry estimates were significantly repeatable

Table 1. Summary of available estimates of brood size and number of broods per year used to calculate pair-wise production of fledged young each year for each species.

Species	Brood size	Broods per year	Fledged juveniles per year	Source(s)
House Sparrow <i>Passer domesticus</i>	2.6	2.3	6.0	1, 2
Dunnock <i>Prunella modularis</i>	1.8	2.0	3.6	3
Blue Tit <i>Cyanistes caeruleus</i>	6.0	1.0	6.0	2, 4
Great Tit <i>Parus major</i>	4.3	1.0	4.3	2, 5
Common Blackbird <i>Turdus merula</i>	–	–	3.8	6
Starling <i>Sturnus vulgaris</i>	3.4	1.5	5.1	2, 7
Robin <i>Erithacus rubecula</i>	4.5	2.0	9.0	8
Wren <i>Troglodytes troglodytes</i>	3.1	1.0	3.1	2, 9

¹Brood size – Siriwardena and Crick (2002a); ²broods per year – www.bto.org; ³Davies (1992); ⁴brood size – average of 5.8 (Cowie & Hinsley 1987) and 6.2 (Perrins 1965); ⁵brood size – average of 4.2 (Perrins 1965) and 4.3 (Cowie & Hinsley 1987); ⁶average of 3.5 (Batten 1973) and 4.1 (Snow 1958; Lack 1966); ⁷brood size – Siriwardena and Crick (2002b); ⁸brood size and broods per year – www.bto.org; ⁹brood size – Garson (1980).

for the tarsus ($F_{9,72} = 3.051$, $P < 0.01$) and primary wing feathers ($F_{9,72} = 143.79$, $P < 0.001$). Consequently, the mean value of the five repeated asymmetry measurements was then calculated for each trait for each individual. Anderson–Darling tests and one-sampled t -tests against a mean of zero were used to examine the distribution of the data and determine the type of asymmetry; in contrast to directional asymmetry and anti-symmetry, fluctuating asymmetry data display an approximately normal distribution of signed asymmetry ($R - L$) scores around a mean of zero (Møller & Swaddle 1997). Although asymmetry data departed from normality for a number of traits (Appendix 1), visual inspection of the data suggested this was because the data were leptokurtic with a high frequency of values near the mean, which is consistent with fluctuating asymmetry (Palmer & Strobeck 1992, Palmer 1994, Leung & Forbes 1997). The relationship between trait asymmetry and trait size was examined using linear regression; no significant relationship was found for tarsus length ($r_{129}^2 = 0.031$, $P = 0.069$) or length of primary wing feathers ($r_{129}^2 = 0.006$, $P = 0.374$). As there was no relationship between absolute degree of fluctuating asymmetry and mean trait size, there was no need to scale these data for trait size (Cuthill *et al.* 1993, Swaddle *et al.* 1994).

Non-parametric tests were used to compare differences in individual characteristics between predated birds and those killed following a collision. Analyses were initially conducted on the full dataset to determine whether potentially confounding factors (season of death, age, body size, body mass) had an effect on the dependent variables (body condition indices, degree of asymmetry). Because species with large sample sizes would dominate any pooled analysis, we took

the conservative approach of reducing data to means for each species and source of mortality, and then treating the species as the unit of analysis (Grafen & Hails 2002). The corresponding data for nine species (Common Blackbird *Turdus merula*, Dunnock *Prunella modularis*, Goldfinch *Carduelis carduelis*, Greenfinch *Carduelis chloris*, House Sparrow *Passer domesticus*, Robin *Erithacus rubecula*, Starling *Sturnus vulgaris*, Blue Tit *Cyanistes caeruleus*, Wren *Troglodytes troglodytes*) were analysed using a series of Wilcoxon matched-pairs signed-rank tests. Due to the large number of statistical tests performed, the overall level of significance was adjusted using the Dunn–Sidak procedure for multiple tests to control for Type I errors (Quinn & Keough 2002).

RESULTS

Of 16 500 questionnaires delivered, 2796 (17%) were collected (2203 original, 593 follow-up; Table 2). Mean (\pm sd) cat density was 348 ± 86 cats/km² or 26 ± 6 cats per 100 households (Table 2). A total of 275 cats from 186 households were included in the study on predation. Overall, 495 prey animals were returned (Table 3), including 309 individuals (62%) from eight mammal species and 92 individuals (19%) from 16 bird species; a further 19 (4%) and 27 (5%) unidentified mammals and birds were recorded, respectively. The most commonly taken species was the Wood Mouse *Apodemus sylvaticus*, which accounted for 53% of all returned prey. The most commonly taken passerines tended to be ground-foraging species such as House Sparrow, Robin, Dunnock and Common Blackbird. In the pilot study, 51–74% of cats surveyed in each season failed to return any prey (Baker *et al.*

Table 2. Summary of original and follow-up questionnaires used to estimate cat density in each of the 10 study sites (see text for details). Each location was a 1-km² Ordnance Survey grid square, except ST5676, which was a 4.2-km² area centred on this location.

Location	Original		Follow-up		Cat density (D) [cats per 100 households]
	Delivered (T_H) [returned (H_O)]	No. of houses with cats [no. of cats (C_O)]	Delivered [returned (H_F)]	No. of houses with cats [no. of cats (C_F)]	
ST5277 Avonmouth	1126 [96]	27 [37]	58 [43]	10 [12]	314 [28]
ST5676 Stoke Bishop	3494 [1027]	246 [353]	216 [216]	37 [52]	229 [28]
ST5768 Bishopsworth	1500 [174]	32 [59]	66 [39]	10 [13]	376 [25]
ST5772 Hotwells	1000 [110]	50 [73]	60 [35]	10 [19]	314 [31]
ST5876 Henleaze	1441 [294]	84 [127]	67 [53]	11 [13]	420 [29]
ST5878 Southmead	1992 [150]	38 [64]	53 [39]	6 [14]	396 [20]
ST5974 Montpelier	1488 [77]	28 [42]	63 [40]	7 [11]	290 [19]
ST6076 Lockleaze	1440 [105]	34 [54]	54 [43]	12 [22]	523 [36]
ST6174 Easton	1725 [117]	47 [74]	54 [38]	4 [7]	262 [15]
ST6272 St Annes	1294 [53]	18 [30]	60 [47]	10 [14]	354 [27]

Table 3. Summary of prey animals returned. *H* indicates the number of households contributing to data collection; *C* is the number of cats in these households. Each location was a 1-km² Ordnance Survey grid square, except ST5676, which was a 4.2-km² area centred on this location.

		ST5277	ST5676	ST5772	ST5876	ST5974	Total
Prey		<i>H</i> 18	89	24	36	19	186
		<i>C</i> 22	131	35	58	29	275
Mammals	Common Shrew <i>Sorex araneus</i>		2				2
	Pygmy Shrew <i>Sorex minutus</i>	1				1	2
	Water Shrew <i>Neomys fodiens</i>					1	1
	Grey Squirrel <i>Sciurus carolinensis</i>		4		1		5
	Wood Mouse <i>Apodemus sylvaticus</i>	16	168	28	18	30	260
	Bank Vole <i>Clethrionomys glareolus</i>		6			5	11
	Field Vole <i>Microtus agrestis</i>					1	1
	Brown Rat <i>Rattus norvegicus</i>	2	6	9		10	27
	Unidentified rodent	2	8	5		4	19
	Birds	House Sparrow <i>Passer domesticus</i>	2	14		3	1
	Dunnock <i>Prunella modularis</i>		6	3	1		10
	Blue Tit <i>Cyanistes caeruleus</i>		8				8
	Great Tit <i>Parus major</i>		1	1		2	4
	Coal Tit <i>Periparus ater</i>	1					1
	Common Blackbird <i>Turdus merula</i>		4		2	1	7
	Song Thrush <i>Turdus philomelos</i>		0			2	2
	Starling <i>Sturnus vulgaris</i>		3				3
	Robin <i>Erithacus rubecula</i>		12	2	2	1	17
	Wren <i>Troglodytes troglodytes</i>		3		1	1	5
	Redstart <i>Phoenicurus phoenicurus</i>	1					1
	Greenfinch <i>Carduelis chloris</i>				1		1
	Whitethroat <i>Sylvia communis</i>				1		1
	Magpie <i>Pica pica</i>	1			1		2
	Woodpigeon <i>Columba palumbus</i>	1	1		1		3
	Feral Pigeon <i>Columba livia</i>	1	3	2	1		7
	Unidentified bird	2	21	1	2	1	27
Other	Common Frog <i>Rana temporaria</i>		1	19			20
	Slow Worm <i>Anguis fragilis</i>			23		2	25
	Invertebrates			3			3
Total		30	271	96	35	63	495

Table 4. Estimates of the minimum and maximum numbers of prey killed each year on the four 1-km² sites surveyed August 2005–July 2006.

	ST5277	ST5772	ST5876	ST5974
No. of prey returned	30	96	35	63
No. of cats surveyed	22	35	58	29
No. of cat days	2276	6199	11850	4131
Minimum predation rate (prey per cat per year)	4.81	5.65	1.08	5.57
Cat density	314	314	420	290
Minimum no. of prey killed per year	4985	5857	1494	5327
No. of cats returning ≥ 1 prey	7	14	21	11
Adjusted no. of cat days	911	4288	8483	2493
Maximum predation rate (prey per cat per year)	12.02	8.17	1.51	9.22
Maximum no. of prey killed per year	12 455	8467	2087	8827

2005); in the four remaining sites, an average of 64% of the cats surveyed failed to return any prey (Table 4). These data indicate that, on average, predation was not observed in approximately 61% of the cats followed.

Estimated total minimum and maximum numbers of prey returned in the four sites surveyed during August 2005 to July 2006 are outlined in Table 4. The pre-breeding densities and estimated patterns of

Table 5. Estimated (a) number of breeding pairs and productivity (number of fledged young), (b) intermediate [minimum – maximum] number of individuals of eight passerine species killed by domestic cats and (c) the intermediate [minimum – maximum] impact scores (see text for details) on each of the five locations. Each location was a 1-km² Ordnance Survey grid square, except ST5676, which was a 4.2-km² area centred on this location. Estimated numbers of prey killed in ST5676 are taken from Baker *et al.* (2005).

(a) Breeding pairs and productivity

Location	House Sparrow	Dunnock	Blue Tit	Great Tit	Common Blackbird	Starling	Robin	Wren
ST5277	121 (724)	8 (29)	5 (30)	3 (13)	40 (152)	41 (209)	4 (36)	10 (31)
ST5676	42 (251)	15 (54)	17 (102)	7 (30)	25 (95)	3 (15)	25 (225)	12 (37)
ST5772	13 (78)	8 (29)	21 (126)	10 (43)	51 (194)	4 (20)	7 (63)	23 (71)
ST5876	115 (688)	10 (36)	17 (102)	4 (17)	41 (156)	42 (214)	10 (90)	13 (40)
ST5974	59 (353)	3 (11)	21 (126)	3 (13)	20 (76)	24 (122)	4 (36)	17 (53)

(b) Number of individuals killed

Location	House Sparrow	Dunnock	Blue Tit	Great Tit	Common Blackbird	Starling	Robin	Wren
ST5277	499 [332–1245]	–	–	–	–	–	–	–
ST5676	358 [245–378]	166 [107–438]	177 [131–475]	23 [16–53]	79 [62–238]	70 [49–162]	288 [202–670]	62 [47–169]
ST5772	–	214 [183–309]	–	71 [61–103]	–	–	142 [122–206]	–
ST5876	151 [128–211]	50 [43–70]	–	–	101 [85–141]	–	101 [85–141]	50 [43–70]
ST5974	95 [85–158]	–	–	190 [169–315]	95 [85–158]	–	95 [85–158]	95 [85–158]

(c) Impact scores

Location	House Sparrow	Dunnock	Blue Tit	Great Tit	Common Blackbird	Starling	Robin	Wren
ST5277	0.7 [0.3–5.1]	–	–	–	–	–	–	–
ST5676	1.4 [0.7–4.5]	3.1 [1.3–14.6]	1.7 [1.0–14.0]	0.8 [0.4–3.8]	0.8 [0.4–4.8]	4.7 [2.3–27.0]	1.3 [0.7–13.4]	1.7 [0.8–7.0]
ST5772	–	7.4 [4.1–19.3]	–	1.7 [1.0–5.2]	–	–	2.3 [1.6–14.7]	–
ST5876	0.2 [0.1–0.9]	1.4 [0.8–3.5]	–	–	0.6 [0.4–1.7]	–	1.1 [0.8–7.1]	1.3 [0.7–2.7]
ST5974	0.3 [0.2–1.3]	–	–	14.6 [8.9–52.5]	1.3 [0.7–4.0]	–	2.6 [1.9–19.8]	1.8 [1.0–4.6]

productivity for the eight most commonly taken passerine species, the minimum, intermediate and maximum numbers killed, and the minimum, intermediate and maximum impact scores across all five sites studied are outlined in Table 5. Mean adult and juvenile densities of these eight species alone were 367 ± 108 and 958 ± 309 birds/km², respectively. The mean (\pm sd) ratios of adults/cats and juveniles/cats across the five sites were 1.17 ± 0.23 and 3.07 ± 0.74 , respectively. Intermediate impact scores for all species except House Sparrows were > 0.6 in all squares where predation was observed for that species (Table 5c), indicating that the estimated number of birds killed was greater than half the estimated number of young produced. The estimated maximum impact was typically substantially greater than adult density.

Physical condition of birds killed by cats

Data from a total of 134 birds from 13 species were analysed, of which 86 and 48 had been killed by cats

and collisions, respectively. Across species, birds killed by cats had significantly lower mass, fat scores (Fig. 1) and pectoral muscle mass scores (Fig. 2). Conversely, there were no significant differences between predated and non-predated birds with respect to measures of fluctuating asymmetry (Table 6). Individuals in these groups did not differ significantly with respect to age, wing length or season of death (Table 6). Those species with a sample size sufficient for within-species analyses (Common Blackbird, Dunnock, House Sparrow, Robin, Starling), all showed the significantly lower mass, fat and muscle scores seen in the cross-species analyses (data not shown).

Analysing the whole pooled dataset, there was a significant association between season of death and pectoral muscle mass score ($H = 12.410$, $df = 2$, $P = 0.002$), being significantly higher in spring than the rest of the year. Age had no significant effect on pectoral muscle mass score ($U_{87,46} = -0.575$, $P = 0.565$), fat score ($U_{87,46} = -1.150$, $P = 0.250$), degree of asymmetry of 8th ($U_{87,46} = -1.001$, $P = 0.317$)

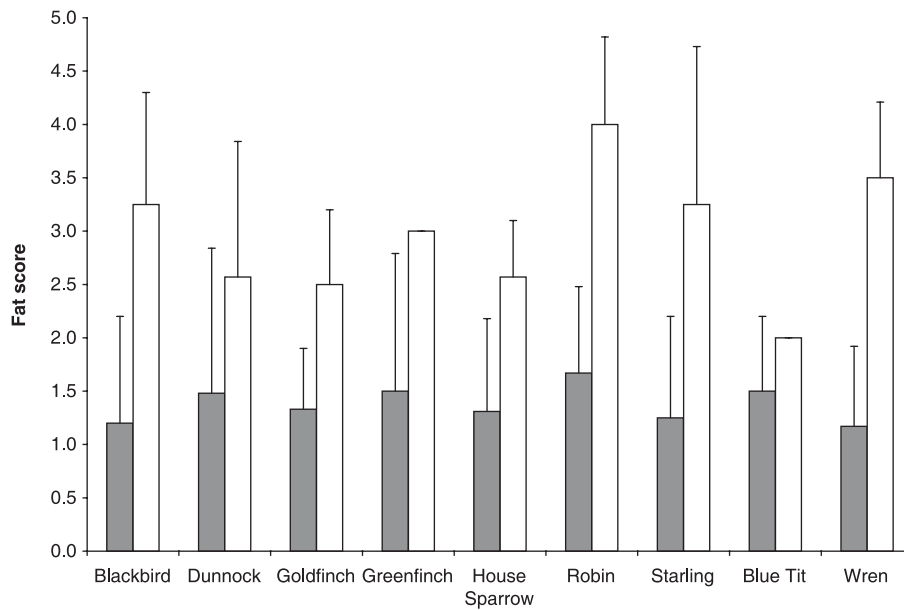


Figure 1. Mean (\pm se) fat score of species killed by cats (filled bars) and those killed following a collision accident (unfilled bars). Sample sizes for each species, respectively for predated and not predated, were: Common Blackbird (10, 12); Dunnock (21, 7); Goldfinch (3, 2); Greenfinch (4, 3); House Sparrow (16, 7); Robin (6, 4); Starling (7, 8); Blue Tit (5, 3); Wren (6, 2).

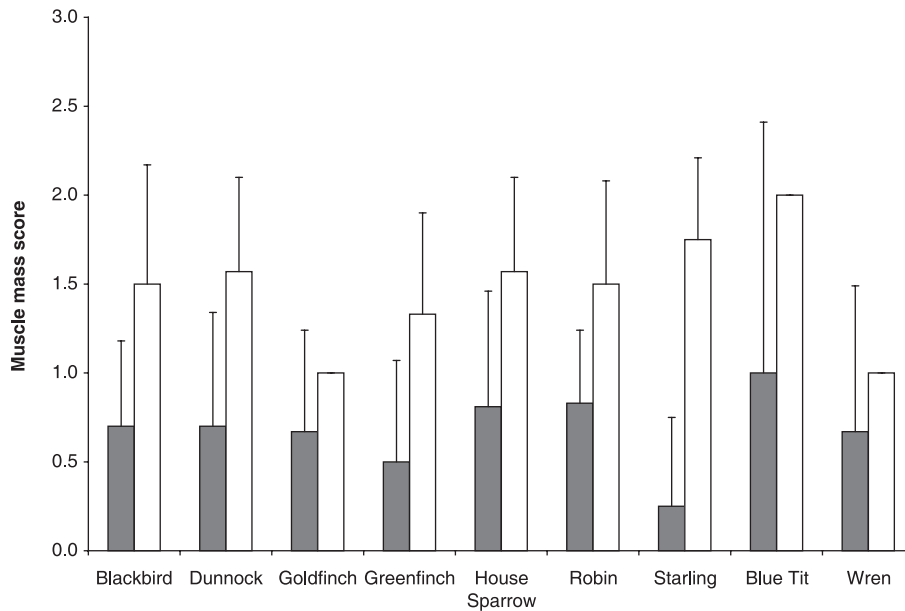


Figure 2. Mean (\pm se) pectoral muscle mass score of species killed by cats (filled bars) and those killed following a collision accident (unfilled bars). Sample sizes are given in Figure 1.

and 9th primary wing feather ($U_{87,46} = -0.795$, $P = 0.427$) or tarsus asymmetry ($U_{87,46} = -0.323$, $P = 0.747$). Nor was there any significant correlation between body size and pectoral muscle mass score ($r_s = 0.073$, $n = 131$, $P = 0.410$) or fat score ($r_s = 0.185$, $n = 131$, $P = 0.340$).

DISCUSSION

The density of cats recorded in this study (229–523 cats/km²) far exceeds the maximum density recorded for other urban carnivores in Britain, e.g. Red Fox *Vulpes vulpes* (37 adults/km²; Baker *et al.*

Table 6. Results of pair-wise comparisons of traits between birds killed by cats and those killed following a collision. Data are based on mean values for nine species: Common Blackbird, Dunnock, Goldfinch, Greenfinch, House Sparrow, Robin, Starling, Blue tit, Wren. Figures are mean \pm sd. *W* is the statistic from Wilcoxon matched-pairs signed-ranks tests.

Variable	Birds killed by cats	Birds killed following collision	Mean difference	Median difference	<i>W</i>	<i>P</i>
Absolute tarsal asymmetry (mm)	0.6 \pm 0.4	0.3 \pm 0.2	0.3 \pm 0.3	0.2	35	0.021
Absolute asymmetry of 8th primary feather (mm)	1.4 \pm 0.9	1.4 \pm 1.1	0.0 \pm 0.4	0	8	1.000
Absolute asymmetry of 9th primary feather (mm)	1.6 \pm 0.8	1.6 \pm 1.1	0.0 \pm 0.6	0	12	0.800
Fat score (0–5)	1.4 \pm 0.2	3.0 \pm 0.6	–1.6 \pm 0.6	–1.5	0	0.009*
Pectoral muscle mass score (0–3)	0.7 \pm 0.2	1.5 \pm 0.3	–0.8 \pm 0.4	–0.8	0	0.009*
Wing length (mm)	80.1 \pm 27.3	83.2 \pm 30.2	–3.1 \pm 3.7	–1.8	6.5	0.066
Age	1.4 \pm 0.3	1.4 \pm 0.3	0.0 \pm 0.4	0.1	23.5	0.953*
Body mass (g)	29.3 \pm 27.0	36.3 \pm 33.6	–7.0 \pm 6.8	–4.5	0	0.009*
Season	2.1 \pm 0.2	2.0 \pm 0.6	0.1 \pm 0.7	–0.1	27	0.636

*Test is significant after sequential Bonferroni correction to retain a table-wide Type I error rate $P < 0.05$.

2001), Eurasian Badger *Meles meles* (7.5 adults/km²; Harris 1984, Harris & Creswell 1987). As a result, the ratio of the density of the eight most commonly taken bird species to cat density was very small (means of 1.17 adults and 3.07 juveniles per cat, respectively). These figures are broadly comparable with those observed in 30 1-km² urban areas surveyed by Sims *et al.* (2008) across Britain, although these authors considered all potential prey species and not just the eight listed in the current study. It is easy to envisage therefore that individual cats would not have to kill many prey each year in order to exert a substantial effect on the dynamics of local bird populations within urban areas.

The potential impact of cat predation (*I*) was estimated in this study according to the general form: $I = [C \times K \times (1/F)]/D$, where *C* is an estimate of cat density, *K* is an estimate of the number of each prey species killed by each cat based on the analysis of the prey returned home by a subset of individuals, *F* is the proportion of prey killed that are returned home, and *D* is an estimate of the density and/or productivity of the bird species in question. Given the simple form of this equation, it is straightforward to determine the directional sensitivity of *I* to changes in the magnitude of each parameter, e.g. a doubling of the estimated density of birds would halve the impact score, whereas a doubling of the estimated number of prey killed per cat would double the impact score. An increase in the proportion of prey returned home would, conversely, lower the estimated impact.

Our estimates of both *C* and *K* are implicitly dependent on the assumption that we randomly sampled the population of householders and their cats in each area. The two-tier approach adopted for

estimating cat density was specifically designed to (1) account for the fact that cat owners may have been unwilling to participate in the study and (2) obtain an estimate of minimum cat density. For example, all extrapolations to houses that did not provide any information were based only on those data obtained during the follow-up phase, where > 50 householders were selected at random and contacted door-to-door; any householder in this phase who did not provide information (because they were not at home when we attempted to contact them) was assumed not to own any cats. Computer simulations to estimate the sampling effort required to estimate cat abundance accurately in urban areas have indicated that 50 households is sufficient for this purpose across a broad range of cat densities (Sims *et al.* 2008). Furthermore, the assumption that non-respondents in the follow-up phase did not own any cats would have had the effect of under-estimating cat density if these householders did own pets.

Recruiting participants into studies is susceptible to non-random sampling. For example, cat owners whose pets were killing lots of birds may have wished to hide the fact; alternatively, they may have been keen to show off their cat's prowess. From conversations with householders, it was clear that both of these influences were present, although the relative importance of each is not known. Owners whose cats consistently do not return any prey home may also have been less likely to volunteer, as they may view this information as unimportant. Given that our objective was to estimate minimum predation rates, the inclusion of such cats was of paramount importance. Consequently, we explicitly requested the assistance of these owners at the outset of the

study; overall > 60% of cats in the study never returned any prey, such that we believe we are justified in treating the estimates of the numbers of prey killed as minimum estimates. Furthermore, predation rates were derived only from animals returned home dead, although additional animals were also frequently brought home alive and released by householders; it is likely that many of these would not have survived the trauma of being captured. The only unambiguous way to address the possible sampling biases outlined would have been to compare the kill rates of cats whose owners volunteered from the outset versus those of cats whose owners agreed to participate only after further discussion, although enlisting the help of sufficient numbers of the latter is likely to be problematic.

To date, only one published study has attempted to calculate the proportion of prey returned home (Kays & DeWan 2004). In that study, the authors radiotracked cats living in suburbs bordering a nature reserve in the USA, and attempted to observe directly the number of kills made that were delivered home versus the number eaten or left *in situ*. Given the disparity in the habitats and bird communities in Kays and DeWan's (2004) study versus the current study, further investigation into the validity of the estimated proportion of prey returned home is warranted. This will pose particular problems in urban areas in Britain, as cats are out of sight for the majority of time. One possible solution may be the use of activity data loggers that are able to identify patterns of hunting and consumption from body posture and movement (Watanabe *et al.* 2005). In addition, there is the need to consider the likelihood that species of different size are more or less likely to be returned. This possible disparity between species could also extend to differences in the return rate of adults versus juveniles within a species.

Intermediate and maximum estimates of the number of each species killed were based upon both identified and unidentified prey animals, the latter being redistributed in direct proportion to the distribution of species observed in the identified sample. The soundness of this approach is dependent on whether householders are considered likely to have been able to identify common species or not. Although we attempted to collect all dead animals, 27 of 119 birds killed (23%) were disposed of by householders before they could be identified. From discussions with participants and notes left with carcasses, it was readily evident that many householders were not able to distinguish even common species, particularly as many were juvenile individuals. Therefore, we

believe it is reasonable to assume that unidentified specimens are more likely to consist of common rather than rare prey species, although we would reiterate that every attempt should be made to collect all dead animals. With the advent of digital cameras and email, animals could easily be identified remotely.

Maximum estimates of the number of each species killed were derived by assuming that those cats that did not return any prey home were killing equivalent numbers of prey to those cats that did. This was clearly not realistic, as the estimated maximum numbers of birds killed typically exceeded breeding density and productivity combined, such that the prey populations studied would probably have gone extinct rapidly at a local level or acted as a major sink for birds immigrating from neighbouring areas. This does not preclude, however, that these cats were not preying on birds to some degree. Given their frequency in the population (> 60% in the sample of cats studied), limited predation by these animals could markedly increase estimates of the number of animals killed. As for other individuals, their predatory behaviour (or lack of it) could be investigated using data loggers (Watanabe *et al.* 2005). Alternatively, stable isotope analysis may enable the consumption of prey animals away from their owner's home to be identified.

Obtaining estimates of bird density in urban areas using DISTANCE sampling is problematic, as much of the available habitat is out of sight behind buildings. Consequently, the estimates of breeding density presented in this manuscript should be regarded as minima. Under-estimating breeding density will tend to over-estimate the impact of cat predation. At present there is no obvious means by which estimates of urban bird densities could easily be improved, although increased sampling effort using point counts within the whole spectrum of habitats is likely to generate better estimates of minimum density. It is also clear that there are relatively few studies on the breeding performance of birds in urban areas, such that the veracity of the values used to estimate annual productivity is not known.

Overall, therefore, our estimates of the numbers of birds killed by cats in this study are based upon several factors, each of which is subject to error. Although the effect of an increase or decrease in any one of these factors will clearly increase or decrease the estimates of the number of birds killed, the magnitude of such errors is not known, such that all these factors require further investigation. Consequently, the

results of this study should be treated as provisional. Despite these caveats, it appears that, for some species in some areas, the number killed by cats is large relative to density and productivity. Dunnocks, Robins and Wrens appear particularly susceptible to cat predation; in over half the sites studied, the estimated number killed exceeded the number of juveniles fledged (Table 5c). A similar pattern was also evident for House Sparrows, Blue Tits, Common Blackbirds, Great Tits and Starlings on some sites. Under these circumstances, the persistence of these local populations would be heavily dependent on immigration from other areas. Furthermore, even in those sites where such significant impacts were not evident, cat predation was still frequently estimated to be equivalent to 20–40% of the total number of adults and juveniles combined, suggesting that it is a major cause of mortality throughout urban areas.

The impact of cat predation is, however, very dependent on whether it is an additive or compensatory form of mortality. Those birds killed by cats in this study had significantly lower fat and pectoral muscle mass scores than those killed by collisions, but there was no significant difference between these two groups in measures of asymmetry. The differences in fat and muscle mass are consistent with the notion that cats were killing poorer quality individuals that would have been likely to die from other causes, i.e. cat predation was mainly compensatory.

However, the relationship between body mass and quality (i.e. likelihood of long-term survival and therefore reproductive potential) in passerines is complex. For example, poor physical condition can affect prey vulnerability directly by reducing an individual's ability to detect and escape from predators (Mesa *et al.* 1994) or indirectly because it may lead to compensatory foraging or other risk-prone behaviours (McNamara & Houston 1987, 1990, McNamara *et al.* 1994, Sinclair & Arcese 1995). Body condition is likely to have a significant effect on predator evasion ability in passerines due to the energetic constraints of flight (Witter & Cuthill 1993). Both fat reserves and muscle condition are integral to flight performance (Gosler & Harper 2000), but whilst fat is an important source of energy, the costs associated with its transport mean that greater reserves may increase predation risk by affecting take-off, velocity and manoeuvrability (Witter & Cuthill 1993, Witter *et al.* 1994, Lind *et al.* 1999). Consequently, dominant and/or better-quality individuals, which may be predicted to have greater access to food resources, may be more likely to reduce fat reserves to maximize flight performance.

Under this hypothesis, the low fat reserves observed in the birds killed by cats in this study could indicate that they were more likely to be breeding individuals, such that cat predation would represent an additive form of mortality. Furthermore, fat reserves fluctuate during daylight hours, tending to be lowest in the morning and increasing towards the evening as birds are not able to forage during the night (Witter & Cuthill 1993, McNamara *et al.* 1994, Thomas & Cuthill 2002). As predation on birds may be highest at dawn (Barratt 1997), when fat reserves are lowest, this again implies that our results could be indicative of an additive effect of cat predation.

Interpretation of these results is therefore problematic. Comparisons of the absolute magnitude of reserves may, however, indicate whether observed fat deposits in cat-killed birds are likely to reflect long- or short-term variations that do or do not reflect a reduced likelihood of survival, respectively; the mean fat scores evident in the cat-killed birds in the current study (Fig. 2) were sufficiently low that these individuals were likely to have had poor long-term survival prospects. The distinction between compensatory and additive mortality does, however, become increasingly redundant as the number of birds killed in a given area increases: where large numbers of prey are killed, predators would probably be killing a combination of individuals with poor and good long-term survival chances. The predation rates estimated in this study would suggest that this was likely to have been the case for some species on some sites. These populations would therefore be reliant on immigration from neighbouring areas to sustain them, leading to source–sink dynamics. Such dynamics could be quantified through intensive studies of individual species within urban areas, but are unlikely to be evident from correlations between bird density and cat density, given that the latter is typically very high (Sims *et al.* 2008).

In summary, there is evidence that cat predation is potentially a significant mortality factor for some localized populations of some species of birds in urban landscapes. Furthermore, as over half of the cats in the current study never returned any prey home, the documented number of prey killed are, in general terms, likely to represent minimum levels of predation. However, there are limitations associated with relying on prey returned home by free-ranging pet cats to estimate the numbers of individual species killed. Future studies must therefore incorporate alternative methodologies to overcome these limitations. Similarly, improved sampling strategies

to estimate breeding density and better estimates of the productivity of breeding birds in urban areas are also warranted. Additional attention must also be focused on whether cat predation is additive or compensatory to other forms of mortality. The only unequivocal way to address this question is by experimentally manipulating cat predation pressure, although this will undoubtedly be logistically difficult. Last, studies of individual species are required to ascertain whether cat predation impacts local populations to the degree that these become 'sinks' for immigrating individuals, and how source and sink populations are inter-connected in the wider urban landscape and neighbouring rural landscapes. It is clear therefore that a great deal of further research is necessary to understand fully the impacts of cats, and other predators, in urban landscapes.

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Appendix 1. Distributional characteristics of (unsigned) asymmetry data.

Group	Trait	N	Mean R-L	SE	Skew	Kurtosis	A-squared ¹	t ²
Predated	Tarsus length	85	−0.709	1.213	−9.500	−3.700	4.792	−5.327
	Length of 8 th primary feather	85	0.879	2.177	0.136	5.566	5.796	3.680
	Length of 9 th primary feather	85	1.132	1.680	0.149	−1.061	2.528	6.140
Collision	Tarsus length	48	0.073	0.500	−1.200	1.083	3.200	1.031*
	Length of 8 th primary feather	48	1.240	2.511	0.932	−5.500	3.745	3.491
	Length of 9 th primary feather	48	0.020	1.708	1.579	2.022	4.524	0.083*

¹ Test statistics from Anderson-Darling tests for normality.

² Test statistics from one-sample t-test: * denotes $P > 0.05$.