

Predation of wildlife by domestic cats *Felis catus* in Great Britain

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ABSTRACT

1. A questionnaire survey of the numbers of animals brought home by domestic cats *Felis catus* was conducted between 1 April and 31 August 1997. A total of 14 370 prey items were brought home by 986 cats living in 618 households. Mammals made up 69% of the items, birds 24%, amphibians 4%, reptiles 1%, fish <1%, invertebrates 1% and unidentified items 1%. A minimum of 44 species of wild bird, 20 species of wild mammal, four species of reptile and three species of amphibian were recorded.

2. Of a sample of 696 individual cats, 634 (91%) brought home at least one item and the back-transformed mean number of items brought home was 11.3 (95% CI 10.4–12.2). The back-transformed means and number of cats retrieving at least one item from each prey group were: 8.1 (7.4–8.9) mammals for 547 (79%) cats, 4.1 (3.8–4.5) birds for 506 (73%) cats, 2.6 (2.2–3.0) herpetofauna for 145 (21%) cats and 2.2 (1.8–2.7) other items for 98 (14%) cats.

3. The number of birds and herpetofauna brought home per cat was significantly lower in households that provided food for birds. The number of bird species brought home was greater in households providing bird food. The number of birds and herpetofauna brought home per cat was negatively related to the age and condition of the cat. The number of mammals brought home per cat was significantly lower when cats were equipped with bells and when they were kept indoors at night. The number of herpetofauna brought home was significantly greater when cats were kept in at night.

4. Based on the proportion of cats bringing home at least one prey item and the back-transformed means, a British population of approximately 9 million cats was estimated to have brought home in the order of 92 (85–100) million prey items in the period of this survey, including 57 (52–63) million mammals, 27 (25–29) million birds and 5 (4–6) million reptiles and amphibians.

5. An experimental approach should be taken to investigate the factors found by this descriptive survey to influence the numbers of prey brought home by cats. In particular, investigation of potential management practices that could reduce the numbers of wild animals killed and brought home by cats will be useful for wildlife conservation, particularly in suburban areas.

Keywords: Felidae, feral cat, house cat, pest management, urban ecology, wildlife conservation

INTRODUCTION

Domestic cats *Felis catus* are the most abundant carnivores in Great Britain and their numbers appear to be growing. In 1981, the national population of cats was estimated to be 6 million (UFAW, 1981). In 1993, the Cats Protection League estimated that approximately 25% of British households owned at least one cat and that the national population was approximately 7.6 million. This was predicted to increase to 8 million by 2000 (Cats Protection League, 1993). A more recent estimate supported this predicted increase and estimated that there were 7.8 million cats in 1998 (Turner & Bateson, 2000). In addition, a minimum of 813 000 cats are estimated to live in a feral or semi-wild state mainly in rural areas and a further unknown number of cats have only loose associations with domestic households in urban areas (Harris *et al.*, 1995). It therefore seems likely that the total cat population in Britain in 2003 is in the region of 9 million. By comparison to native carnivores, this is nearly 20 times the estimated pre-breeding populations of stoats and weasels and 38 times the estimated pre-breeding population of foxes *Vulpes vulpes* (Harris *et al.*, 1995).

Most domestic cats depend on food supplied by their owners. Therefore, their populations are not limited by the availability of wild prey. Cats frequently kill wild animals and the combined impact of predation by millions of cats may have a substantial effect on wildlife. This prospect has previously been highlighted by several authors (Churcher & Lawton, 1987; May, 1988; Barratt, 1997, 1998). The recent rapid declines seen in British populations of many farmland and garden birds (Mead, 2000), and the increasing importance of gardens for a range of small birds (Mead, 2000), has led to renewed concern over the potential impact of cat predation on bird populations. However, experimental evaluations of the impact of cat predation on wildlife remain scarce and assessments of factors that might mitigate any such impact often lead to public controversy, arising from concern about the welfare of cats (May, 1988; Proulx, 1988; Fitzgerald, 1990; Jarvis, 1990).

Churcher & Lawton (1987) calculated that in a single English village, cats were responsible for up to 30% of mortality in a house sparrow population and concluded that domestic cats were a major predator in a typical English village. They found that the average cat caught and brought home approximately 14 prey items over the 12 months of their survey. May (1988) extrapolated from this figure and suggested that about 100 million wild birds and small mammals could be killed by 6 million cats every year in Britain. Mead (1982) ascribed 31% of recoveries of ringed robins and dunnocks to cat predation, but believed that there was no evidence that cats affected the overall populations of these species. Sharing this view, Fitzgerald (1988) and Fitzgerald & Turner (2000) asserted that on continental landmasses, wildlife had co-evolved with cats for hundreds of generations and that any species that were susceptible to predation would be 'long extinct'. It has also been argued that in many situations cats may limit populations of other predators, such as rats *Rattus* spp., that could have a more pronounced effect on wildlife (Fitzgerald, 1990; Fitzgerald, Karl & Veitch, 1991). However, while cats may eat *Rattus* spp., larger individuals of one of the most damaging rat species *Rattus norvegicus* are often avoided since they are hard to handle (Childs, 1986). Most authors do agree, however, that wildlife on oceanic islands is likely to be particularly susceptible to the impact of predation by cats. A particularly well-known example is that of the Stephens Island wren *Xenicus lyalli*, the entire population of which was eliminated by a single cat belonging to the island's lighthouse keeper (Oliver, 1955). Likewise, the Socorro dove *Zenaida graysoni* has also been driven to extinction primarily by cats (Jehl & Parks, 1983). Similarly, mammalian species such as hutias *Geocapromys* spp. have been exterminated from several Caribbean islands as the result of predation by cats (Fitzgerald, 1988).

Previous investigators of predation of wildlife by cats have frequently taken advantage of their habit of bringing back their prey to their owners' houses. Owners have been asked to record the species caught and the date it was retrieved or have retained the prey animal and given it to investigators for identification (Borkenhagen, 1978; Howes, 1982; Churcher & Lawton, 1987; Barratt, 1997, 1998). Similarly, but working at a smaller scale, Carss (1995) recorded the captures of his own two domestic cats over two periods of 2 years. There are several qualifications for the use of this method to describe the killing behaviour of cats, as opposed to alternatives such as analysing faeces or gut contents (reviewed by Fitzgerald, 1988; Fitzgerald & Turner, 2000). Qualifications include the following: the prey brought home by cats should be representative of the total and variety of prey they actually kill; cats belonging to households participating in the survey should exhibit behaviour representative of the killing behaviour of cats in general; cat owners should be competent and honest recorders of the items their cats bring home. Unfortunately, for logistical reasons, these qualifications have usually remained untested. Nevertheless, the participation of cat owners is the only logistically feasible method of investigating cat predation of a range of species at a large scale.

Since it seems unlikely that trends in cat ownership and numbers in Britain will reverse, non-invasive measures that could be taken to reduce the number of animals killed by cats, while avoiding public concern for cat welfare, could be useful from a conservation perspective. For this study, a large-scale descriptive survey was conducted of the animals brought home by domestic cats living in Britain. We investigated factors influencing predation rates and which might be the focus of experimental work to evaluate strategies for minimizing the numbers of wild animals killed by cats.

The scientific names for prey species mentioned in this paper are provided in the Appendix and follow Arnold & Burton (1978), Chinery (1989), Corbet & Harris (1991) and Cramp (1994).

METHODS

The methods applied during this survey were based on the work of Churcher & Lawton (1987) and Barratt (1997, 1998). A survey was conducted by The Mammal Society between 1 April and 31 August 1997. Participants were recruited through Society membership and appeals through the national media, including radio, newspapers and magazines. Forms were sent out to approximately 1400 households. Cat owners were asked to record in as much detail as possible the prey items brought home by each cat in their ownership. Where several cats lived in the same house, it was not always possible to separate the items brought home by individual cats. In these cases, records were included in our basic description of prey items, but were omitted from statistical analysis, which was based on households that could assign all retrieved items to individual cats. In common with previous investigators, we have assumed that the numbers of prey brought home by the cats was closely related to the numbers and variety of prey they actually kill. We have also assumed that the cat owners participating in the survey were representative, competent and honest recorders of the items their cats brought home. The validity and consequences of these assumptions are discussed below.

The following information was recorded by each household: the total number of cats in the household, whether the householders provided food for birds, the county of residence and the residence type. Counties were classified into five regions of England (north, midlands, south east, south west and East Anglia), Scotland and Wales. Because of small sample sizes, households from Ireland and the Channel Islands were excluded from statistical analysis. Residence types were: detached house (a multi-storey house with garden on up to four sides),

semi-detached house (a house attached to one other and with garden on up to three sides), terraced house (predominantly urban housing that is adjoined on both sides and with usually small garden to front and rear only), bungalow (a single storey detached house with surrounding garden) and flat. For each cat the owners recorded: age, sex, condition (on a qualitative scale of 1 = thin to 3 = fat), whether the cat wore a bell and whether it was allowed out at night or kept indoors.

Prey items were grouped by taxonomic class and order where possible. In some cases, householders were unable to identify the prey remains brought home by their cat at all and these items were omitted from statistical analysis and were included only in total counts of prey items brought home (Appendix). Statistical analyses were conducted first on the numbers of birds, mammals and herpetofauna (reptiles and amphibians) and then on the numbers of bird and mammal species brought home by each cat. Counts of prey and prey species were $\log_{10}(n + 1)$ transformed and cat ages were $\sqrt{(n + 0.375)}$ transformed to improve their approximation to normality (Zar, 1996). Four analyses of covariance (ANCOVA) were conducted. The first investigated the factors associated with the household that influenced the numbers of animals brought home by cats to the house. Region, residence type and the provision of bird food were factors and the total number of cats in the household was a covariate. The second ANCOVA investigated the factors associated with individual cats that influenced the numbers of animals they brought home. This analysis considered only the cats that lived in households with no other cats. This was in order to avoid possible pseudoreplication (Hurlbert, 1984) arising from similar conditions being applied to several cats living in one household. Sex, allowing the cat out at night and equipping the cat with a bell were factors and the age and condition of the cat were covariates. Both of these analyses included cats that did not bring home any animals, that is, zero counts. These analyses were then repeated, but with the number of bird and mammal species brought home as the dependent variables and the total number of birds and mammals brought home as an additional covariate, to control for the effect of predation rate on species range. In this case, since the identification of species clearly required at least one animal to have been brought home, these analyses included only cats that had brought home at least one bird or mammal. Few herpetofauna were identified to species and the range of species was small, hence analysis of the number of species was not undertaken. Interaction terms were initially included in both analyses but were removed if found not to be significant and the analyses were rerun. No statistical analysis was made of other prey groups. Residuals from the ANCOVAs were checked for normality. Adjusted group means, corrected for covariates, of significant factors from ANCOVAs were compared using the Bryant-Paulson-Tukey test with Kramer's modification for unequal sample sizes (Bryant & Paulson, 1976; Day & Quinn, 1989).

To estimate the order of magnitude of the total numbers of animals that may be brought home by cats in Britain, we first estimated the population of cats likely to bring home prey of each group. This was achieved by multiplying the estimated cat population, here taken to be 9 million, by the proportion of this sample that brought home at least one of each prey type. Then, for all the cats that did bring home at least one of each prey category, we calculated the mean and 95% CI of the log-transformed data. The number of prey animals brought home by all cats in Britain was then estimated by multiplying the estimated population of cats that retrieved that prey type by the back-transformed means and the associated, asymmetric 95% confidence limits. In order to be sure of the CI for this estimate, it was derived from the records from households where all prey items were assigned to individual cats, rather than the returns from households where the kills of several cats could not be distinguished.

RESULTS

The survey received prey records from 618 of the 1400 (44%) households (Table 1). A total of 14 370 prey items were brought home by 986 cats (Table 2). A minimum of 20 species of wild mammal, 44 species of wild bird, four species of reptile and three species of amphibian were recorded (Appendix). The numbers of prey items brought home was recorded for 696 individual cats living in 506 households (Table 3). The frequency distribution of the numbers of animals brought home by each cat was markedly skewed (Fig. 1). For 467 cats that brought home mammals that could be identified to species, the mean number of species brought home was 2.4 (95% CI 2.2–2.5, range 1–9). For 475 cats that brought home birds that could be identified to species, the mean number of species brought home was also 2.4 (95% CI 2.3–2.6, range 1–10). There was a significant but weak relationship between the number of mammal species and the number of bird species brought home by cats that brought home at least one identifiable species of mammal or bird ($r_s = 0.121$, $n = 277$, $P < 0.05$). The number

Table 1. Location and residence type of the 618 households responding to the survey. Households in the Channel Islands and Ireland were excluded from statistical analyses because of small sample sizes

Region	Detached	Semi-detached	Terraced	Bungalow	Flat	Unknown	Total
South east	45	41	28	12	6	41	173
East Anglia	17	23	4	9	2	11	66
South west	30	13	13	13	0	21	90
Midlands	35	27	7	6	0	13	88
North	39	28	19	11	2	26	125
Scotland	15	13	0	4	1	14	47
Wales	9	3	3	0	1	6	22
Ireland	3	1	0	0	0	1	5
Channel Islands	1	0	0	0	0	0	1
Unknown	0	0	0	0	0	1	1
Total	194	149	74	55	12	134	618

Table 2. Prey items, grouped by taxon, that were brought home by 986 cats in 618 households. For a more detailed list of prey items see the Appendix

Class/order	Total	%	Class/order	Total	%	Class/order	Total	%
Mammalia	9852	68.6	Reptilia	144	1.0	Arachnida	9	0.1
Insectivora	1852	12.9			1.0			
Chiroptera	30	0.2	Amphibia	590	4.1	Crustacea	1	<0.1
Carnivora	17	0.1	Anura	568	3.9			
Rodentia	6369	44.3	Urodela	22	0.2	Gastropoda	6	<0.1
Lagomorpha	1243	8.6	Osteichthyes	31	0.2			
Unidentified mammal	341	2.4			0.2	Oligochaeta	21	0.1
Aves	3391	23.6	Insecta	134	0.9			
Anseriformes	6	<0.1	Coleoptera	4	<0.1	Unidentified	191	1.3
Charadriiformes	1	<0.1	Dermaptera	1	<0.1	Total	14370	100.0
Columbiformes	147	1.0	Diptera	6	<0.1			
Galliformes	21	0.1	Hymenoptera	7	0.2			
Passeriformes	2698	18.8	Lepidoptera	84	<0.1			
Piciformes	2	<0.1	Odonata	25	0.6			
Ralliformes	9	0.1	Orthoptera	7	<0.1			
Unidentified bird	507	3.5						

Table 3. Summary of prey items brought home by 696 individual cats

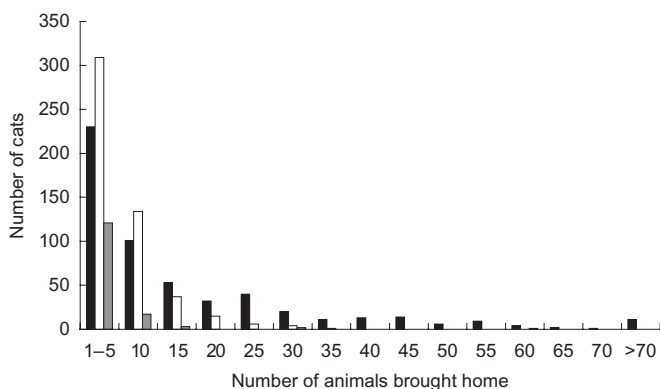
Prey group	Mammals	Birds	Herpetofauna	Other items§	Total
Total	7837	2809	549	342	11537
Average items per cat*	11.3	4.0	0.8	0.5	16.6
Maximum	139	35	56	64	151
Number of cats bringing home at least one item from that prey group (%)	547 (78.6)	506 (72.7)	145 (20.8)	98 (14.1)	634 (91.1)
Back-transformed mean (95% CI)†	8.1 (7.4–8.9)	4.1 (3.8–4.5)	2.6 (2.2–3.0)	2.2 (1.8–2.7)	11.3 (10.4–12.2)

*The average number of items per cat is the total divided by the complete sample and so includes cats that did not bring home any items from that group. This measure is equivalent to the averages provided in other studies (Churcher & Lawton, 1987; Barratt, 1998, etc.). The minimum number of prey items brought home per cat was zero in all cases.

†Means and 95% CI are back-transformed from the \log_{10} -transformed data and include only the cats that brought home at least one item from that prey group.

§Other items include fish, invertebrates and unidentified prey items, some of which will be mammals, birds or herpetofauna.

Fig. 1. Frequency distribution of the number of mammals (black columns), birds (white columns) and herpetofauna (grey columns) brought home by 696 individual cats. For numbers of cats that brought home none of these prey groups, see Table 3.



of species brought home was a function of the number of animals brought home (number of bird species = $0.484 \times \text{number of birds} + 0.174$, $r^2 = 0.61$, $F_{1,473} = 734.9$, $P < 0.001$; number of mammal species = $0.306 \times \text{number of mammals} + 0.225$, $r^2 = 0.52$, $F_{1,465} = 508.8$, $P < 0.001$).

Full details of all factors and covariates relating to households were collated for 396 households owning 555 cats. The number of cats varied between households: 297 (75%) households had only one cat, 65 (16%) had two cats, 20 (5%) had three cats, 9 (2%) had four cats. Five, six, seven and eight cats were owned by one, two, one and one households, respectively. The mean number of cats per household was 1.4 (95% CI 1.3–1.5), though the median was one cat per household. Food was provided for birds by 265 (67%) households. The number of herpetofauna brought home per household was positively related to the total number of cats living in the household, but no effect was observed for mammals or birds (Table 4). Region significantly affected the numbers of herpetofauna brought home, but had

no significant effect on the numbers of birds or mammals. There were, however, no significant pairwise differences between regions in the numbers of herpetofauna brought home, probably due to limited sample sizes in certain regions. Nonetheless, there was a general trend of decreasing numbers of herpetofauna brought home with increasing latitude (Fig. 2). The numbers of both birds and mammals, but not herpetofauna, brought home were significantly affected by residence type (Fig. 3). Greater numbers of birds were brought home by cats living in bungalows than in terraced houses or flats. Greater numbers of mammals were brought home by cats living in detached houses than in semi-detached and terraced houses. The mean number of birds and herpetofauna brought home per cat was significantly lower in households that provided food for birds but no significant effect of providing bird food was observed for mammals (Fig. 4). In contrast, the number of bird species brought home was significantly greater in households that provided food for birds than in those that did not ($F_{1,363} = 4.11, P < 0.05$) (Fig. 4). No other factors relating to households significantly affected the numbers of bird or mammal species brought home.

Full details of all factors and covariates relating to individual cats were collated for 282 cats living in households with no other cats. The sex ratio of these cats (male : female = 147 : 135) was not significantly different from parity (G -test with Yates' correction for continuity $G = 0.43, \text{d.f.} = 1, P > 0.05$). Bells were worn by 92 (33%) cats. At night, 90 (32%) cats were kept indoors. There was no significant association between bell-wearing and being kept indoors at nights (χ^2 test with Yates' correction for continuity: $\chi^2 = 1.96, \text{d.f.} = 1, P > 0.05$). The mean age of the cats was 5.5 years (95% CI 5.1–5.9) and the mean condition was 2.0 (95% CI 1.9–2.1). There was a significant positive correlation between the numbers of mammals and birds brought home ($r = 0.23, \text{d.f.} = 280, P < 0.001$), though 94% of the variation in the numbers of birds brought home remained unexplained by the number of mammals. The sex of the cat did not significantly affect either the numbers of mammals, birds or herpetofauna brought home (Table 5). The numbers of mammals brought home was significantly lower if the cat wore a bell, but no similar effect was observed for birds or herpetofauna (Fig. 5). The numbers of mammals brought home were significantly lower and numbers of herpetofauna were significantly higher if the cat was kept indoors at night, but no effect was observed for birds (Fig. 6). The age and condition of the cat were both negatively related to the numbers of birds and herpetofauna brought home, but not to the numbers of mammals. No factors relating to individual cats were found significantly to affect the number of bird or mammal species brought home.

The total number of animals brought home by about 9 million cats living in Great Britain during the 5-month period April–August 1997 was estimated to be in the order of 92.4 million (95% CI 85.1–100.2). This estimate can be broken down to 57.4 (52.1–63.1) million mammals, 27.1 (25.1–29.2) million birds, 4.8 (4.1–5.6) million reptiles and amphibians and 2.8 (2.3–3.4) million other items.

DISCUSSION

By virtue of their abundance in many ecosystems, domestic and feral cats are a major predator of wild animals in Great Britain. While their impact as predators and the necessity of measures to mitigate this are controversial, there is a clear need for analysis of the numbers of animals affected and of the factors influencing kill rates. It was our aim to report on the numbers of animals brought home by cats at a national scale and to establish hypotheses for some of the factors affecting this. This descriptive survey was not intended to gauge the impact of predation by cats on the population dynamics of their prey, and so no data on prey populations were collected.

Surveys that require the participation of the public should be considered in the light of several limitations. It was not possible to determine how representative this sample is of cats in general, nor how representative the behaviour of the cats surveyed was. A major caveat is the likely bias of this survey towards cat owners who have a particular interest in wildlife biology and conservation (Fitzgerald & Turner, 2000). Equally, there is a potential bias towards cats that have predilections for killing wild animals and for bringing home their prey. Approximately 20–30% of cats brought home either no birds or no mammals during this survey while cats that brought home no prey items at all made up 8.9% of the sample. In their exhaustive survey of all the cats living in one village, Churcher & Lawton (1987) found that six of approximately 70 cats (8.6%) did not bring home any prey during the year of their study. This similar figure encourages the conclusion that the cats in this survey were comparable to cats in at least one other detailed study. Cats that do not bring home prey may either not be killing wild animals at all or they could be killing them but not then bringing them home. A failure to consider greater numbers of these two 'non-predatory' and 'non-retrieving' types of cat would lead to a considerable difference between our measures of the total numbers of wild animals brought home and the actual number of wild animals killed by cats in general. The fact that 'predatory' cats will not bring home all the prey they kill and that our estimates are therefore a minimum number of prey killed may compensate for this potential bias to some extent.

Clearly, cats will not bring home all the prey they kill. Some smaller prey will be completely eaten while other items too large to transport large distances may be abandoned or eaten *in situ*. Nonetheless, the number of prey items brought home and recorded by householders is an index representing the minimum number of animals killed by cats. The quality of this index has not been investigated in detail here or elsewhere, though George (1974) found that three farm cats never ate or deposited their prey where it was caught, but always carried it to his house or lawn. Our main aim was to determine which factors influence the prey capture rates of domestic cats. Therefore, an index of the number of animals killed is adequate, if we can assume that it is the cat's ability or inclination to capture prey that is influenced by the factors being investigated and not its inclination to bring prey home, that is, it seems safe to assume that by wearing a bell a cat's ability to catch a mouse may be affected, but not the cat's tendency then to bring the mouse home.

We have confirmed the findings of numerous previous investigators that there is great variation between individual cats in the numbers of wild animals they bring home (Churcher & Lawton, 1987; Barratt, 1998). The simple average number of animals brought home in this 5-month survey (total items/number of cats, 16.6) was rather higher than other studies; over 12 months Churcher & Lawton (1987) recorded an average of 'about 14' items per cat, though this average included only vertebrate prey. Barratt (1998) recorded a 12-month average of 10.2 vertebrate prey items and Borkenhagen (1978) recorded a mean of 5.7 items per cat. Howes (1982) found that young cats between 18 months and 2-year-old caught an average of 33 vertebrate prey items a year, though this declined to 12 items a year in older cats. Our survey took place during the period April–August when most animals were brought home by cats in the other surveys (Churcher & Lawton, 1987). Nonetheless, ours is still rather a high average and further studies are required to account for this high figure. It should be noted that in all of the above cases, the simple average number of animals brought home is not a useful measure of central tendency because of the skewed frequency distribution of the numbers of prey items brought home (Fig. 1). Hence our consideration of these figures is limited to comparisons between studies. In our estimates of the total animals killed by cats, we used the back-transformed mean and CI of the log-transformed data.

Table 4. ANCOVA of household-related factors affecting the numbers of animals brought home to 396 households by 555 cats. Number of cats in the household was a covariate

Source of variation	Coefficient of covariate (S.D.)	d.f.	Adjusted mean square	F	P
Mammals					
Region		6	0.488	1.95	0.072
Residence type		4	1.734	6.94	<0.001
Bird food		1	0.002	0.01	0.937
Number of cats	-0.001 (0.029)	1	0.001	0.00	0.966
Error		383	0.250		
Total		395			
Birds					
Region		6	0.205	1.30	0.256
Residence type		4	0.527	3.34	0.010
Bird food		1	1.268	8.04	0.005
Number of cats	0.037 (0.023)	1	0.410	2.60	0.108
Error		383	0.158		
Total		395			
Herpetofauna					
Region		6	0.176	2.21	0.042
Residence type		4	0.036	0.45	0.772
Bird food		1	0.454	5.69	0.018
Number of cats	0.062 (0.016)	1	1.178	14.75	<0.001
Error		383	0.080		
Total		395			

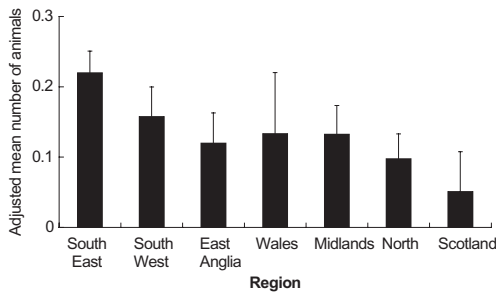


Fig. 2. Adjusted means (\pm S.D.) of \log_{10} -transformed numbers of herpetofauna brought home by cats to households in each of seven regions. While region significantly affected the number of animals brought home, there were no significant pairwise comparisons during *post-hoc* testing.

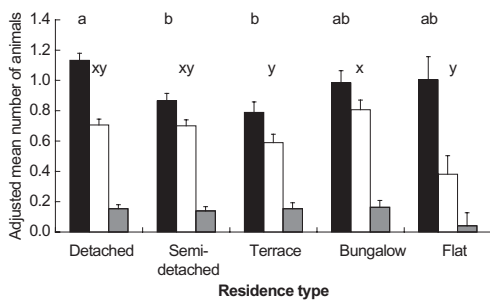


Fig. 3. Adjusted means (\pm S.D.) of \log_{10} -transformed numbers of mammals (black columns), birds (white columns) and herpetofauna (grey columns) brought home by cats living in residences of different types. Residence types that did not differ significantly are marked with the same letter (a, b for mammals and x, y for birds). Residence type did not significantly affect the number of herpetofauna brought home.

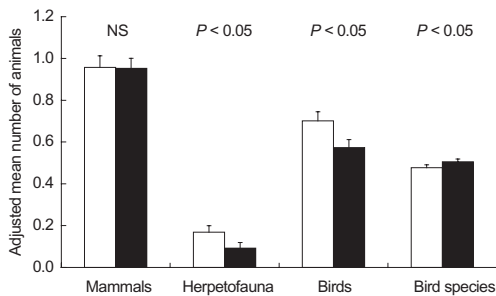


Fig. 4. Adjusted means (\pm S.D.) of \log_{10} -transformed number of mammals, herpetofauna and birds and number of bird species brought home by cats living in households that did not provide food for birds (white columns) and that did provide food for birds (black columns).

Table 5. ANCOVA of cat-related factors affecting the numbers of animals brought home by 282 cats living in households with no other cats. Age and condition of the cat were covariates

Source of variation	Coefficient of covariate (S.D.)	d.f.	Adjusted mean square	<i>F</i>	<i>P</i>
Mammals					
Sex		1	0.064	0.26	0.608
Indoors/outdoors		1	1.861	7.71	0.006
Bell		1	3.545	14.69	<0.001
Age	-0.075 (0.042)	1	0.764	3.17	0.076
Condition	-0.076 (0.054)	1	0.486	2.01	0.157
Error		276	0.241		
Total		281			
Birds					
Sex		1	0.030	0.24	0.628
Indoors/outdoors		1	0.063	0.49	0.484
Bell		1	0.005	0.04	0.847
Age	-0.214 (0.031)	1	6.226	48.84	<0.001
Condition	-0.109 (0.039)	1	1.007	7.90	0.005
Error		276	0.128		
Total		281			
Herpetofauna					
Sex		1	0.008	0.17	0.681
Indoors/outdoors		1	0.310	6.26	0.013
Bell		1	0.001	0.01	0.913
Age	-0.072 (0.019)	1	0.712	14.40	<0.001
Condition	-0.048 (0.024)	1	0.197	3.99	0.047
Error		276	0.049		
Total		281			

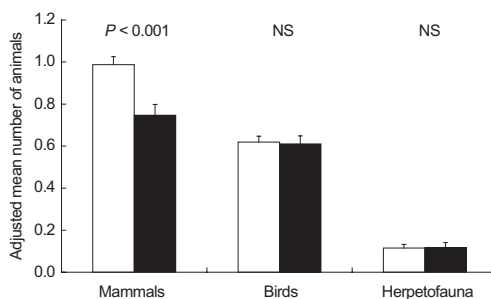


Fig. 5. Adjusted means (\pm S.D.) of \log_{10} -transformed numbers of mammals, birds and herpetofauna brought home by cats that did not wear bells (white columns) and that did wear bells (black columns).

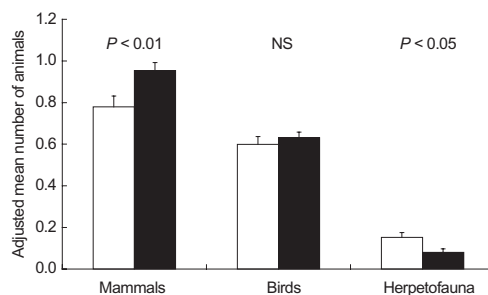


Fig. 6. Adjusted means (\pm S.D.) of \log_{10} -transformed numbers of mammals, birds and herpetofauna brought home by cats that were not allowed outdoors at nights (white columns) and that were allowed out at nights (black columns).

Variation in the numbers of animals killed per cat may in part be explained by characteristics of the household, the cat and by the management regime adopted by cat owners. However, in our analyses, and in most previous studies, a large part of the variation in prey capture rates remained unexplained by the factors we measured. This residual variation is most likely to arise from individual-based differences in cat behaviour (Turner & Bateson, 1988). For example, the early experience of juvenile cats in relation to parental capture of wild prey, as well as random factors such as weather conditions, can influence their inclination and aptitude for capturing wild prey (Turner & Bateson, 1988).

Perhaps not surprisingly, given differences in appropriate hunting techniques and prey availability, our results have suggested that the factors influencing the rate of prey capture differ between prey groups. The regional effect on numbers of herpetofauna brought home likely reflects the distribution of these species, several of which are found mainly in southern regions of Britain. Curiously, cats living in households that provided food for birds brought home fewer birds and fewer herpetofauna than cats living in houses that did not provide bird food. When the effect of bird capture rate on species range was controlled for, cats living in households where birds were fed brought home a wider range of species. It may have been expected that feeding birds attracted both a greater number of birds and a wider range of species to the garden and placed them within easy reach of predators. This appears to be the case at least in terms of the range of bird species brought home. Dunn & Tessaglia (1994) asserted that predation rates in gardens where birds were fed were similar to predation rates in other areas. In support of our findings, however, several authors have suggested that feeding birds may reduce susceptibility to predation in two ways. A greater number of birds may enhance group vigilance behaviour and thus warn against predator presence (Siegfried & Underhill, 1975; Waite, 1987; Popp, 1988). Alternatively, extra food supply may reduce foraging time and thus the time at which the birds are at risk of being captured by cats (Jansson, Ekman & Von Bromssen, 1981). The range of species would not necessarily be affected in this way, since foraging responses to predation risk vary between species (Giesbrecht & Ankney, 1998) and such mechanisms may be more significant in common, flocking species. While such biological explanations are appealing, it remains a possibility that households that owned cats they knew to be prodigious killers of birds or herpetofauna chose not to feed the birds. This alternative explanation also seems plausible for the observed pattern in herpetofauna and for the pattern in species range, since owners are likely to decide not to feed birds on the basis of numbers rather than diversity of birds brought home.

We found that younger or thinner cats brought home more birds and herpetofauna. As cats get older or fatter, the rates of retrieval of these groups declined. Fewer mammals were brought home by cats that were equipped with bells and by those that were kept in at nights. These results were intuitive. Bells may serve as a warning to mammals of a predator's approach. The capture rates of neither birds nor herpetofauna were affected by equipping cats with bells. It is possible to speculate that this may be because birds rely largely on visual cues in predator avoidance behaviour, or because the acoustic qualities of cat bells may not lend themselves to warning birds or herpetofauna. Alternatively, a cat may have been equipped with a bell because without a bell it was a prodigious killer. Cats that were kept in at night brought home fewer mammals and greater numbers of herpetofauna than cats that were allowed out at night. Wild mammals are predominantly nocturnal and so keeping cats indoors at night would reduce their access to mammalian prey. Producing a similar pattern, some cat owners may encourage their cats to be outdoors at night, in order that they 'keep down vermin' and so these cats bring back higher numbers of mammalian prey. It is not clear why patterns of retrieval of herpetofauna should differ in relation to being kept in at nights,

though it is possible that cats that are let out early in the morning and are keen to hunt are able to catch reptiles and amphibians while they are still cold and inactive. The same would not apply to birds. Clearly, it is essential that an experimental approach be taken to identify which of the factors we have identified as influencing prey capture rates are causally related to the numbers of wild animals killed. This aim has recently been realized by the experimental work of Ruxton, Thomas & Wright (2002), who have confirmed that the numbers of wild animals killed and brought home by cats can be reduced by equipping them with bells.

Our estimates of the total numbers of animals brought home by cats throughout Britain should be treated with requisite caution and these figures do not equate to an assessment of the impact of cats on wildlife populations. Nonetheless, they represent an early assessment of the likely order of magnitude of wild animals killed by a very large population of domestic cats. While a figure of 92 million wild animals being killed by an estimated 9 million cats over the 5 months (April–August 1997) is doubtless striking, this amounts to the average cat bringing in only one item every two weeks. The critical element in this equation is the very large number of cats living in Britain, and so an accurate estimate of the British cat population is essential to improving the accuracy of these calculations. Likewise, it may not be appropriate to include feral cats in these calculations, since their killing rates may be substantially different from truly domestic cats. Our estimates took into account that sizeable proportions of the cat population are likely not to bring home any items from some prey groups (20% for mammals and birds, 80% for herpetofauna). Taking into account the fact that we may have focused on predatory cats, if the true rates of predatory behaviour were half those we observed, there would remain the probability that the equally striking figure of 46 million wild animals are killed by the remaining 'predatory' half of the population.

In Britain, most prey species have evolved under the selective pressure of predation by numerous species of wild mammalian and avian predator, albeit living at relatively low densities. Thus, these species are likely to be relatively tolerant of predation when compared to the more vulnerable fauna of oceanic islands. Nevertheless, the continuous pressure of predation by carnivores living at high densities and that are not in any way regulated by the availability of wild prey could be considered analogous to the process of hyperpredation on oceanic islands (Smith & Quin, 1996; Courchamp, Langlais & Sugihara, 1999). This is the process whereby native species are threatened by occasional predation by a large population of introduced predators that is sustained by abundant introduced prey species that are in turn well adapted to high predation pressure. A constantly renewed food source, that is, provision of food by householders, may be compared to the ready availability of introduced rats or rabbits on oceanic islands (Courchamp *et al.*, 1999). It is conceivable that predation by superabundant and well-fed predators such as domestic cats could lead to the decline of continental species, if only on a local or temporary basis. Baker *et al.* (2003) recorded a negative relationship between numbers of wood mice and the numbers of cats visiting suburban gardens. This suggests that high levels of cat activity may deplete the numbers of otherwise common species, such as wood mice, in local areas. It is not possible directly to discern the process of hyperpredation in the data recorded here, though the occurrence of species of growing conservation concern among the prey records, such as water shrews, yellow-necked mice and harvest mice (Marsh, Poulton & Harris, 2001; Greenwood, Churchfield & Hickey, 2002; Moore, Askew & Bishop, 2003) gives additional cause for concern. Churcher & Lawton (1987) concluded that cats had a significant impact on house sparrows in the village they studied. A potential link between the frequent occurrence of sparrow predation in this and other studies and the pronounced decline in this species throughout Britain should, therefore, be considered and experimental work is called for in the light of this descriptive

study. This echoes the recent suggestion of Crick, Robinson & Siriwardena (2002) that targeted studies are required to investigate the role of predation by domestic cats in the decline of house sparrows, particularly in urban areas.

In conclusion, this survey confirms that cats are major predators of wildlife in Britain. Further investigation of the extent and nature of predatory behaviour among domestic cats is clearly warranted by this initial work. In particular, detailed observation of cats in the field and description of the numbers of animals they kill and the proportion they retrieve are essential. Investigation of the response and attitude of cat owners living in a range of environments to the predatory behaviour of their cats would also be valuable (Coleman & Temple, 1993). Although this was not an experimental study, there were differences in the numbers of wild animals brought home by cats subjected to different management regimes. Experimental studies of the effects of equipping cats with bells (Ruxton *et al.*, 2002) or other devices, keeping cats indoors at night and feeding birds will all be essential for evaluating the desirability and likely success of attempts to reduce the numbers of animals killed by growing cat populations.

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APPENDIX

Descriptions and frequencies of prey items brought home to 618 households by 986 cats. A total of 191 prey items could not be identified by the householder

Class	Prey description	Scientific name	Total	Class	Prey description	Scientific name	Total			
Mammalia	Mouse	Muridae	1765	Aves	Siskin	<i>Carduelis spinus</i>	7			
	Wood mouse	<i>Apodemus sylvaticus</i>	1617		Partridge	Perdidae	6			
	Rabbit	<i>Oryctolagus cuniculus</i>	1242		Ducklings	Anatidae	6			
	Field vole	<i>Microtus agrestis</i>	853		Jackdaw	<i>Corvus monedula</i>	5			
	Common shrew	<i>Sorex araneus</i>	807		Coal tit	<i>Parus ater</i>	5			
	House mouse	<i>Mus domesticus</i>	622		Swift	<i>Apus apus</i>	5			
	Shrew	Soricidae	599		Crow	<i>Corvus corone</i>	5			
	Vole	Muridae	552		Bird's egg	–	4			
	Bank vole	<i>Clethrionomys glareolus</i>	544		Bullfinch	<i>Pyrrhula</i>	4			
	Unidentified mammal	–	341		Treecreeper	<i>Certhia familiaris</i>	4			
	Pygmy shrew	<i>Sorex minutus</i>	320		Sparrow	Passer spp.	2			
	Harvest mouse	<i>Micromys minutus</i>	177		Skylark	<i>Alauda arvensis</i>	2			
	Rat	<i>Rattus norvegicus</i>	162		Flycatcher	Muscicapidae	2			
	Mole	<i>Talpa europaea</i>	99		Rook	<i>Corvus frugilegus</i>	2			
	Water shrew	<i>Neomys fodiens</i>	27		Yellow wagtail	<i>Motacilla flava</i>	2			
	Squirrel	<i>Sciurus</i> spp.	26		Great spotted woodpecker	<i>Dendrocopos major</i>	1			
	Bat	Chiroptera	22		Green woodpecker	<i>Picus viridis</i>	1			
	Water vole	<i>Arvicola terrestris</i>	20		Red grouse	<i>Lagopus lagopus scoticus</i>	1			
	Yellow-necked mouse	<i>Apodemus flavicollis</i>	17		Herring gull	<i>Larus argentatus</i>	1			
	Dormouse	Gliridae	12		Nuthatch	<i>Sitta europaea</i>	1			
	Weasel	<i>Mustela nivalis</i>	10		Jay	<i>Garrulus glandarius</i>	1			
	Stoat	<i>Mustela erminea</i>	7		Budgerigar	<i>Melopsittacus undulatus</i>	1			
	Long eared bat	<i>Plecotus auritus</i>	4		Goldcrest	<i>Regulus regulus</i>	1			
	Pipistrelle	<i>Pipistrellus</i> spp.	4		Frog	<i>Rana</i> spp.	545			
	Hamster	<i>Mesocricetus auratus</i>	2		Toad	<i>Bufo</i> spp.	23			
	Hare	<i>Lepus</i> spp.	1		Newt	<i>Triturus</i> spp.	22			
	Aves	House sparrow	<i>Passer domesticus</i>		961	Amphibia	Slowworm	<i>Anguis fragilis</i>	87	
		Unidentified bird	–		503		Lizard	<i>Lacerta</i> spp.	45	
		Blue tit	<i>Parus caeruleus</i>		344		Grass snake	<i>Natrix natrix</i>	10	
		Blackbird	<i>Turdus merula</i>		316		Sand lizard	<i>Lacerta agilis</i>	2	
		Starling	<i>Sturnus vulgaris</i>		228		Osteichthyes	Goldfish	<i>Carassius auratus</i>	31
		Robin	<i>Erithacus rubecula</i>		142			Insecta	Moth	Lepidoptera
		Thrush	<i>Turdus</i> spp.		128		Butterfly		Lepidoptera	26
		Pigeon	Columbiformes		114		Dragonfly	Odonata	25	
		Wren	<i>Troglodytes troglodytes</i>		105		Large white	<i>Pieris brassicae</i>	9	
		Greenfinch	<i>Carduelis chloris</i>		82		Tortoiseshell	<i>Nymphalis polychloros/Aglais urticae</i>	8	
		Chaffinch	<i>Fringilla coelebs</i>		70		Bee	Hymenoptera	7	
		Great tit	<i>Parus major</i>		52		Fly	Diptera	6	
		Dunnock	<i>Prunella modularis</i>		34		Red admiral	<i>Vanessa atalanta</i>	6	
		Collared dove	<i>Streptopelia decaocto</i>		33		Beetle	Coleoptera	4	
		Tree sparrow	<i>Passer montanus</i>		27		Caterpillar	Lepidoptera	4	
		Swallow	<i>Hirundo rustica</i>		22		Cricket	Orthoptera	4	
Finch		Fringillidae	20	Grasshopper	Orthoptera		3			
Goldfinch		<i>Carduelis carduelis</i>	19	Hawk-moth	Sphingidae		2			
Magpie		<i>Pica pica</i>	18	Orange tip	<i>Anthocharis cardamines</i>		1			
Song thrush		<i>Turdus philomelos</i>	17	Painted lady	<i>Vanessa cardui</i>		1			
Pied wagtail		<i>Motacilla alba</i>	14	Earwig	Dermaptera		1			
Pheasant		<i>Phasianus colchicus</i>	14	Spider	Araneae		9			
Warbler		Sylviidae	14	Crab	Decapoda		1			
Tit		Paridae	11	Slug	Pulmonata		5			
House martin		<i>Delichon urbica</i>	9	Snail	Pulmonata		1			
Moorhen		<i>Gallinula chloropus</i>	9	Earthworm	Lumbricidae		21			
Yellowhammer		<i>Emberiza citrinella</i>	8	Unidentified			191			
Meadow pipit	<i>Anthus pratensis</i>	8								
			Total			14370				