Mammal Rev. 2005, Volume 35, No. 3&4, 302–312. *Printed in Singapore.*

Impact of predation by domestic cats *Felis catus* in an urban area

PHILIP J. BAKER, AMY J. BENTLEY, RACHEL J. ANSELL and STEPHEN HARRIS
School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

ABSTRACT

1. As companion animals, domestic cats *Felis catus* can attain very high densities, and have the potential to exert detrimental effects on prey species. Yet, there is a paucity of information on the impact of cat predation in urban areas, where most cats are likely to be present.
2. We quantified the minimum number of animals killed annually by cats in a 4.2-km^2 area of Bristol, UK, by asking owners to record prey animals returned home by their pets. The potential impact of cat predation on prey species was estimated by comparing the number of animals killed with published estimates of prey density and annual productivity.
3. Predator density was 229 cats/km^2.
4. Five mammal, 10 bird and one amphibian prey species were recorded. Mean predation rate was 21 prey/cat/annum. The most commonly recorded prey species was the wood mouse *Apodemus sylvaticus*.
5. Predation on birds was greatest in spring and summer, and probably reflected the killing of juvenile individuals. For three prey species (house sparrow *Passer domesticus*, dunnock *Prunella modularis*, robin *Erithacus rubecula*), estimated predation rates were high relative to annual productivity, such that predation by cats may have created a dispersal sink for juveniles from more productive neighbouring areas. The impact of cats on these species therefore warrants further investigation.

Keywords: conservation, feral cat, house cat, hyperpredation, urban ecology

INTRODUCTION

Hyperpredation is the process whereby one prey species exerts an indirect effect on a second species by causing an increase in the abundance of a common shared predator. For vertebrates, this process has generally been considered in the context of the detrimental impact of introduced wild animals on endemic species (e.g. Courchamp, Langlais & Sugihara, 1999, 2000; Roemer *et al*., 2001). However, similar effects may arise where the predator is a domestic or companion animal of humans, with human provisioning of food analogous to the role of the primary prey species (see also Kristan & Boarman, 2003). Furthermore, because of their reliance on artificial food sources, predator abundance may substantially surpass the carrying capacity of the environment, such that the impact of predation may be severe, even though artificial food may reduce individual predation rates. The most widespread example of such a system is that of the domestic cat *Felis catus*.

Cat populations exhibit varying degrees of dependence on humans. Truly, feral populations live completely independently of humans, whereas urban colonies, farm colonies and stray cats are generally reliant in part on people for food. However, in many developed countries,

Correspondence: P. J. Baker. E-mail: p.j.baker@bristol.ac.uk

the largest fraction probably comprises free-ranging pet or house cats that are regularly fed by their owners. In the UK, there are estimated to be around 813 000 feral (Harris *et al.*, 1995) and eight million pet cats (Cats Protection League, 1993).

Individual pet cats vary considerably in the degree to which they predate wild animals, with most probably taking few or no prey (Churcher & Lawton, 1987; Barratt, 1997, 1998; Robertson, 1998; Ruxton, Thomas & Wright, 2002). Collectively, however, cat populations may kill very large numbers of prey. For example, Woods, McDonald & Harris (2003) estimated that pet cats in Britain killed 52–63 million mammals, 25–29 million birds and 4–6 million reptiles and amphibians during a 5-month survey period. However, despite the fact that large numbers of prey are certainly taken, the impact of predation on prey populations is equivocal (e.g. Barratt, 1997, 1998), and is dependent on the degree to which cat predation is additive or compensatory to other sources of mortality.

With the continued expansion of urban areas into rural habitats, the importance of cat predation as an ecological factor is potentially increasing. Urban areas currently occupy up to 10% of the total land area of Britain and Ireland (Haines-Young *et al.*, 2000), with around 6000 ha of rural land converted to urban use in Britain annually (Department of Environment, Food and Rural Affairs, 2003). For a number of bird species, urban populations comprise a substantial component of the total national population (Bland, Tully & Greenwood, 2004), including some that are of conservation concern, e.g. house sparrow *Passer domesticus*, starling *Sturnus vulgaris*. Conversely, cat predation may be beneficial where pest species, such as common rat *Rattus norvegicus* and house mouse *Mus domesticus*, are taken.

At present, there are few data on the pattern and extent of predation by domestic cats in Britain (but see Howes, 2002; Woods *et al.*, 2003), in particular for urban areas where most cats are likely to be present. For example, approximately 70% of UK inhabitants live in settlements of > 10 000 residents (2001 UK National Census, Office for National Statistics, http://www.statistics.gov.uk), although the distribution of cats is unlikely to exactly mirror the distribution of humans as patterns of pet ownership are likely to be influenced by where people live. Therefore, we undertook a questionnaire survey of householders within north-west Bristol, UK, to (i) quantify cat density and (ii) quantify the number of prey killed, by asking cat owners to record prey animals returned home during each of four survey periods. The potential impact of predation was then estimated by comparing annual predation rates with published estimates of prey density and productivity.

METHODS

A questionnaire was delivered to all 3494 householders in a 4.2-km^2 area in north-west Bristol during October – December 2002. This is an area of predominantly semidetached housing built during the interwar years, but also comprises regions of private flats, terraced and detached housing, and council housing; other major habitats include sports fields, woodland, churchyards and a cemetery (see Harris, 1981). The questionnaire requested: the number of pet cats owned; each cat's sex and age; whether they had been neutered; whether they wore an antipredation device (bell, sonic emitter); whether they were typically allowed out during the day only, during the night only or during both the day and night; and to estimate the approximate number of birds, mice/voles and amphibians/reptiles that each cat brought home each month. Finally, each owner was asked whether he/she would assist with the study by keeping a simple diary recording the prey items the cat(s) brought home.

We initially asked householders to leave the completed form on their doorstep on a given day for collection (hereafter termed 'original' questionnaires). Following this, a subset of householders that failed to return the form were then contacted door-to-door and asked to complete the form ('follow-up' questionnaires). In all analyses, original and follow-up questionnaires were first compared to determine if the two data sets were statistically different. In those cases where differences were detected, the mean values from the follow-up questionnaires were used to extrapolate the responses of non-respondents, assuming that follow-up questionnaire results were more representative of non-respondents.

All cat owners who stated that they would keep a diary were contacted and asked to record the number of dead and living prey items brought in by their pet(s) during 5 December 2002 – 13 January 2003 (winter: $n = 40$ days), 28 April – 1 June 2003 (spring: $n = 35$ days), 4 October – 2 November 2003 (autumn: $n = 30$ days) and 24 July – 31 August 2004 (summer: $n = 39$ days) inclusive. Householders were asked to report all dead animals brought in by their cat(s) so that they could be collected for identification: prey recorded as, e.g. 'mouse' or 'small bird', and not identified by us, were classified as unidentified. Sampling periods were spaced out throughout the year in an attempt to reduce participant dropout. At the end of each sampling period, non-respondents were contacted up to five times in an attempt to minimize biases arising from, for example, the disproportionate loss of owners whose cats failed to return any prey during the sampling period. Where possible, owners were asked to identify which cat brought in each prey item.

Estimating predation rates

The potential impact of cat predation on prey populations was estimated by comparing the minimum, intermediate and maximum number of animals killed annually with published estimates of prey abundance and productivity. Predation rates were based only on those animals returned home dead. Minimum predation rates in each season were calculated as the total number of identified dead prey returned divided by the total number of cats in the survey period. Intermediate and maximum predation rates were derived by first classifying unidentified prey, assuming that they exactly mirrored the distribution of identified prey. It is possible that householders were most likely to be able to identify common prey species, such that unidentified prey would have tended to consist of other less common species: redistributing these less readily identified prey would therefore have the effect of elevating true rates of predation on common species. Alternatively, householders may have simply been unable to identify species generally, in particular juvenile birds: in this case, redistributing unidentified prey would reflect rates of predation on common species. Unidentified mammal and bird remains were redistributed among identified small mammal and passerine categories (i.e. excluding grey squirrel *Sciurus carolinensis* and columbiforms). Intermediate predation rates were then calculated by dividing the number of dead prey returned by the total number of cats. Maximum predation rates were calculated by dividing the number of dead prey returned by the total number of cats that returned ≥ 1 prey, including instances where, for example, only one prey was recorded for a household containing two cats. All predation rates were then multiplied by a factor of 3.3: Kays & DeWan (2004) recorded a return rate of 1.67 prey/cat/month ($n = 12$ cats) using a similar approach to that adopted in the current study, compared with a kill rate of 5.54 prey/cat/month for 11 radio-collared cats whose hunting behaviour was observed directly. The number of prey killed annually per unit area (km^2) was then calculated by multiplying the predation rate in each corresponding survey period by 91 days and summing across the year.

Potential impact of cat predation

Pre-breeding small mammal density was derived from the adjusted density estimates for woodland (9% of study area), scrub (24%), gardens of semidetached houses (20%) and gardens of detached houses (8%) quoted by Dickman & Doncaster (1987): data quoted for semidetached houses and woodlands were utilized to estimate density in the gardens of terraced houses (5%) and allotment gardens (1%), as these habitats appear comparable (Ansell, 2004). All other habitats were assumed to be unproductive. Grey squirrel density was taken as 0.1/ha (Harris *et al*., 1995). Common rat density was estimated assuming that 13% of households were infested (Langton, Cowan & Meyer, 2001), with a mean of 2.2 rats per infestation (Harris *et al*., 1995).

Maximum productivity was estimated from the length of the breeding season divided by the length of each breeding attempt (gestation plus lactation) multiplied by average litter size (Corbet & Harris, 1991), i.e. ignoring any effect of density on the proportion of females breeding. For rats, it was assumed that 30% of breeding females produced a maximum of five litters throughout the year (Corbet & Harris, 1991): this is equivalent to each female producing 1.5 litters/year.

Breeding bird density in the City of Bristol has been measured annually in selected 1 km squares as part of the British Trust for Ornithology's Breeding Bird Survey for a number of years, and during 2001, over 58% of the city was surveyed (Bland, 2001). In each survey square, two 1-km transects were walked early in the morning twice each year, first between 1 April – 15 May, and then again at least 4 weeks later before the end of June. Surveyors were able to recognize species by sight and song. Average densities of species in the nine 1 km squares centred on the study site (OS grid co-ordinate: 356176) were obtained from R. Bland and J. Tully (personal communication). Productivity was estimated by multiplying prey density by the number of broods raised and average brood size at fledging (http://www.bto.org). For both birds and mammals, the pre-breeding population sex ratio was assumed to be equal.

The minimum impact of cat predation was calculated by dividing the minimum number of animals killed by the sum of pre-breeding density and productivity. As the number of offspring produced annually typically exceeds the size of the pre-breeding density, maximum impact was calculated by dividing the maximum number of animals killed by pre-breeding density alone. Intermediate impacts (ranging from smallest to largest) were calculated by dividing the intermediate number of animals killed by pre-breeding density and productivity combined, productivity alone and pre-breeding density alone, respectively. In all cases, we have assumed that live individuals rescued by owners and released would have survived.

RESULTS

Overall, 1243 questionnaires (36%) were collected (1027 original, 216 follow-up). There was a significant difference between the proportion of 'original' (24%) and 'follow-up' (17%) respondents owning cats ($\chi^2_1 = 4.64$, $P < 0.05$). Assuming that the same proportion of non-respondents on the study site owned cats as in the follow-up survey, it was estimated that 674 householders (19%) owned cats on the study site. There was no significant difference between original and follow-up respondent cat owners with respect to the mean number of cats they owned (Mann–Whitney test: $W = 4458.5$, $N_1 = 246$, $N_2 = 37$, NS; mean = 1.43 cats/household). Overall, cat density was 229 cats/km^2, with a total population of 962 cats (28 cats per 100 households).

Eighty-nine householders ($n = 131$ cats) participated in data collection, although not all householders collected data in all seasons. Overall, 271 dead and 87 living prey items were recorded (Table 1). The most commonly recorded prey species was the wood mouse *Apodemus sylvaticus*, accounting for 62% and 82% of records of dead and living prey, respectively. Estimated intermediate predation rates for each season were: spring, 1348 prey/km^2; summer,

Table 1. Summary of prey items brought home

Species	Spring ($n = 121$ cats) ($n = 81$ houses) ($n = 35$ days)		Summer ($n = 92$ cats) ($n = 63$ houses) ($n = 39$ days)		Autumn ($n = 102$ cats) ($n = 72$ houses) ($n = 30$ days)		Winter ($n = 117$ cats) ($n = 80$ houses) ($n = 40$ days)		Total ($n = 131$ cats) ($n = 89$ houses) ($n = 144$ days)	
	Dead	Living	Dead	Living	Dead	Living	Dead	Living	Dead	Living
Mammals										
Common shrew *Sorex araneus*	2 [2.3]	0	0 [0.0]	0	0 [0.0]	0	0 [0.0]	0	2	0
Grey squirrel *Sciurus carolinensis*	0 [0.0]	0	0 [0.0]	0	2 [2.0]	0	2 [2.0]	0	4	0
Wood mouse *Apodemus sylvaticus*	28 [32.1]	14	54 [54.0]	25	51 [51.9]	17	35 [36.9]	15	168	71
Bank vole *Clethrionomys glareolus*	1 [1.1]	0	5 [5.0]	0	0 [0.0]	0	0 [0.0]	0	6	0
Common rat *Rattus norvegicus*	3 [3.4]	1	1 [1.0]	0	1 [1.0]	1	1 [1.1]	1	6	3
Unidentified rodent	3 –	1	0 –	0	0 –	0	1 –	0	4	1
Unidentified mammal	2 –	0	0 –	0	1 –	0	1 –	0	4	0
Birds										
House sparrow *Passer domesticus*	8 [11.4]	3	6 [9.0]	0	0 [0.0]	0	0 [0.0]	1	13	4
Dunnock *Prunella modularis*	4 [5.7]	0	1 [1.5]	0	1 [2.0]	0	0 [0.0]	0	2	0
Blue tit *Parus caeruleus*	3 [4.3]	0	2 [3.0]	0	0 [0.0]	0	3 [3.4]	0	8	0
Great tit *Parus major*	1 [1.4]	0	0 [0.0]	0	0 [0.0]	0	0 [0.0]	0	1	0
Blackbird *Turdus merula*	2 [2.8]	0	0 [0.0]	0	0 [0.0]	0	2 [2.3]	0	4	0
Starling *Sturnus vulgaris*	3 [4.3]	0	0 [0.0]	0	0 [0.0]	0	0 [0.0]	0	1	0
Robin *Erithacus rubecula*	8 [11.4]	0	3 [4.5]	0	0 [0.0]	0	1 [1.1]	0	7	0
Wren *Troglodytes troglodytes*	2 [2.8]	0	0 [0.0]	0	0 [0.0]	0	1 [1.1]	0	3	0
Wood pigeon *Columba palumbus*	0 [0.0]	0	0 [0.0]	0	0 [0.0]	0	1 [1.0]	0	1	0
Feral pigeon *Columba livia*	0 [0.0]	0	1 [1.0]	0	2 [2.0]	0	0 [0.0]	0	3	0
Unidentified bird	13 –	4	6 –	2	1 –	0	1 –	0	33	6
Herpetofauna										
Common frog *Rana temporaria*	1 [1.0]	2	0 [0.0]	0	0 [0.0]	0	0 [0.0]	0	1	2
Total	84 [84.0]	25	79 [79.0]	27	59 [59.0]	18	49 [49.0]	17	271	87

Data in square brackets indicate revised seasonal totals after redistribution of unidentified prey remains (see text for details).

1514 prey/km^2; autumn, 1324 prey/km^2; and winter, 720 prey/km^2 (Table 2). This was equivalent to an annual rate of 4906 prey/km^2 or 21 prey/cat/annum. However, in all seasons, the majority of cats (57%, 51%, 73% and 74%, respectively) did not return any dead prey (Table 2). Pre-breeding prey abundance and productivity is summarized in Table 3, and the potential impact on prey populations is outlined in Table 4.

Fifty-two households, containing 77 cats, recorded data in all four seasons. Collectively, these returned 212 dead prey items, an average of 2.8 prey items per cat in the sampling periods ($n = 144$ days) or 7.0 prey/cat/annum. There was no significant difference between seasons in the predation rate per household for this subsample (Friedman test: $\chi^2_3 = 5.64$, $P > 0.05$), although a large number of these households had zero rates for three ($n = 9$ households) or four ($n = 17$) seasons.

DISCUSSION

The intermediate predation rate observed in this study (21 prey/cat/annum) was at the low end of the spectrum reported in similar previous studies in the UK (14 – Churcher & Lawton, 1987; 28.9 – Howes, 2002; 71.7 – Ruxton *et al.* (2002), based on an average of 5.5 prey per cat in a sampling period of 28 days; and 27.0 – Woods *et al*. (2003), based on an average of 11.3 prey per cat in a sampling period of 153 days), principally because in each sampling period, the majority of cats (51–74%) failed to return any prey. However, there are a number of problems inherent with drawing direct comparisons between studies.

First, the predation rates determined in this study were most reliant on cat density, as this parameter had the greatest magnitude (229 cats/km^2). We adopted a two-sampling protocol to adjust for the fact that cat owners may have been more likely to leave the original questionnaire on the doorstep as requested. Yet, the follow-up survey could still have overestimated cat density if some householders were more likely to have been absent when we called and these absent householders were less likely to own cats. However, given that the major demographic groupings on the study site were pensioners and middle-class families with children of school age, and given that we attempted to contact residents both during the day and in the evening, it is our opinion that the magnitude of any bias against non-cat-owning households is likely to be minimal.

Second, recruiting participants into surveys is also susceptible to biases. For example, owners whose cats kill large numbers of prey may be over-represented if owners are keen to demonstrate their pet's hunting prowess and/or if owners of cats that kill very few or no prey consider that such information is not important. We attempted to control for this problem by including a section on the original questionnaire asking householders to estimate the approximate number of prey that each of their cats brought home each month. These data could then have been used to estimate whether the composition of participating owners was biased towards cats that tended to bring large numbers of prey home (which would have overestimated the true pattern of predation) or that tended to bring no prey home (which would have underestimated predation rates). Unfortunately, the vast majority of cat owners did not answer this question or gave information that could not be readily quantified. Consequently, we considered this comparison unreliable. Yet, it must be noted that the majority of cats in each survey period did not bring home any prey, and that half of the households providing year-round data had zero counts in three or four seasons, indicating that the estimated predation rates are not likely to be excessive in magnitude. This is particularly true if cats that did not return any prey were actually taking prey (see below). Predation rates would also be higher if, as seems probable, some live prey individuals rescued by owners subsequently perished.

Table 2. Estimated minimum (min.), intermediate (int.) and maximum (max.) seasonal predation rates (prey killed per km^2)

Species	Spring			Summer			Autumn			Winter			Annual intermediate predation rate (minimum–maximum)
	Min. ($n = 121$)	Int. ($n = 121$)	Max. ($n = 52$)	Min. ($n = 92$)	Int. ($n = 92$)	Max. ($n = 45$)	Min. ($n = 102$)	Int. ($n = 102$)	Max. ($n = 28$)	Min. ($n = 117$)	Int. ($n = 117$)	Max. ($n = 30$)	
Mammals													
Common shrew	32	37	87	0	0	0	0	0	0	0	0	0	37 (32–87)
Grey squirrel	0	0	0	0	0	0	45	45	164	29	31	120	76 (74–284)
Wood mouse	455	521	1213	1035	1035	2116	1146	1166	4249	514	542	2115	3265 (3150–9692)
Bank vole	16	18	42	96	96	196	0	0	0	0	0	0	114 (112–237)
Common rat	49	55	128	19	19	39	22	22	82	15	16	63	113 (105–313)
Birds													
House sparrow	130	185	431	115	172	353	0	0	0	0	0	0	358 (245–783)
Dunnock	65	93	215	19	29	59	22	45	164	0	0	0	166 (107–438)
Blue tit	49	70	162	38	57	118	0	0	0	44	50	195	177 (131–475)
Great tit	16	23	53	0	0	0	0	0	0	0	0	0	23 (16–53)
Blackbird	32	45	106	0	0	0	0	0	0	29	34	132	79 (62–238)
Starling	49	70	162	0	0	0	0	0	0	0	0	0	70 (49–162)
Robin	130	185	431	57	86	176	0	0	0	15	16	63	288 (202–670)
Wren	32	45	106	0	0	0	0	0	0	15	16	63	62 (47–169)
Wood pigeon	0	0	0	0	0	0	0	0	0	15	15	57	15 (15–57)
Feral pigeon	0	0	0	19	19	39	45	45	164	0	0	0	64 (64–203)
Total	1055	1348	3136	1399	1514	3096	1281	1324	4822	676	720	2808	4906 (4412–13862)

Minimum predation rates were determined by dividing the number of identified prey by the total number of cats in each season. Maximum predation rates were determined by dividing the total number of dead prey (unidentified prey redistributed in accordance with distribution of identified prey) by the number of cats returning ≥1 prey in each season. Intermediate rates were determined by dividing the total number of dead prey by the total number of cats in each survey period. Figures in brackets indicate the number of cats used in each calculation. Rates were then multiplied by a factor of 3.3 to account for the proportion of prey killed that was returned home (see text for details). Each season was assumed to last 91 days. Note that subtotals for minimum estimates excluded unidentified prey and are therefore not true totals.

Table 3. Estimated patterns of prey density and productivity (see text for details)

Species	Pre-breeding density (prey/km^2)	Productivity (young per year)		
		Litter/brood per year	Litter/brood size	Annual production
Mammals				
Common shrew	1382	3.8	6.0	15 755
Grey squirrel	100	1.6	3.0	240
Wood mouse	2051	5.1	5.5	28 770
Bank vole	623	4.6	3.6	5 162
Common rat	238	1.5	7.5	1 338
Birds				
House sparrow	120	2.5	2.84	426
Dunnock	50	2.0	3.67	184
Blue tit	120	1.0	7.50	450
Great tit	60	1.0	6.56	197
Blackbird	180	2.5	3.36	756
Starling	60	1.5	3.86	174
Robin	80	2.0	4.50	360
Wren	100	1.0	5.16	258

Table 4. Comparison of the minimum (m), intermediate (I) and maximum (M) predation rates (Table 2) with pre-breeding prey abundance (A) and productivity (P) (Table 3)

Species	Predation rate (prey/km^2/year)	Impact				
		Minimum	Intermediate			Maximum
		{m/(A + P)}	{I/(A + P)}	{I/P}	{I/A}	{M/A}
Mammals						
Common shrew	37 (32–87)	<0.01	<0.01	<0.01	0.03	0.06
Grey squirrel	76 (74–284)	0.22	0.22	0.32	0.76	2.84
Wood mouse	3265 (3150–9692)	0.10	0.11	0.11	1.59	4.73
Bank vole	114 (112–237)	0.02	0.02	0.02	0.18	0.38
Common rat	113 (105–313)	0.07	0.07	0.08	0.48	1.31
Birds						
House sparrow	358 (245–783)	0.45	0.65	0.84	2.98	6.53
Dunnock	166 (107–438)	0.46	0.71	0.91	3.33	8.76
Blue tit	177 (131–475)	0.23	0.31	0.39	1.48	3.96
Great tit	23 (16–53)	0.06	0.09	0.12	0.38	0.88
Blackbird	79 (62–238)	0.07	0.08	0.10	0.44	1.32
Starling	70 (49–162)	0.21	0.30	0.40	1.16	2.71
Robin	288 (202–670)	0.46	0.65	0.80	3.59	8.38
Wren	62 (47–169)	0.13	0.17	0.24	0.62	1.69

Third, studies of cat predation are drawn from different habitats with different prey bases, such that predation rates of cats in rural areas with increased levels of available prey may be substantially higher (e.g. Howes, 2002). The relatively small number of prey species taken during this study is consistent with the reduction in species' diversity typically observed in urban areas, where communities tend to consist of a small number of synanthropic species tolerant of human activities, but which may be very abundant (Luniak, 2004). In high-density predator populations, such as in this study, individuals may also be restricted to small home ranges (Kays & DeWan, 2004), thereby reducing the range of prey they can encounter and their impact, but which may enhance localized effects (see Baker *et al.*, 2003).

Last, the method utilized implicitly assumes that the rate at which prey is returned home is consistent across populations, yet the magnitude of any difference between populations is unknown. In this study, we have utilized a conversion factor of 3.3 to estimate the actual number of prey killed, based on the work of Kays & DeWan (2004). To the best of our knowledge, this is the only study that has managed to quantify this parameter. Consequently, there is the need for additional studies to determine the consistency of this estimate. Furthermore, attention must also be paid to cats that fail to return any prey home; the assumption that these individuals had not killed anything would have significantly underestimated predation rates if they were taking prey.

Impact of cat predation

Minimum predation rates were moderately high for three species: house sparrow (predation equivalent to 45% of the combined total of pre-breeding density and annual productivity), dunnock (46%) and robin (46%: Table 4). In these species, intermediate predation rates were equivalent to 80–91% of productivity alone and 65–71% of the combined total of pre-breeding density and annual productivity. Such losses are likely to be non-trivial and warrant further investigation, in particular whether cat predation is additive or compensatory to other forms of mortality.

The difference in magnitude of these estimates is dependent on the treatment of unidentified prey remains. Minimum rates were derived solely from identified prey items, whereas intermediate rates were estimated from both identified and unidentified prey remains under the assumption that unidentified prey consisted of the same species, and in the same relative abundance, as those that had been identified. We believe that this was likely to be true since the majority of unidentified prey probably related to predation on juvenile birds in spring and summer, which householders were unlikely to be able to identify even if they were common species. The assumption of identical distributions is less clear, and future studies should therefore aim to recover all carcasses for positive identification.

The house sparrow has previously been identified as potentially vulnerable to the impact of cat predation (Churcher & Lawton, 1987), and is typically the most common avian species taken in UK studies (Howes, 2002; Woods *et al*., 2003; but see Mead, 1982). Nationally, this species is declining in urban areas (Siriwardena, Robinson & Crick, 2002), but numbers appear to be stable in Bristol as a whole (J. Tully, personal communication). However, given that house sparrow distribution is highly heterogeneous and that the study site was an area of low density (Bland, 1998), it is possible that cat predation was significantly affecting levels of recruitment and creating a dispersal sink for more productive neighbouring areas: similar effects may also have been evident for robins and dunnocks. Consequently, we would recommend quantification of age-specific patterns and rates of mortality, predation and dispersal in these species.

Overall, therefore, the levels of predation by individual cats observed in this study were towards the lower end of rates quantified in previous studies, yet direct comparisons between studies are difficult. Collectively, despite occurring at very high densities, the summed effects on prey populations appeared unlikely to affect population size for the majority of prey species. This may be attributable to selection for prey species that have successfully adapted to the urban environment, including the predation pressure exerted by cats. However, for three species there was evidence that the impact of cat predation may be significant. Consequently, the overall impact of predation by domestic cats in urban areas warrants further investigation, including: (i) consideration of prior species' loss in the formation of current urban animal communities; (ii) the use of manipulative experiments and/or comparative studies to quantify the effects of reduced predation pressure on prey population growth; (iii) quantifying the relative importance of cat predation within the guild of mammalian and avian predators present in urban areas; and (iv) monitoring of the relative importance of cat predation in different urban habitats and over time.

ACKNOWLEDGEMENTS

We would like to express our gratitude to: Philippa Bulman, Eve Jackson, Louise Jasper, Fiona Strouts, Stephanie Thein and members of the general public for help in collecting the data; Richard Bland and John Tully for providing data on bird densities; and Stuart Newson and colleagues at the British Trust for Ornithology for help in identifying bird carcasses.

REFERENCES

Ansell, R.J. (2004) The spatial organization of a red fox (*Vulpes vulpes*) population in relation to food resources. Unpublished PhD Thesis, University of Bristol, Bristol.

Baker, P.J., Ansell, R.J., Dodds, P.A.A., Webber, C.E. & Harris, S. (2003) Factors affecting the distribution of small mammals in an urban area. *Mammal Review*, **33**, 95–100.

Barratt, D.G. (1997) Predation by house cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. *Wildlife Research*, **24**, 263–277.

Barratt, D.G. (1998) Predation by house cats, *Felis catus* (L.), in Canberra, Australia. II. Factors affecting the mount of prey caught and estimates of the impact on wildlife. *Wildlife Research*, **25**, 475–487.

Bland, R.L. (1998) House sparrow densities in Bristol. *Avon Bird Report 1998*, 145–148.

Bland, R.L. (2001) The survey of breeding birds of Bristol – 2001. *Avon Bird Report 2001*, 154–157.

Bland, R.L., Tully, J. & Greenwood, J.J.D. (2004) Birds breeding in British gardens: an underestimated population? *Bird Study*, **51**, 97–106.

Churcher, P.B. & Lawton, J.H. (1987) Predation by domestic cats in an English village. *Journal of Zoology*, **212**, 439–455.

Corbet, G.B. & Harris, S. (1991) *The Handbook of British Mammals*, 3rd edn. Blackwell Scientific Publications, Oxford.

Courchamp, F., Langlais, M. & Sugihara, G. (1999) Control of rabbits to protect island birds from cat predation. *Biological Conservation*, **89**, 219–225.

Courchamp, F., Langlais, M. & Sugihara, G. (2000) Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology*, **69**, 154–164.

Department of Environment, Food and Rural Affairs (2003) *DEFRA Digest of Environmental Statistics*. Available at: http://www.defra.gov.uk/environment/statistics/des/land.

Dickman, C.R. & Doncaster, C.P. (1987) The ecology of small mammals in urban habitats. I. Populations in a patchy environment. *Journal of Animal Ecology*, **56**, 629–640.

Haines-Young, R.H., Barr, C.J., Black, H.I.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M.T., Gillespie, M.K., Hill, R., Hornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A.P., Stuart, R.C. & Watkins, J.W. (2000) *Accounting for Nature: Assessing Habitats in the UK Countryside*. Department of the Environment, Transport and the Regions, London.

Harris, S. (1981) An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *Journal of Applied Ecology*, **18**, 455–465.

Harris. S., Morris, P., Wray, S. & Yalden, D. (1995) *A Review of British Mammals: Population Estimates and Conservation Status of British Mammals other than Cetaceans.* Joint Nature Conservation Committee, Peterborough.

Howes, C.A. (2002) Red in tooth and claw: 2. Studies on the natural history of the domestic cat *Felis catus* Lin. in Yorkshire. *Naturalist*, **127**, 101–130.

Kays, R.W. & DeWan, A.A. (2004) Ecological impact of inside/outside house cats around a suburban nature preserve. *Animal Conservation*, **7**, 273–283.

Kristan, W.B. & Boarman, W.I. (2003) Spatial pattern of risk of common raven predation on desert tortoises. *Ecology*, **84**, 2432–2443.

Langton, S.D., Cowan, D.P. & Meyer, A.N. (2001) The occurrence of commensal rodents in dwellings as revealed by the 1996 English House Condition Survey. *Journal of Applied Ecology*, **38**, 699–709.

Luniak, M. (2004) Synurbization – adaptation of animal wildlife to urban development. In: *Proceedings of the 4th International Symposium on Urban Wildlife Conservation, May 1–5 1999* (Ed. by W.W. Shaw, L.K. Harris & L. VanDruff), pp. 50–55. University of Arizona, Tucson, Arizona.

Mead, C.J. (1982) Ringed birds killed by cats. *Mammal Review*, **12**, 183–186.
Robertson, I.D. (1998) Survey of predation by domestic cats. *Australian Veterinary Journal*, **76**, 551–554.
Roemer, G.W., Coonan, T.J., Garcelon, D.K., Bascompte, J. & Laughrin, L. (2001) Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation*, **4**, 307–318.
Ruxton, G.D., Thomas, S. & Wright, J.W. (2002) Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of Zoology*, **256**, 81–83.
Siriwardena, G.M., Robinson, R.A. & Crick, H.Q.P. (2002) Status and population trends of the house sparrow *Passer domesticus* in Great Britain. In: *Investigation into the Causes of the Decline of Starlings and House Sparrows in Great Britain* (Ed. by H.Q.P. Crick, R.A. Robinson, G.F. Appleton, N.A. Clark, & A.D. Rickard), pp. 33–52. BTO, Thetford.
Woods, M., McDonald, R.A. & Harris, S. (2003) Predation of wildlife by domestic cats *Felis catus*. Great Britain. *Mammal Review*, **33**, 174–188.

Submitted 8 February 2005; returned for revision 11 May 2005; revision accepted 1 July 2005
Editor: RM