UNIVERSITY OF DERBY

THE IMPACT OF PREDATION BY DOMESTIC CATS (*FELIS CATUS*) ON BRITISH WILDLIFE POPULATIONS

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List of abbreviations

AIC	Akaike Information Criterion
BBS	Breeding Bird Survey
BTO	British Trust for Ornithology
CEH	Centre for Ecology and Hydrology
FO	Frequency of Occurrence
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
IDW	Inverse-Distance Weighted
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
PCA	Principal Component Analysis
PDSA	People's Dispensary for Sick Animals
PFMA	Pet Food Manufacturers Association
P Mean	Posterior Mean
RFO	Relative Frequency of Occurrence
RSPB	Royal Society for the Protection of Birds

List of country codes

AU	Australia
BR	Brazil
CH	Switzerland
EC	Ecuador
ES	Spain
FI	Finland
FR	France
HR	Croatia
HU	Hungary
IL	Israel
IT	Italy
JP	Japan
MX	Mexico
NZ	New Zealand
PL	Poland
UK	United Kingdom
US	United States
ZA	South Africa

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Abstract

Non-native predators can cause great harm to natural ecosystems, through competition for resources and by directly predating on native species. Despite decades of research into predation by domestic cats (*Felis catus*) globally, the impacts on British wildlife populations are less clear than, for example, Australasian species. Since predation by cats is dependent on prey availability and local faunal composition, capture rates of different taxa can vary throughout the world. In order to assess impact, reliable and representative prey return data must be gathered, and total predation estimated (since it is unlikely that cats return all prey caught).

Here, prey return rates were established using a 'cat diary' where cat owners (n=553 cats) recorded all prey items returned home each month, yielding a total of 4,674 data months. This dataset was also used to investigate the key influencers of predation, finding that return rates were linked to the sex and age of the cats, with males returning larger numbers than females, and younger cats returning the most prey. Overall, most cats returned fewer than 0.5 prey per month. However, despite a monthly median of 0.3 prey, the mean was 1.57 prey per month owing to a small number of 'super predator' cats returning up to 61 prey in a single month.

Collar-mounted video cameras were used on a subset of these 'diary' cats, observing their behaviour outdoors and how they treated prey after capture (whether returned, eaten, or discarded). These video data were then used to calculate a coefficient by which return rates can be multiplied in order to estimate total predation (between 1.22 and 1.57 for vertebrate prey). This study is the first piece of video research in the UK and gives an important insight into cats' behaviour after prey capture.

It was apparent that shrews and other insectivores may be unpalatable to cats, as just under 97% of shrews returned were 'whole', suggesting that there had been no attempt by the cat to consume them. It was concluded that, due to this difference between taxa, insectivore capture rates should be extrapolated separately. Similarly, the potential differences in detectability by cat owners of prey remains may also vary dependent on taxon (for example, with bird remains being more readily detected than small mammals). Therefore, using a single multiplier to

estimate all prey species was found to be inappropriate, and the most reliable approach is to apply taxon-specific multipliers.

Mapping techniques were used to assess the overall impact of pet cats in the UK on the five most frequently returned bird species. This found that the relationships between cats and their prey are complex and dependent on environmental variables, and potentially other anthropogenic factors.

Overall, prey populations are currently stable or increasing, although data are lacking for some mammalian species. This research suggests that while cats do kill millions of prey per year in the UK, there is no measurable effect on prey at a population level, likely because British prey species have evolved alongside similar terrestrial predators.

Chapter 1

Literature review

Hannah Lockwood

1.1 Cats as invasive species

The domestic cat (*Felis catus*), hereafter 'cat', is one of the most ubiquitous predators in the world, having established populations on all continents, with the exception of Antarctica (Nogales *et al.*, 2013). First domesticated in the Near East around 10,000 years ago, cats were found to be useful in controlling rodent populations and were transported around the World by whalers and sealers (Driscoll *et al.*, 2007).

Cats are now cited as contributing to the decline and extinction of 367 and 63 species, respectively, according to a meta-analysis comparing the impacts of invasive mammalian predators (Doherty *et al.*, 2016). Their effects as predators are particularly apparent on oceanic islands, where high species endemism and poorly developed predator defence strategies can lead to severe declines and extinctions of native species (Medina *et al.*, 2011). However, in the UK, prey species have evolved alongside the European wildcat (*Felis silvestris*) and mustelid species, exerting similar pressure on populations (Beaumont *et al.*, 2001; Clegg, 2017). Therefore, prey present in the UK are better adapted to either avoid predation (through crypsis, escape, or defence), or able to cope with losses (through high productivity rates) than on remote islands where prey species have not faced such predation pressures previously (Bradshaw *et al.*, 2012; Clegg, 2017).

1.2 Hunting success

The majority of work on the impacts of cat predation has been conducted on birds (Møller and Erritzøe, 2000; Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012). However, cats are better adapted for hunting small mammals such as mice and voles (Leyhausen, 1979). Hunting success is dependent on their prey's predator defence mechanisms, and will therefore vary across the world, depending on evolved predator responses. It has been found through the use of video cameras that 44% (in Georgia, USA, Hernandez *et al.*, 2018) and 31.7% (in Australia,

McGregor *et al.*, 2015) of hunts end in successful capture, where hunting behaviour is defined as stalking, pouncing, and capturing. These figures would be reduced, were it not for invertebrates, reptiles, and amphibians, where hunting success was much higher (82%, 69%, and 76%, respectively, Hernandez *et al.*, 2018). For birds however, this figure is much lower (16.7%), suggesting that birds are not as easy to catch (Hernandez *et al.*, 2018).

1.3 **Impact**

1.3.1 Exclusion

There are a number of ways that authors have attempted to investigate the impact of cats on local wildlife populations (Frank *et al.*, 2014; Stokeld *et al.*, 2018). Ideally, one would remove cats from an area and monitor the wildlife populations post-exclusion. However, this is not possible on a large scale. Similarly, cats being introduced to a thriving ecosystem would not be ethically sound. There have been a number of experimental exclusion studies in Australia. For example, Frank *et al.* (2014) used four 6.25 ha enclosures (two accessible to cats and two inaccessible) to test whether cat exclusion would affect the persistence of native long-haired rats (*Rattus villosissimus*). Cats were not detected in either of the inaccessible enclosures, however they were found to be accessing the open enclosures, albeit infrequently. The native rats went extinct in both accessible areas within 16 months, whereas they persisted in the closed enclosures, although experienced slight declines (Frank *et al.*, 2014). In a more recent study, Stokeld *et al.* (2018) used much larger enclosures (each 64 ha) and included reptile fencing to prevent digging. They found that the exclusion of cats led to a significant increase in reptile abundance over a two-year period. The key issue with such exclusion studies is that they do not only exclude cats, but also dogs (*Canis lupus familiaris*) and dingoes (*Canis lupus dingo*) which may also predate on the prey monitored.

1.3.2 Eradication

There have been a number of studies which monitor the health of prey populations after cat eradication on small islands. Bergstrom *et al.* (2009) showed that post-eradication of cats, the non-native rabbit (*Oryctolagus cuniculus*) population increased substantially on Macquarie Island. While this shows that cats were suppressing the rabbit population, their increase after cat eradication is an undesirable effect as it led to widespread vegetation damage. This is known as the mesopredator release effect, where the removal of a carnivore species (in this case, cats) leads to a population boom in a species of lower trophic level, having a damaging effect. Despite this, grey petrels (*Procellaria cinerea*) were found to be breeding on Macquarie Island post-eradication for the first time in over 80 years and the overall positive impacts on seabirds were rapid (Schulz *et al.*, 2005).

1.3.3 Additive and compensatory predation

Predation can be additive or compensatory to natural mortality. Additive predation occurs when cats take healthy breeding adults out of the prey population (Péron, 2013), whereas compensatory predation occurs when juveniles and those in poor health are removed from the population, as this would likely happen despite the presence of predators (Zager and Beecham, 2006). Examining the condition of prey caught is a way of testing whether predation by cats is likely to be additive or compensatory, as individuals of a poorer body condition are likely to be predisposed to greater mortality (Bender and Rosas-Rosas, 2016). Baker *et al.* (2008) found that birds killed by cats had lower mass, fat, and muscle mass scores than those killed in collisions. Although this indicates compensatory predation, mass can fluctuate throughout the day and during the breeding season (Baker *et al.*, 2008). However, the same is true of those killed in collisions. Møller and Erritzøe (2000) used measurements of spleen size as a proxy for bird condition and found that of 18 species studied, 16 had a smaller spleen (and therefore a poorer condition) if killed by a cat, as opposed to accidental mortality, again suggesting that predation

by cats is compensatory. Péron (2013) suggests that distinguishing between additive and compensatory predation requires knowledge of 1) prey survival rate in the absence of cats, 2) mortality rate of prey due to cats, and 3) the correlation between 1) and 2). Since cats are such a ubiquitous carnivore, there is great difficulty in obtaining data for point 1), and point 2) is hard to measure due to the secretive and poorly understood predatory behaviour of cats (Loss and Marra, 2017). It is therefore important to gain a thorough understanding of cat behaviour, particularly what they do with prey after capture, for example, whether they return prey home, eat it, or discard it. This will be examined further in Chapter 4.

1.3.4 Productivity of prey species

Although not strictly looking at impact, Churcher and Lawton (1987) found that 30% of house sparrow (*Passer domesticus*) deaths in a UK village were due to predation by cats. Using productivity data, it was estimated that the local house sparrow population increased by 300-400 individuals per breeding season, before returning to a stable level the following year (Churcher and Lawton, 1987). A prey return survey then suggested that around 30% of annual house sparrow mortality is due to cats (Churcher and Lawton, 1987). However, it is not possible to relate this to the impact of cats without also monitoring population trends, as this mortality level may be sustainable. In a more recent study, Baker *et al.* (2005) used the productivity of bird species to measure the impact of predation by cats. They found that overall, cats do not appear to be endangering prey populations in the UK, although for three bird species (house sparrow, dunnock *Prunella modularis*, and robin *Erithacus rubecula*), impacts may be substantial. Similarly, Thomas *et al.* (2012) found that the maximum estimated number of birds killed exceeded the number of adults in the population for five out of the six species studied (in some, but not all locations), suggesting a direct deleterious effect of cat predation. However, it should be noted that prey return studies were conducted for only 6 weeks per season, in a small area of Reading, UK and it was only the maximum estimate that exceeded the number of adults in the prey population. If this were true of the UK as a whole, widespread declines would be rapid, leading

to imminent extinction of bird species in the UK. The British Trust for Ornithology (BTO), however, determined that garden bird populations in some areas of the UK are increasing (such as the house sparrow in the west of the region, BTO, 2011).

1.3.5 Density comparison

Another measure used to monitor impact is the comparison between cat density and prey density. If cats are having a negative impact on prey populations, one would expect that prey density is reduced in areas of high cat density such as cities. Sims *et al.* (2008) found a positive correlation between bird and cat densities in the UK, suggesting that cats do not have a negative impact on populations. However, this may have been due to a lack of variation of cat density between sites (cat density = 132 – 1580/km^2, median = 417/km^2). Another study in the USA found that the number of cats roaming within a woodland area did not impact the density of any small mammal species or biodiversity (Kays and DeWan, 2004). In studies like these, it should be noted that habitat and land use are potentially large confounding factors. This will be investigated further in Chapter 5.

1.4 **Global impact**

Doherty *et al.* (2016) conducted a meta-analysis, comparing the impacts of invasive mammalian predators. This research states that cats are implicated in the extinction of 63 species, and the population declines of a further 367 species, globally. These statistics have been routinely cited throughout the literature without being questioned (e.g. Loss and Marra, 2017). On review of the supplementary information available, it is clear that of the 63 species extinctions described, evidence is provided in just one case, the Choiseul pigeon (*Microgoura meeki*). This is however a correlative piece of evidence and therefore does not mean causation. There are no empirical data available to support the claims regarding the remaining 62 species, only anecdotal evidence. While local knowledge and anecdotal information can be valuable, especially where empirical

data collection is problematic (or species of interest are already extinct), it remains concerning that the data sources are not scrutinised in citing literature. Despite the problems surrounding the conclusions of this study, it is suggested that rodents have an impact on prey species, comparable to cats (Doherty *et al.*, 2016). Therefore, removing cats from these ecosystems will likely result in the release of rodents as a mesopredator, further damaging prey populations (Tidemann *et al.*, 1994; Nogales *et al.*, 2013).

Globally, the areas of greatest concern are small islands, of which there are around 179,000 (Medina *et al.*, 2011). These small areas hold a disproportionate amount of the world's biodiversity and are home to many endemic species, not adapted to ground predators (Medina *et al.*, 2011). This is one reason that there is global concern over the impacts of invasive species such as cats (Bonnaud *et al.*, 2011).

1.5 **The average cat**

In order to estimate total predation rates of all cats in an area, a large sample size is required to give a reliable estimate of predation per cat per year. Many studies have shown large variability between individual cats' return rates (Barratt, 1998; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Kauhala *et al.*, 2015). For example, Kauhala *et al.* (2015) found that 9% of the pet cats studied returned 40% of the total prey recorded, and Morgan *et al.* (2009) state that 80% of pet cats in the study returned 10 or fewer prey over the whole year. This skew in return rates is also illustrated by a mean prey return that is over three times larger than the median (van Heezik *et al.*, 2010), suggesting that most owned cats return few prey, but there are some 'super predators' which return a vast number. What is not clear is whether this skew in return rate is echoed in actual kill rates or whether some cats return a greater proportion of their kills than others. However, it is clear from video studies that, although only monitored for a short time, some pet cats hunt a great amount of prey whereas the majority do not successfully hunt at all (70.9% of cats; Loyd *et al.*, 2013).

It is likely that cats do not return home all prey captures. A proportion may be eaten or discarded elsewhere, remaining undetected by owners. It is therefore important to consider this when producing estimates of total predation. The proportion of kills returned home and detected by cat owners has been estimated to be from 8.8% (Krauze-Gryz *et al.*, 2012) to 50% (George, 1974). One figure which is frequently used in extrapolations (see Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012 as examples) comes from Kays and DeWan (2004), who estimate that cats return 30% of total kills. This estimate is the result of comparing prey returns of pet cats (n = 12) with direct observations of cats outdoors 11 years earlier (n = 11), which leads to questions around the temporal differences in habitat, prey availability, and the individual cats themselves. While these methods were once very useful, with the development of small, collar-mounted digital cameras, the reliability of such studies can now be improved upon. Furthermore, while providing an insight into total predation rates, the use of a universal multiplication factor may result in vast over- or under-estimation of predation and potential impacts on wildlife when used in further studies, as different taxa may be returned in differing proportions.

1.6 **Influencers of predation**

There are a number of factors which might influence a cat's ability or propensity to hunt wild prey. Some of these factors can be controlled by humans, and others are uncontrollable (e.g. age) and vary between cats. There is much concern over the impacts of cats on local wildlife systems (Doherty *et al.*, 2016) and it is therefore important that the controllable differences between cats (e.g. fed diet, Cecchetti *et al.*, 2021) are identified and managed. In order to minimise the negative effects that cats can have on native wildlife, much research has looked at such factors, and measures to reduce the number of successful kills.

1.6.1 Bells and bibs

The use of detachable 'cat bibs' prevented 81% of cats from catching and returning birds (Calver *et al.*, 2007), while similar success has been found with the use of a bell attached to the cats' collar, reducing total prey returned by 53% (Gordon *et al.*, 2010). However, Morgan *et al.* (2009) found no difference between the return rates of those wearing a bell and those not, and Barratt (1998) showed that the number of bells worn had no effect on return rates. The effectiveness of these measures appears to vary by prey group. Woods *et al.* (2003) found that a belled collar may reduce mammal mortality, but a similar effect was not found for birds or herptiles. Similarly, Ruxton (2002) showed that a bell was effective at halving bird and mammal returns, while not affecting amphibians. Other measures which have seen similar success are sonic devices (Nelson *et al.*, 2005) and 'Birds Be Safe' ruff collars (Figure 1.1, Willson *et al.*, 2015; Pemberton and Ruxton, 2020).

Figure 1. 1. A cat wearing a Birds Be Safe ruff collar (Birdsbesafe, 2019)

1.6.2 Domestic diet

A key difference between feral and owned cats is that owned cats receive regular food and therefore do not need to hunt for survival. However, the feeding regime and quality of diet given to pet cats varies around the world. Silva-Rodriguez and Sieving (2011) conducted owner interviews and reported that 57% of cats were fed household scraps and 5% were fed wheat bran in Chile. Further, the same study reports a higher number of wild prey caught when anthropogenic food provision is reduced. This suggests that the quantity of diet provided can impact a cat's propensity to hunt. Similarly, in Australia, cats which were not fed meat returned more prey than those fed meat, although feeding offal, snacks, or supplements did not have a significant effect (Robertson, 1998). This suggests that there may be a link between fed diet and hunting behaviour of cats, although more research is required to make solid conclusions.

In the UK, the Pet Food Manufacturers' Association (PFMA) estimates that a population sample of 7.5 million cats were fed 382,000 tonnes of pet food in 2018, equating to 140g per day (PFMA, 2020b). According to the calorie content of various wet and dry foods available (Iams, Purina, Whiskas, Felix), this 140g equates to around 250kcal per day, half of what is recommended for carnivore species (Nagy *et al.*, 1999; Matias and Catry, 2008). However, the PFMA advise that a 4.5kg active cat requires just 274 kcal per day, suggesting that food given by owners in the UK is slightly below their requirements (PFMA, 2020a), therefore perhaps increasing the cats' need to supplement their diet with wild prey. However, the caloric requirement is reduced for smaller individuals and commercial cat food may therefore be ample for some individuals.

1.6.3 Body condition and sex

The cats' overall body condition may affect hunting ability. While the condition of prey returned has been monitored (Baker *et al.*, 2008), the influence of cat condition on prey mortality is not currently understood. Woods *et al.* (2003) found that overweight cats returned fewer birds than

their thinner conspecifics, perhaps because agility and speed were reduced in larger individuals. However, there was no association between body condition and the number of mammals returned home (Woods *et al.*, 2003). Sex does not appear to be a predictor of predation rate in cats (Barratt, 1998; Gillies and Clout, 2003; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Kutt, 2011; Tschanz *et al.*, 2011; Loyd *et al.*, 2013; Kauhala *et al.*, 2015; McDonald *et al.*, 2015).

1.6.4 Neutering status

There is evidence to suggest that neutering status can affect predation rates, or at least the number of prey returned home (Robertson, 1998), although it is a seldom reported factor. Robertson (1998) found that neutered cats (both male and female) return prey more frequently and spend more time outdoors than entire individuals. However, with a high proportion of cats having been neutered (95-98%, Barratt, 1998; Kauhala *et al.*, 2015), the sample size of entire cats may be too low to detect any real patterns in many studies. While the age at which a cat is neutered appears to have no effect on predation rates (Barratt, 1998), lactating females appear to predate more often than those without kittens (Robertson, 1998).

1.6.5 Age

While age appears to be an influencing factor in some studies (Barratt, 1998; Woods *et al.*, 2003; Flux, 2007; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Kauhala *et al.*, 2015; Bruce *et al.*, 2019), it is not found to be a significant influencer in many others (Robertson, 1998; Tschanz *et al.*, 2011; Loyd *et al.*, 2013; Yip *et al.*, 2014). Loyd *et al.* (2013) found that while age did not have a significant impact on predation (overall), it did influence the number of prey caught by hunting cats (excluding those which did not return any prey), with younger individuals returning a greater number of prey. It can also be dependent on the prey groups concerned. For example, Gillies and Clout (2003) found a significant negative correlation between age and the number of

invertebrates, birds, and lizards returned, but not between age and the number of mammals returned. As a cat gets older, the proportions of prey returned change. Older cats may return fewer birds, but a greater proportion of mammals (Kauhala *et al.*, 2015). It is reasonable to assume that this is due to older cats not having the agility and speed required to catch bird species. Older cats may also have more blunt carnassial teeth (Leyhausen, 1979), therefore being perhaps less likely to eat their prey.

1.7 **Summary**

Cats are a non-native species in the vast majority of their present-day range and are kept as pets, as well as the existence of feral colonies around the world. While their impact on native wildlife populations can be great in some areas, such as small islands with many endemic prey species, where native terrestrial predators have evolved alongside prey, the population impact is likely to be reduced.

Pet cats generally exist in great densities, mirroring that of the human population. They are largely well fed and therefore do not need to hunt to survive. While a minority appear to be very adept at hunting ('super predators'), most return very few prey by comparison. There are a number of factors which have been found to influence predation (or at least return) rates, including age and body condition score. In addition, the use of bells and bibs has been found to be effective in reducing prey return rates. These influencing factors will be further explored in Chapter 3 (predation survey).

Chapter 2

Meta-analyses

Hannah Lockwood

2.1 **Introduction**

2.1.1 Cats in the UK and around the World

Cats in the UK are mostly owned, with around 1 million feral cats (but there is no evidence more recent than Harris *et al.*, 1995), and an estimated 11.1 million owned cats (People's Dispensary for Sick Animals, PDSA, 2022). However, estimates are highly variable due to a lack of cat registration legislation. Recently, it was estimated that 73.9% of owned cats in the UK (or 8.2 million individuals) have access to the outdoors (Finka *et al.*, 2019). Pet cats have regular access to anthropogenic food sources including commercial cat food (Bradshaw *et al.*, 2012). In contrast, island populations are often made up of feral individuals, relying solely on wild food sources and therefore killing a far greater number of wild prey animals (Bonnaud *et al.*, 2007). Since pet cat populations are not limited by the same factors as wild predators (habitat and food resource availability, disease), they occur in far greater densities (Liberg *et al.*, 2000; Sims *et al.*, 2008). While hunting does still occur amongst owned cats, this can be expected to be far greater in feral individuals (Krauze-Gryz *et al.*, 2012). Although pet cats likely do not impact wild prey species to the same degree as feral cats (as discussed in this section), concerns have been raised about their impacts as well (Doherty *et al.*, 2016).

The location of a study may influence the results. For example, a number of studies have suggested that cats hunt in accordance with prey availability (Churcher and Lawton, 1987; Molsher *et al.*, 1999; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015; Krauze-Gryz *et al.*, 2017; Read *et al.*, 2018). Since the availability of different taxa can vary between locations (e.g. oceanic islands and mainland sites), the prey proportions of cats in these areas can also be expected to vary accordingly. There is also seasonal variability in prey availability, such that studies monitoring diet over a short period are unsuitable for extrapolation across a full year. As the breeding season for most birds and mammals begins in the spring (Hume *et al.*, 2016; Couzens *et al.*, 2017), predation by pet cats will likely be higher during the spring and summer periods than the winter months. Studies which monitor cats across one or two seasons (e.g. Woods *et*

al., 2003) can bias the results, either over- or under-estimating prey caught annually. McGregor *et al.* (2015) found that cats in Australia have greater hunting success in open environments over those of a more closed nature. This finding is perhaps echoed in other research, finding a difference in prey returns between urban and rural cats (with urban areas being more closed habitats, Brickner-Braun *et al.*, 2007; Blancher, 2013; Kauhala *et al.*, 2015; Krauze-Gryz *et al.*, 2017).

2.1.2 **Monitoring** methods

There are four key methods employed to measure the number of prey captured or returned by cats. Commonly, pet cats are monitored using owner surveys, providing estimates of prey returned home (Robertson, 1998; Woods *et al.*, 2003; Kays and DeWan, 2004; Baker *et al.*, 2005; Thomas *et al.*, 2012; McDonald *et al.*, 2015). This is an effective and popular method, since it is non-invasive and does not require land-owner permissions or extensive fieldwork. There can, however, be problems with owner identification skills and there may be misidentified prey items if photographs are not provided for researchers to check identification. Owned cats can also be monitored using scat analysis, although scats are commonly buried by pet cats due to high territory overlap (Gorman and Trowbridge, 1989). In feral cats, this method is frequently used to monitor the daily prey intake (Nogales and Medina, 1996; Molsher *et al.*, 1999; Pontier *et al.*, 2002; Krauze-Gryz *et al.*, 2012) as feral cats will often leave scats in the open as a scent mark (Gorman and Trowbridge, 1989). The third method often used is stomach and gut analysis, which is appropriate for feral cats which are under population control measures (Fitzgerald *et al.*, 1991; Tidemann *et al.*, 1994; Paltridge *et al.*, 1997; Brickner-Braun *et al.*, 2007). Finally, the use of video cameras attached to a cat's collar can be employed to get an accurate estimate of daily predation, although the battery life of these devices can be variable (Loyd *et al.*, 2013; McGregor *et al.*, 2015; Hernandez *et al.*, 2018; Bruce *et al.*, 2019). There are clear differences between the methods used and the resulting data can often reflect this. For example, all stomach analyses are

typically conducted on feral individuals, increasing the estimates of prey caught per year. Similarly, return studies cannot be conducted on feral cats, so cats in these studies are all owned. Due to this relationship between method used and cat type, one cannot directly compare the two approaches. Also, it can be difficult to identify whether differences in prey proportions are due to method or cat type.

2.1.3 Aims and hypotheses

Here, the aim is to investigate the potential explanatory variables which influence the prey proportions reported in studies across the World, and to explore the biases produced by using different methods of data collection. It is hypothesised that (1) since cats are better adapted to hunting small ground-dwelling prey (Leyhausen, 1979), mammals will be the top component in the cats' wild prey diet. Secondly, (2) there will be an important difference between the prey recorded for each different method used, as some studies use owner questionnaires (thus not seeing all captured prey), whereas others use technology like cat-mounted video cameras (showing all prey captured). Since Australia and New Zealand do not share the faunal composition of areas such as mainland Europe and the United States (Inns, 2009; Cogger, 2018), it is also hypothesised that (3) there will be an important effect of the location of studies on the prey proportions reported.

2.2 **Methods**

2.2.1 Literature compilation and selection

In order to determine whether the sometimes contradictory findings outlined above showed general patterns, allowing more general conclusions, a meta-analytical study combining findings

from all relevant published scientific sources was conducted. These were analysed using both beta-regression models and Principal Component Analysis.

A Web of Science and Google Scholar search for the following terms was conducted, including studies up until March 2022:

(cat OR cats OR catus) AND (predat* OR prey OR threat OR kill OR risk*) AND (wildlife OR bird* OR "small mammal*" OR amphibian* OR reptile*)

The studies retrieved through this initial search were then filtered to retain the following Level 1 criteria:

a) Articles on prey preference, diet, predation rate, return rate, and impact of cats
b) Articles on influencing factors of predation by cats (e.g. bell on collar)
c) Multi-predator articles, including cats

This left 142 studies which met the above criteria, all of which were then examined and either deemed suitable or unsuitable for review (Figure 2. 1). These were then reviewed a second time (level 2 criteria), and suitable studies gave a total number of prey captured (using the video approach), returned (questionnaires), or eaten (scat and stomach analyses), along with a breakdown of prey, either by taxon or, where available, species. Where consumption studies (scat and stomach) gave Relative Frequency of Occurrence (RFO, the number of occurrences of a prey type divided by total number of occurrences of all prey types x 100) data, these were recalculated to provide the number of prey consumed (*N* data). Frequency of Occurrence (FO, percentage of a scats or stomachs containing a prey type) and biomass (biomass ratio of each prey type) studies were excluded. Although FO and biomass are useful measures of consumption (Reynolds and Aebischer, 1991) and are widely used (Nogales *et al.*, 1988; Tidemann *et al.*, 1994; Medina *et al.*, 2008; Shionosaki *et al.*, 2015), they are not comparable with prey caught or prey returned studies, since they do not express the total number of prey consumed.

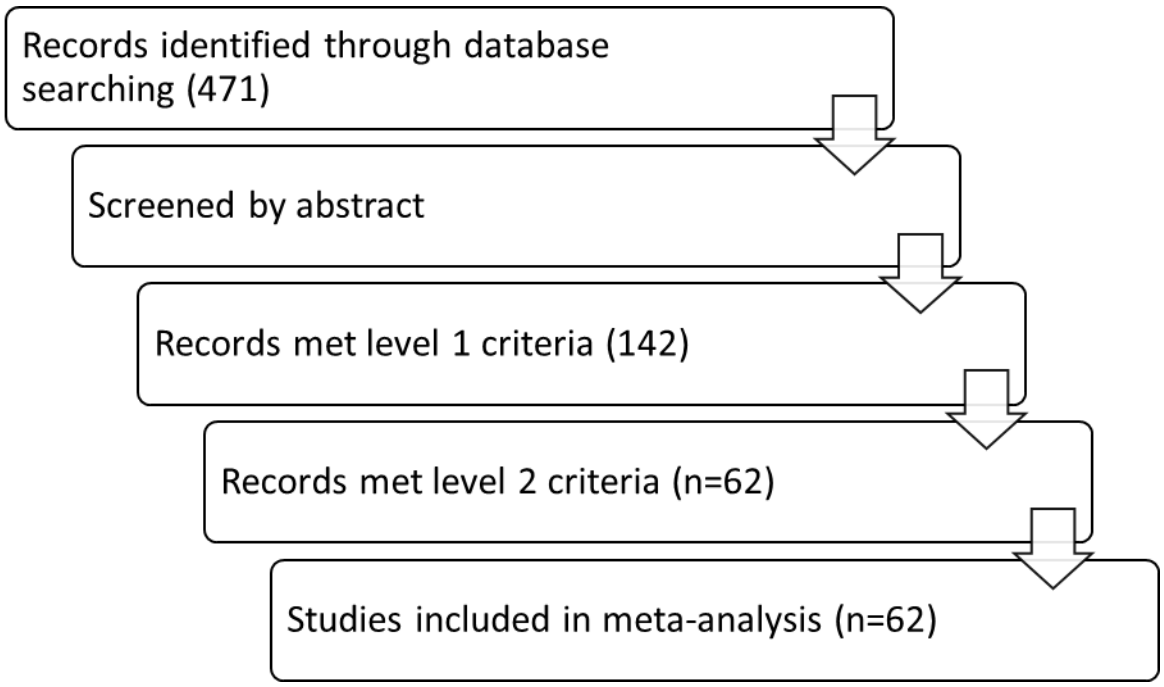


Figure 2. 1. The process of study selection.

2.2.2 Analysis

Since data for invertebrates do not appear to have been consistently recorded (particularly in return questionnaires), data on such species were omitted from analyses here. Invertebrates usually have a high productivity rate, do not constitute a large amount of cat dietary biomass, and are not recorded by all authors or data collection methods. Where a study reported invertebrates in their results, the proportions have been recalculated to exclude this group.

Scat and stomach methods were combined into one category (consumed) to examine the influence of the three key methods used (returned as identified by questionnaires, consumed, and caught via video footage). Data were first analysed including five video studies with video footage data. Due to this low sample size, and therefore reduced reliability, this category was then removed and the data re-analysed to investigate the influence that this had on analytical

outputs and statistical importance. Where 'herpetofauna' was stated in a study's results, this was removed from the analyses for reptiles and amphibians (three studies). Location was split into three categories (island, mainland, and Australia and New Zealand- 'AN') to assess the influence on reported prey proportions, as Australasian faunal composition is known to differ from the rest of the world with New Zealand having no native terrestrial mammals (IUCN, 2020). For the purposes used here, an island is defined as being an area of land no larger than 100,000 km^2. Studies were classified according to their length, i.e. whether they lasted for at least 12 months, or less. Due to the seasonal variability of prey availability, this is of high importance when compiling data for annual extrapolation. It was also noted whether cats in each study were owned (being intentionally provided with food and shelter) or feral (no intentional feeding). There was a strong correlation between the methods used and cat type (feral or owned) (Pearson R_{69} = -0.686, $p < 0.001$) and therefore, only one of these two factors would be considered for model inclusion, the most influential being selected for the final model. The effect of method or cat type, location, and duration were tested on the dependent variables, which were the proportional data for each taxon. Mammal and bird data were tested using a simple beta-regression for both 'including video' and 'no video' datasets (Table 2. 1), following a backward stepwise approach. Due to the presence of one zero for birds and a further zero in the mammal data ('including video' dataset), these data were initially not suitable for beta regression (as data cannot contain zeros or ones), and were therefore transformed using the following equation, where N is the sample size and Y_i represents individual prey proportions (Zuur and Ieno, 2016):

$$(Y_i \times (N-1) + 0.5) / N$$

A high number of zeros in the reptile and amphibian data led to zero-one inflated beta-regressions being considered most appropriate (Table 2. 1). While zero-inflation models are an option in many cases, only 13 (81.7%) of the data points for fish were above zero, and just one was above 3 (% of diet). This indicates that while a zero-inflation model could be applied, results may be difficult to accurately interpret. Therefore, no statistical analyses were conducted on fish data. All beta-regression tests were applied in a Bayesian framework, due to a lack of suitable

frequentist software packages. Goodness of fit was determined by plotting the posterior mean of Y against observed Y.

Table 2. 1. The type of test applied to each taxon and whether transformation took place (Y-yes or N-no).

Inc. Video	Taxa	Transformed?	Test
	Mammals	N	Beta-regression (simple)
	Birds	Y	Beta-regression (simple)
	Reptiles	N	Beta-regression (zero-one inflated)
	Amphibians	N	Beta-regression (zero-one inflated)
No Video			
	Mammals	N	Beta-regression (simple)
	Birds	Y	Beta-regression (simple)
	Reptiles	N	Beta-regression (zero-one inflated)
	Amphibians	N	Beta-regression (zero-one inflated)

The proportions of each taxon reported were used in a Principal Component Analysis (PCA), and a further cluster analysis to identify clustered studies and possible outlier studies, for which, fish data were included. The number and content of clusters which best described the proportional data were identified using the K-means method and Euclidean distance.

For a more detailed analysis on different prey types, a sub-set of 13 studies were found after a thorough search (six using scat and stomach analysis, and a further seven regarding prey returned). These articles were selected as being mainland studies and from European (including UK) countries, to ensure comparability of prey species, which provide in-depth prey species information, allowing for the grouping of species into the following:

1. Rodents, including mice, rats, and voles
2. Insectivores, including shrews, moles, and bats
3. Medium mammals, including rabbits, hares, and mustelids
4. Birds, including eggs

5. Reptiles
6. Amphibians
7. Fish

After checking test assumptions of normality (using Shapiro-Wilk tests) and homogeneity of variances (using Fligner-Killeen tests, see Appendix 2. 1 for details), the prey proportions recorded were compared depending on the method employed, i.e. consumed or returned prey, to ultimately see whether some species groups may have been under- or over-estimated in previous studies (Wilcoxon Rank Sum). Fish were not included here, as a very high number of zeros were recorded. All analyses were carried out using R version 4.0.2 and R Studio version 1.0.153 (R Core Team, 2016; R Studio Team, 2020), and using the packages 'R2jags' (Su and Yajima, 2020), 'zoib' (Liu and Kong, 2019), 'NbClust' (Charrad *et al.*, 2014), 'vegan' (Oksanen *et al.*, 2019), and 'flexclust' (Leisch, 2006).

2.3 **Results**

2.3.1 Overview

Sixty-two articles were found to meet the inclusion criteria (Tables 2.2 and 2.3). Studies were compiled from across the globe, including data from 18 countries. Although 62 articles were found to be suitable, these contained details of 75 separate studies, for example, where research was conducted using more than one method. Of these 75, the number conducted in each of the three location categories, along with the three methodologies, are given in Table 2. 4.

Table 2. 2. Number of studies according to sampling description of the owned and feral cat studies used in these analyses. The total number of studies is 62 (found in Table 2. 3), although sums for specific sampling features can exceed this where, for example, a study uses both feral and owned cats.

Sampling	Owned cat	Feral cat
Sample type		
Scat	2	21
Stomach	1	17
Return	29	-
Video	3	2
Location		
Mainland	26	16
Island	1	14
Australia & New Zealand	8	10
Sample size (cats)		
1-50	13	-
51-100	7	-
101-150	6	-
151-200	1	-
201+	5	-
Sample size (scat/stomach)		
1-50	-	8
51-100	1	4
101-150	-	8
151-200	-	3
201+	1	17
Sample size (prey)		
1-250	13	20
251-500	7	10
501-1000	4	5
1001+	10	2
Study period		
12 months +	23	29
Less than 12 months	12	11

Table 2. 3. Percentage of mammals, birds, reptiles, amphibians, and fish in the diets of cats recorded in 75 studies (62 articles) estimating cat predation rates (retrieved through Web of Science and Google Scholar search). Under 'method', 'Qu' stands for questionnaire studies. An island is classed as a piece of land no larger than 100,000 km^2. Where there are multiple values, more than one treatment was applied. Australia and New Zealand are denoted as 'AU/NZ'. Where 'herpetofauna' was stated, cells are merged (n = 3). Dark grey shading denotes a higher percentage, and light grey a lower percentage. Longer studies (over 12 months) are marked with an *.

Reference	Year	F/O	Method	Country	Location	12 months +	Mammals	Birds	Reptiles	Amphibs	Fish
Churcher & Lawton	1987	O	Qu	UK	Mainland	*	64.4%	35.8%	0.0%	0.0%	0.0%
Mitchell & Beck	1992	O	Qu	US	Mainland	*	54.0%	19.8%	22.5%	3.7%	0.0%
Carss	1995	O	Qu	UK	Mainland	*	85.0%	14.7%	0.2%	0.0%	0.0%
Barratt	1997	O	Qu	AU	AU/NZ	*	65.0%	27.0%	6.7%	1.1%	0.2%
Howes	2002	O	Qu	UK	Mainland	*	69.1%	30.5%	0.0%	0.2%	0.1%
Ruxton *et al.*	2002	O	Qu	UK	Mainland		69.5%	22.0%	0.0%	8.5%	0.0%
Ruxton *et al.*	2002	O	Qu	UK	Mainland		73.9%	21.2%	0.0%	4.9%	0.0%
Gillies & Clout	2003	O	Qu	NZ	AU/NZ	*	59.9%	25.7%	14.4%	0.2%	0.0%
Woods *et al.*	2003	O	Qu	UK	Mainland		70.4%	24.2%	1.0%	4.2%	0.2%
Kays & DeWan	2004	O	Qu	US	Mainland		86.4%	13.6%	0.0%	0.0%	0.0%
Baker *et al.*	2005	O	Qu	UK	Mainland	*	71.6%	28.0%	0.0%	0.4%	0.0%
Baker *et al.*	2005	O	Qu	UK	Mainland	*	75.1%	24.0%	0.0%	0.8%	0.0%
Nelson *et al.*	2005	O	Qu	CH	Mainland		65.0%	32.3%	0.6%	2.0%	0.1%
Brickner-Braun *et al.*	2007	O	Qu	IL	Mainland	*	55.6%	20.1%	24.4%	0.0%	0.0%

Reference	Year	F/O	Method	Country	Location	12 months +	Mammals	Birds	Reptiles	Amphibs	Fish
Calver *et al.*	2007	O	Qu	AU	AU/NZ		56.7%	15.4%	28.0%		0.0%
Calver *et al.*	2007	O	Qu	AU	AU/NZ		54.7%	25.5%	19.8%		0.0%
Flux	2007	O	Qu	NZ	AU/NZ	*	58.2%	40.0%	1.6%	0.2%	0%
Baker *et al.*	2008	O	Qu	UK	Mainland	*	69.3%	20.6%	5.5%	4.4%	0.0%
Morgan *et al.*	2009	O	Qu	NZ	AU/NZ	*	50.2%	26.2%	22.6%	0.6%	0.3%
van Heezik *et al.*	2010	O	Qu	NZ	AU/NZ	*	42.7%	46.9%	10.1%	0.2%	0.0%
Tschanz *et al.*	2011	O	Qu	UK	Mainland		87.9%	12.1%	0.0%	0.0%	0.0%
Krauze-Gryz *et al.*	2012	O	Qu	PL	Mainland	*	76.0%	14.3%	7.8%	0.8%	1.0%
Thomas *et al.*	2012	O	Qu	UK	Mainland	*	64.7%	30.5%	0.5%	4.4%	0.0%
Kauhala et al.	2015	O	Qu	FI	Mainland		79.2%	17.8%	3.0%		0.0%
McDonald et al.	2015	O	Qu	UK	Mainland	*	62.5%	28.3%	9.3%	0.0%	0.0%
Krauze-Gryz et al.	2017	O	Qu	PL	Mainland	*	72.7%	15.5%	9.7%	0.9%	1.2%
Mori et al.	2019	O	Qu	IT	Mainland	*	37.8%	35.4%	23.7%	3.1%	0.0%
Piontek *et al.*	2021	O	Qu	PL	Mainland	*	73.2%	23.2%	3.6%	0.0%	0.0%
Mella-Méndez *et al.*	2022	O	Qu	MX	Mainland		10.1%	20.1%	46.6%	23.3%	0.0%
Loyd et al.	2013	O	Video	US	Mainland	*	32.2%	16.1%	45.2%	6.4%	0.0%
McGregor et al.	2015	F	Video	AU	AU/NZ	*	21.5%	10.7%	17.5%	50.1%	0.0%
Hernandez et al.	2018	F	Video	US	Mainland		9.7%	2.1%	31.3%	57.1%	0.0%
Bruce et al.	2019	O	Video	NZ	AU/NZ		0.0%	11.1%	88.9%	0.0%	0.0%
Seymour et al.	2020	O	Video	ZA	Mainland		31.3%	2.1%	64.6%	2.1%	0.0%

Reference	Year	F/O	Method	Country	Location	12 months +	Mammals	Birds	Reptiles	Amphibs	Fish
Nilsson	1940	F	Scat	US	Mainland	*	66.1%	33.9%	0.0%	0.0%	0.0%
Eberhard	1954	F	Scat	US	Mainland	*	73.5%	26.5%	0.0%	0.0%	0.0%
Karl & Best	1982	F	Scat	NZ	AU/NZ	*	59.9%	15.9%	24.3%	0.0%	0.0%
Apps	1983	F	Scat	ZA	Island	*	62.4%	37.6%	0.0%	0.0%	0.0%
Nogales et al.	1988	F	Scat	ES	Island		58.5%	4.7%	36.6%	0.0%	0.0%
Fitzgerald et al.	1991	F	Scat	NZ	AU/NZ		86.9%	13.1%	0.0%	0.0%	0.0%
Weber & Dailly	1998	F	Scat	CH	Mainland	*	94.6%	5.4%	0.0%	0.0%	0.0%
Smucker et al.	2000	F	Scat	US	Island	*	68.3%	31.7%	0.0%	0.0%	0.0%
Bonnaud et al.	2007	F	Scat	FR	Island	*	91.2%	6.9%	1.9%	0.0%	0.0%
Phillips et al.	2007	F	Scat	US	Island	*	66.1%	4.7%	29.2%	0.0%	0.0%
Matias & Catry	2008	F	Scat	UK	Island		77.8%	22.2%	0.0%	0.0%	0.0%
Medina et al.	2008	F	Scat	ES	Island		78.7%	5.9%	15.6%	0.0%	0.0%
Peck et al.	2008	F	Scat	FR	Island		75.5%	21.7%	2.8%	0.0%	0.0%
Faulquier et al.	2009	F	Scat	FR	Island	*	53.5%	46.5%	0.0%	0.0%	0.0%
Millán	2010	F	Scat	ES	Island	*	89.2%	9.7%	1.1%	0.0%	0.0%
Krauze-Gryz *et al.*	2012	F	Scat	PL	Mainland	*	74.2%	17.4%	3.4%	5.0%	0.0%
Ferreira *et al.*	2014	F	Scat	BR	Mainland	*	76.6%	22.1%	0.0%	1.3%	0.0%
Kitts-Morgan	2015	F	Scat	US	Mainland	*	81.5%	18.5%	0.0%	0.0%	0.0%
Lanszki *et al.*	2015	F	Scat	HR	Island	*	74.7%	5.0%	18.4%	0.0%	1.9%
Lanszki *et al.*	2015	O	Scat	HR	Island	*	58.1%	18.2%	3.4%	0.0%	20.2%

Reference	Year	F/O	Method	Country	Location	12 months +	Mammals	Birds	Reptiles	Amphibs	Fish
Shionosaki *et al.*	2015	F	Scat	JP	Island	*	96.8%	2.5%	0.7%	0.0%	0.0%
Carrion & Valle	2018	F	Scat	EC	Island		42.5%	0.0%	57.5%	0.0%	0.0%
Piontek *et al.*	2021	O	Scat	PL	Mainland	*	76.9%	23.1%	0.0%	0.0%	0.0%
Errington	1936	F	Stomach	US	Mainland	*	86.4%	13.6%	0.0%	0.0%	0.0%
Nilsson	1940	F	Stomach	US	Mainland	*	72.7%	26.3%	0.0%	1.0%	0.0%
McMurray & Sperry	1941	F	Stomach	US	Mainland	*	90.2%	6.5%	3.3%	0.0%	0.0%
Hubbs	1951	F	Stomach	US	Mainland	*	76.5%	19.5%	2.6%	0.0%	1.4%
Parmalee	1953	F	Stomach	US	Mainland	*	75.7%	10.8%	13.5%	0.0%	0.0%
Eberhard	1954	F	Stomach	US	Mainland	*	73.3%	26.7%	0.0%	0.0%	0.0%
Jones	1977	F	Stomach	NZ	AU/NZ	*	58.5%	41.5%	0.0%	0.0%	0.0%
Fitzgerald *et al.*	1991	F	Stomach	NZ	AU/NZ		86.7%	13.3%	0.0%	0.0%	0.0%
Biró *et al.*	2005	F	Stomach	HU	Mainland	*	87.8%	11.2%	0.6%	0.0%	0.4%
Brickner-Braun *et al.*	2007	F	Stomach	IL	Mainland	*	75.0%	6.0%	9.0%	10.0%	0.0%
Peck *et al.*	2008	F	Stomach	FR	Island		57.6%	30.8%	11.6%	0.0%	0.0%
Kutt	2011	F	Stomach	AU	AU/NZ	*	36.8%	13.6%	45.3%	4.3%	0.0%
Krauze-Gryz *et al.*	2012	F	Stomach	PL	Mainland	*	82.2%	8.0%	6.4%	3.2%	0.0%
Yip *et al.*	2014	F	Stomach	AU	AU/NZ		49.0%	12.6%	24.2%	11.6%	2.7%
Yip *et al.*	2015	F	Stomach	AU	AU/NZ		52.2%	12.2%	27.9%	6.4%	1.3%
Read et al.	2018	F	Stomach	AU	AU/NZ	*	51.2%	17.9%	30.9%	0.0%	0.0%

Reference	Year	F/O	Method	Country	Location	12 months +	Mammals	Birds	Reptiles	Amphibs	Fish
Woinarski *et al.*	2018	F	Stomach	AU	AU/NZ	*	29.4%	10.7%	59.0%	0.9%	0.0%
Piontek *et al.*	2021	O	Stomach	PL	Mainland	*	80.0%	20.0%	0.0%	0.0%	0.0%

Table 2. 4. Total number of studies for each location category and method used. Three studies included herpetofauna as a single category and therefore were excluded from amphibian and reptile analyses, affecting total sample sizes (marked with * and **).

Location	**Method**			**Totals**
	Returned	Caught	Consumed	
Mainland	22*	3	17	**42**
Island	0	0	15	**15**
Australasia	7**	2	9	**18**
Totals	**29**	**5**	**41**	

* Amphibians and reptiles were merged in one study
* Amphibians and reptiles were merged in two studies

2.3.2 Including video studies

The model best fitting mammals included the methods used in studies and the location of data collection (V1, Table 2. 5). This model found that the difference between video capture studies and other methods was statistically important, with video studies reporting lower proportions of mammals (Figure 2. 2). This was mirrored in the reptile data (V3), reporting far higher proportions in video studies. The mammal model also found an important difference between Australasian studies and those conducted in mainland environments elsewhere in the world, reporting lower proportions of mammals in Australasia. In contrast, for reptiles, proportions were higher in Australasia compared to other mainland locations (Figure 2. 3**Error! Reference source not found.**).

The model used to analyse the bird data (V2) included the cat type (feral or owned), with birds making up a greater proportion of wild-caught diet for owned cats. There was also a difference between long and short study duration, with studies lasting at least 12 months reporting a higher proportion of birds. The amphibian model (V4) likewise found a difference in study duration, showing that shorter studies reported higher proportions than those lasting 12 months or longer. Cat type (feral or owned) was, again, an important variable in the amphibian model, with feral individuals typically having a higher proportion of this taxon in their diet.

Table 2. 5. The beta-regression outputs (posterior mean (P Mean) and credible interval) described by variables used. Statistically important values are shown in bold text. Re = returned, Ca = caught, Co = consumed, Ml = mainland, Is = island, AN = Australia and New Zealand; L = long, S = short; F = feral, O = owned. Data here included video studies and models are therefore labelled V1-V4.

Model	Variables	P Mean	2.5%	97.5%
V1	Mammals ~ Methods (Re, Ca, Co) + Location (Ml, Is, AN)			
	Methods: Re > Ca	-2.07	**-2.89**	**-1.36**
	Re < Co	0.40	**0.04**	**0.77**
	Ca < Co	2.48	**1.76**	**3.30**
	Location: Ml = Is	-0.25	-0.71	0.22
	Ml > AN	-0.73	**-1.10**	**-0.35**
	Is = AN	-0.48	-0.98	0.03
V2	Birds ~ Type (F, O) + Duration (L, S)			
	Type: F < O	0.54	**0.25**	**0.83**
	Duration: L > S	-0.45	**-0.78**	**-0.13**
V3	Reptiles ~ Methods (Re, Ca, Co) + Location (Ml, Is, AN)			
	Methods: Re < Ca	1.90	**0.95**	**2.82**
	Re = Co	0.42	-0.26	1.09
	Ca > Co	-1.48	**-2.41**	**-0.53**
	Location: Ml = Is	0.02	-0.79	0.81
	Ml < AN	0.82	**0.17**	**1.44**
	Is = AN	0.81	-0.06	1.65
V4	Amphibians ~ Type (F, O) + Duration (L, S)			
	Type: F > O	-0.76	**-1.41**	**-0.07**
	Duration: L < S	0.91	**0.18**	**1.58**

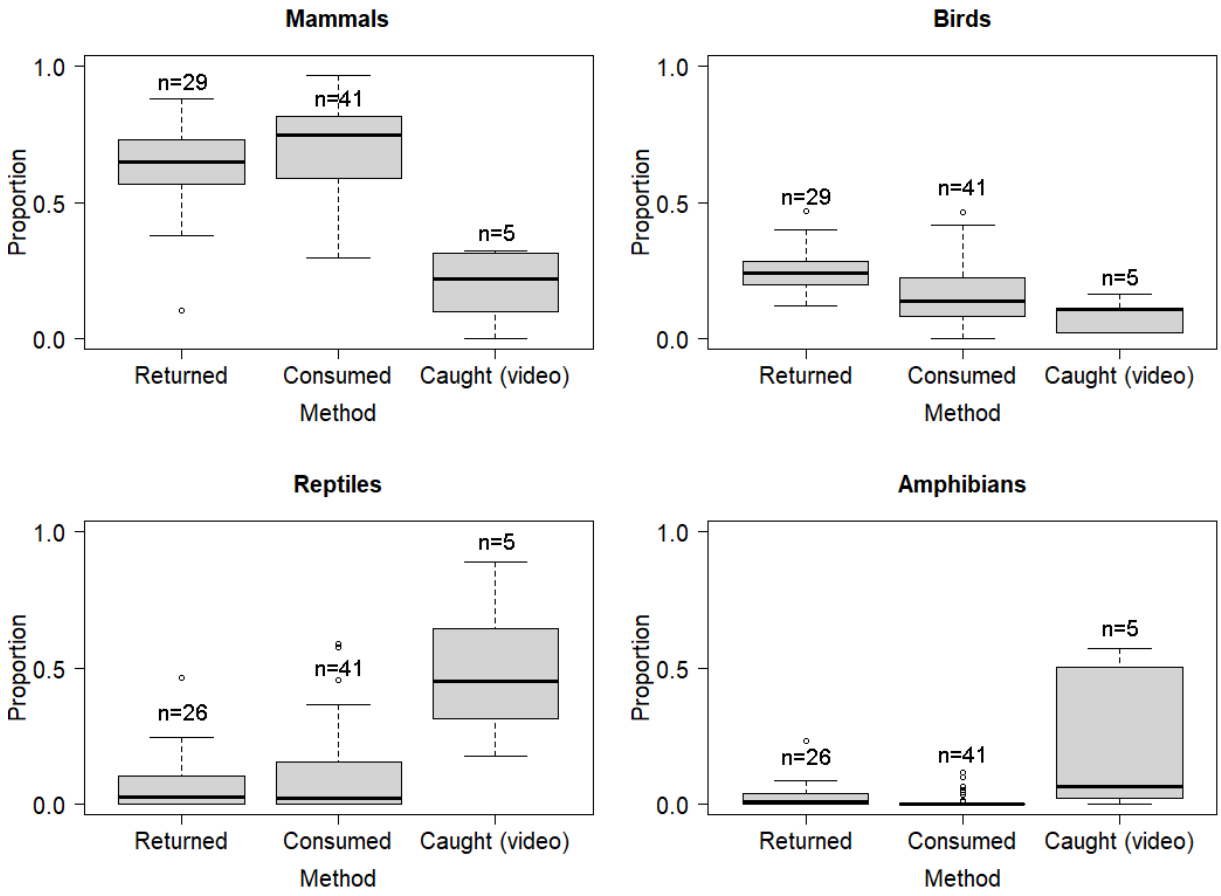


Figure 2. 2. Effect of method used to determine predation on the estimated proportion of total prey returned, consumed, and caught for four main prey groups. Returned = questionnaire studies, consumed = scat and stomach studies, Caught = video studies.

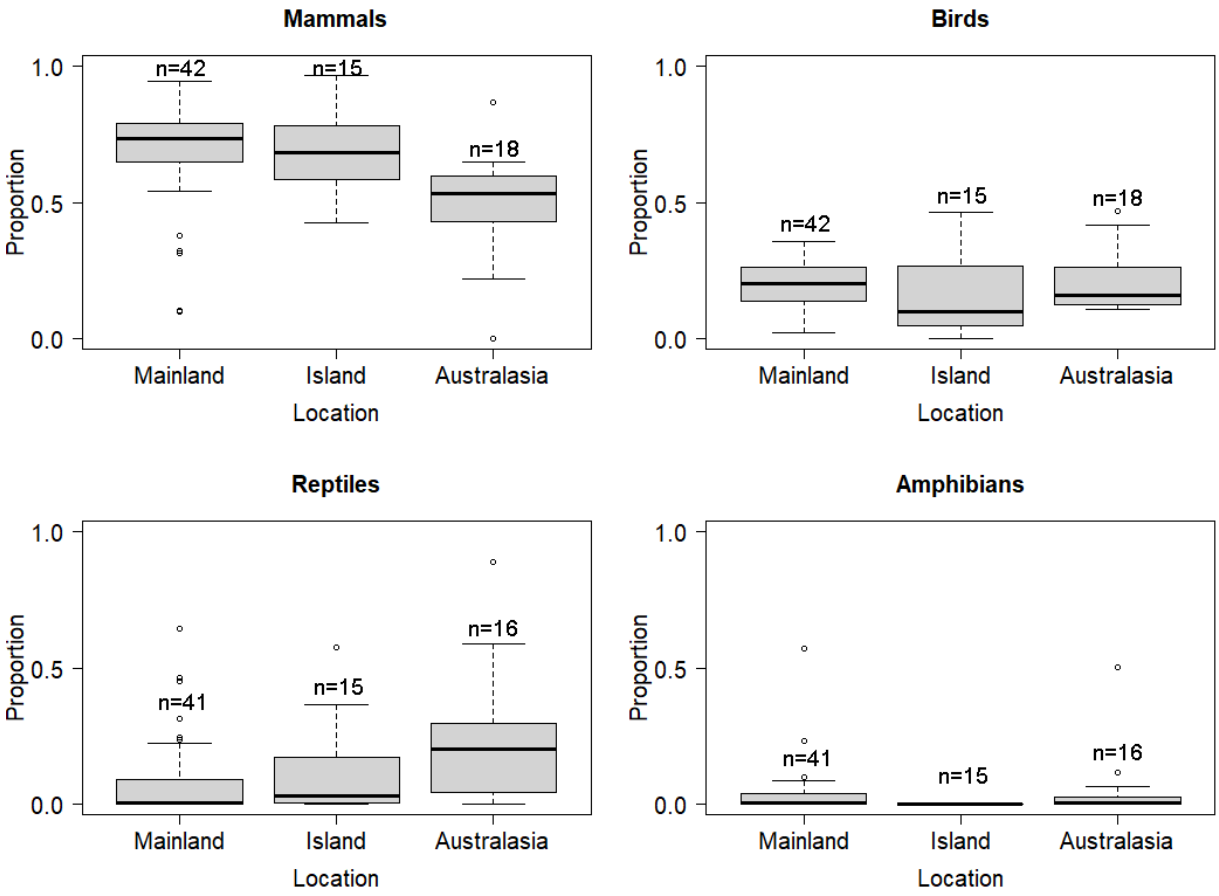


Figure 2. 3. Effect of location (mainland, island, or Australasia) on estimated proportion of total prey recorded for the four main prey groups.

2.3.3 Removing video studies

Removing the five very influential video studies gave qualitatively similar results (Table 2. 6**Error! Reference source not found.**). With video removed, cat type (feral or owned) became a more influential variable than the methods used, and was therefore included in the mammal, bird, and amphibian models. Feral diets contained a higher proportion of mammals and a lower proportion of birds, with the result for amphibians being borderline. Study location was included in the

mammal (NV1, Table 2. 6) and reptile models (NV3), whereby cats in Australasia had a higher proportion of reptiles in their diet, and a lower proportion of mammals than on mainland areas elsewhere.

Table 2. 6. The beta-regression outputs (posterior mean (P Mean) and credible interval) described by variables used. Statistically important values are shown in bold text. Ml = mainland, Is = island, AN = Australia and New Zealand; L = long, S = short; F = feral, O = owned.

Model	Variables	P Mean	2.5%	97.5%
NV1	Mammals ~ Type (F, O) + Location (Ml, Is, AN)			
	Type: F > O	-0.41	**-0.77**	**-0.05**
	Location: Ml = Is	-0.22	-0.68	0.24
	Ml > AN	-0.71	**-1.11**	**-0.30**
	Is = AN	-0.48	-0.99	0.02
NV2	Birds ~ Type (F, O) + Duration (L, S)			
	Type: F < O	0.58	**0.30**	**0.86**
	Duration: L = S	-0.30	-0.63	0.01
NV3	Reptiles ~ Location (Ml, Is, AN)			
	Location: Ml = Is	0.29	-0.43	1.00
	Ml < AN	0.93	**0.23**	**1.61**
	Is = AN	0.64	-0.14	1.42
NV4	Amphibians ~ Type (F, O) + Duration (L, S)			
	Type: F = O	-0.52	-1.09	0.09
	Duration: L < S	1.21	**0.57**	**1.79**

2.3.4 Principal Component Analysis (PCA) and cluster analysis

Cluster analysis divided the studies into two distinct clusters. Cluster one included studies which comprised mostly mammals, followed by birds, reptiles, amphibians, and fish. Cluster two contained those studies which found a high proportion of reptiles and reduced proportions of mammals. Cluster two was made up of 14 studies including all five using video, seven consumption studies (five in Australia, two on islands), and four questionnaires (Figure 2. 4).

There was no clear divide between studies on feral and owned cats, with nine of the 14 studies in cluster two being on feral individuals.

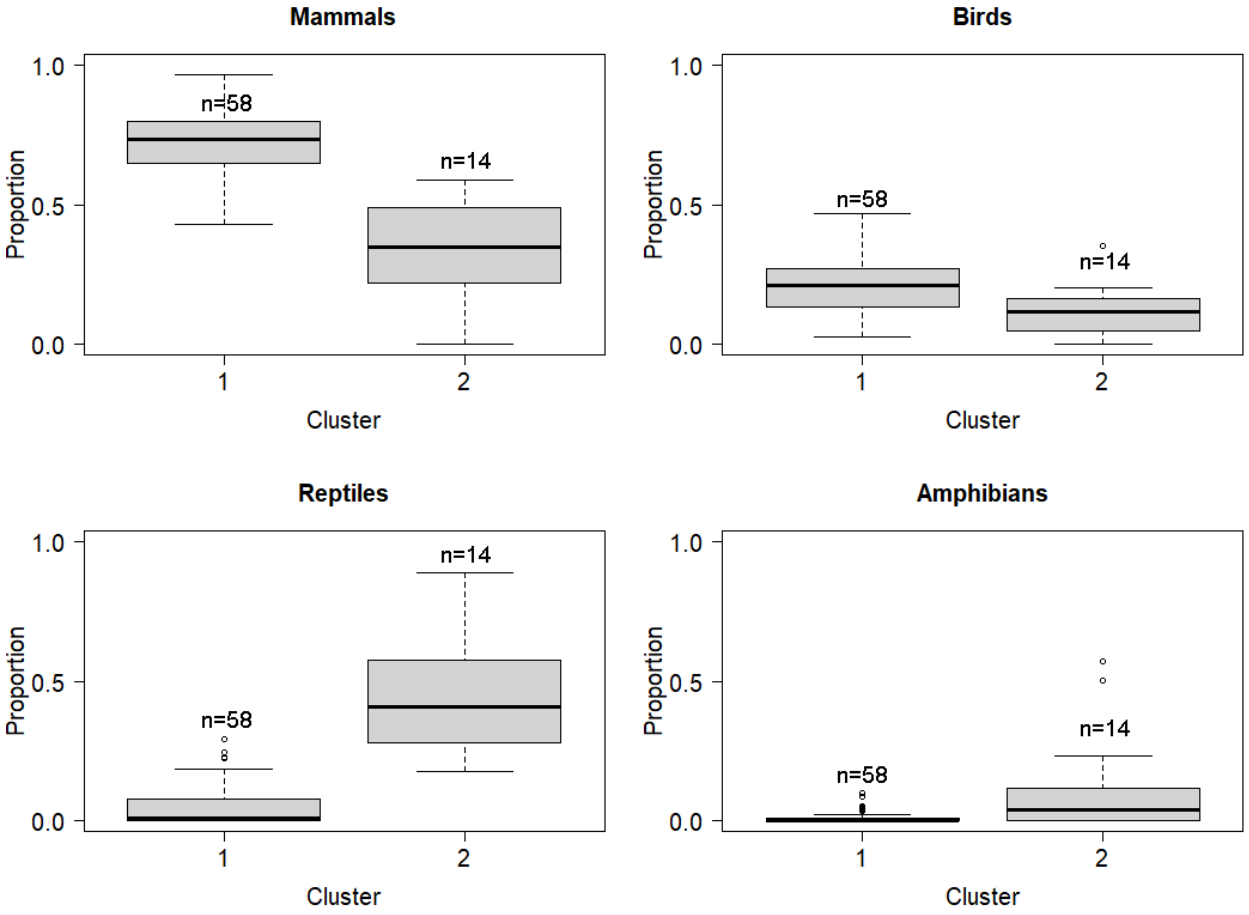


Figure 2. 4. The proportion of prey reported in studies grouped into cluster one and cluster two, for the four main prey groups.

The PCA showed that two principal components were sufficient to explain the data (Figure 2. 5**Error! Reference source not found.**). The scree plot in Figure 2. 5 shows that the first two components have Eigenvalues >1, which means that these components explain more than one explanatory variable. Therefore, two PCs were included here. A PCA biplot (loadings plot) illustrates how strongly each item influences a principal component, and the correlation between different studies (Figure 2. 6, loadings listed in Appendix 2. 2). Thus, amphibians and reptiles were

not related, while proportions of birds and fish were strongly correlated (Figure 2. 6). The convex hulls on the biplot (Figure 2. 6) show large overlap between return and consumption studies, whereas video studies report somewhat unusual proportions of herptiles.

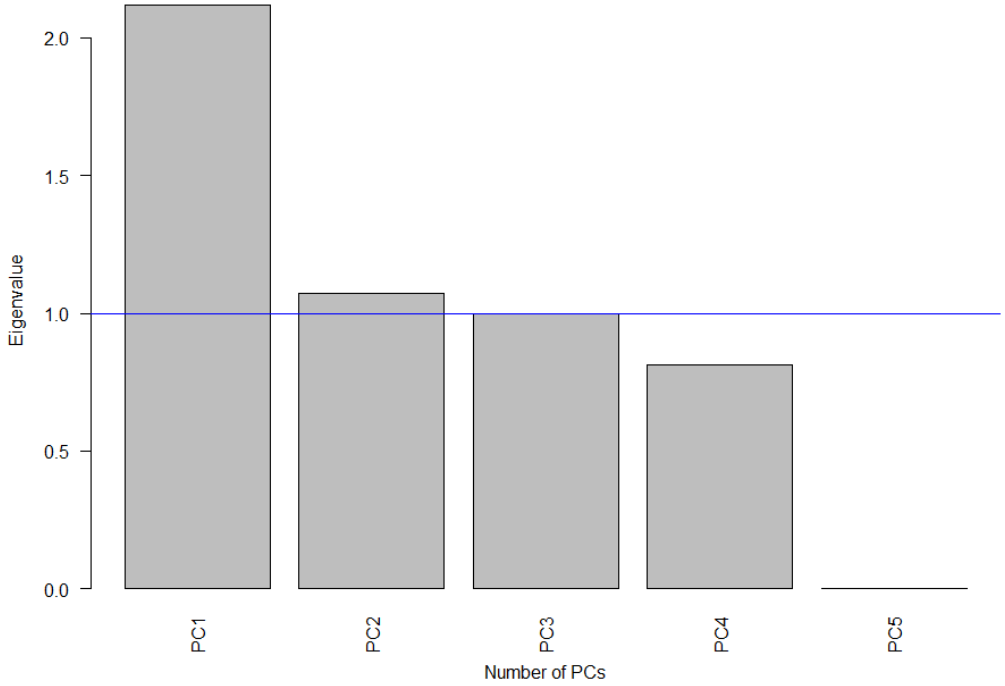


Figure 2. 5. Scree plot showing the Eigenvalues corresponding with each Principal Component (PC). Eigenvalue 1 is represented by a blue line.

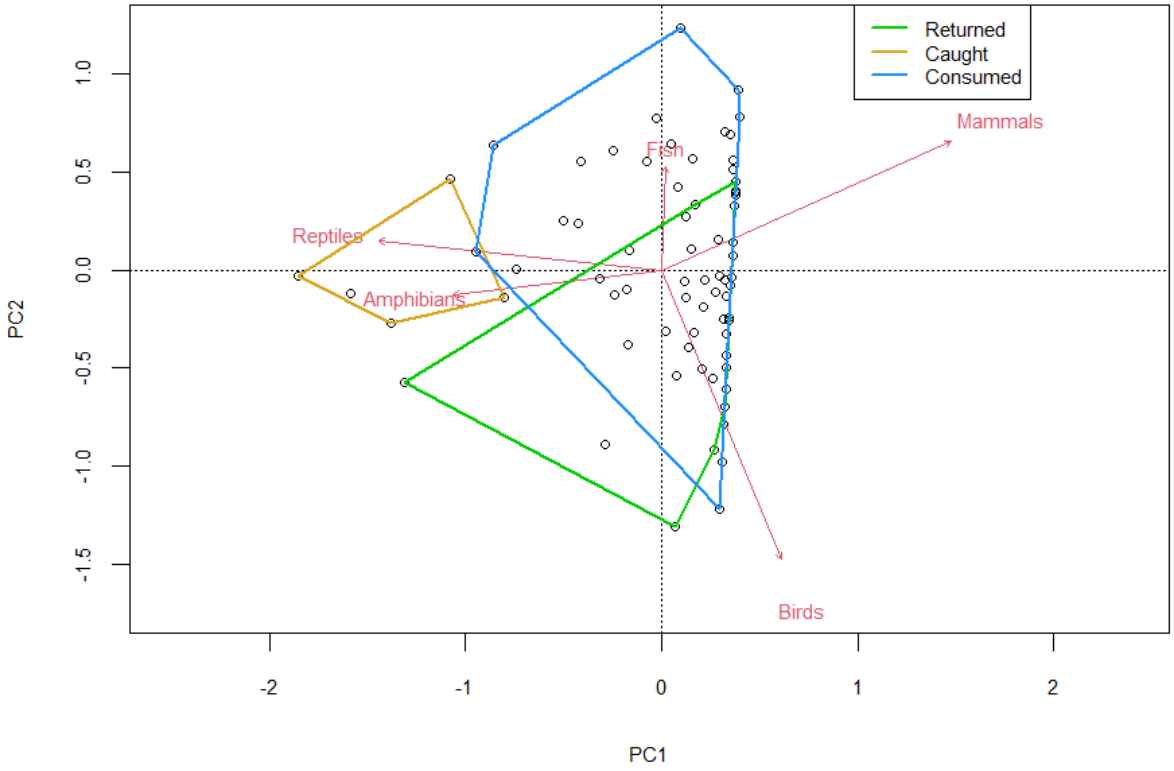


Figure 2. 6. PCA biplot using two principal components where each study is individually represented (scaling=2). Convex hulls are used to highlight studies using each of the three methods: caught (using video footage), consumed (scat and stomach analysis), and returned (using questionnaire methods).

2.3.5 Consumed and returned prey

The subset of studies with more detailed information on prey type (Table 2. 7) found that a significantly higher proportion of rodents were eaten than returned (Wilcoxon rank sum test: $W_{5,6}$ = 37.5, p = 0.022, Table 2. 8, Figure 2. 7). In contrast, a lower proportion of birds and insectivores were eaten than returned, although this was not a significant difference.

Table 2. 7. Proportion of prey groups consumed or returned by cats in six consumption (scat and stomach) and seven return (questionnaire) studies.

Reference	Year	Consumed/ returned	Location	Rodents	Insectivores	Medium Mammals	Birds	Reptiles	Amphibians	Fish
Weber & Daily	1998	Consumed	CH	0.89	0.05	0.00	0.05	0.00	0.00	0.00
Biró *et al.*	2005	Consumed	HU	0.86	0.00	0.02	0.11	0.01	0.00	0.00
Krauze- Gryz *et al.*	2012	Consumed	PL	0.71	0.01	0.01	0.19	0.03	0.05	0.00
Krauze- Gryz *et al.*	2012	Consumed	PL	0.81	0.02	0.00	0.08	0.07	0.03	0.00
Piontek *et al.*	2021	Consumed	PL	0.63	0.11	0.03	0.23	0.00	0.00	0.00
Piontek *et al.*	2021	Consumed	PL	0.68	0.12	0.00	0.20	0.00	0.00	0.00
Churcher & Lawton	1987	Returned	UK	0.38	0.16	0.11	0.36	0.00	0.00	0.00
Woods *et al.*	2003	Returned	UK	0.47	0.14	0.09	0.25	0.01	0.04	0.00
Baker *et al.*	2005	Returned	UK	0.76	0.01	0.01	0.22	0.00	0.01	0.00
Thomas *et al.*	2012	Returned	UK	0.55	0.04	0.00	0.35	0.00	0.05	0.00
Krauze- Gryz *et al.*	2012	Returned	PL	0.66	0.09	0.01	0.15	0.08	0.01	0.01
Krauze- Gryz *et al.*	2017	Returned	PL	0.63	0.09	0.00	0.16	0.10	0.01	0.01
Piontek *et al.*	2021	Returned	PL	0.58	0.14	0.01	0.23	0.04	0.00	0.00

Table 2. 8. Prey composition reported as mean proportion (±SE) for a sample of prey return studies (n = 7) and consumption studies (n = 6). Significant results are marked with an * (Wilcoxon rank sum tests).

Prey category	**Proportion of returned prey: mean (±SE)**	**Proportion of consumed prey: mean (±SE)**	***W***	***p***	**n**
Rodents	0.58 (±0.05)	0.76 (±0.04)	37.5	0.022*	13
Insectivores	0.1 (±0.02)	0.05 (±0.02)	11.5	0.197	13
Medium mammals	0.03 (±0.02)	0.01 (±0.01)	16.5	0.551	13
Birds & eggs	0.25 (±0.03)	0.14 (±0.03)	7.5	0.063	13
Reptiles	0.03 (±0.02)	0.02 (±0.01)	17	0.598	13
Amphibians	0.02 (±0.01)	0.01 (±0.01)	15.5	0.449	13

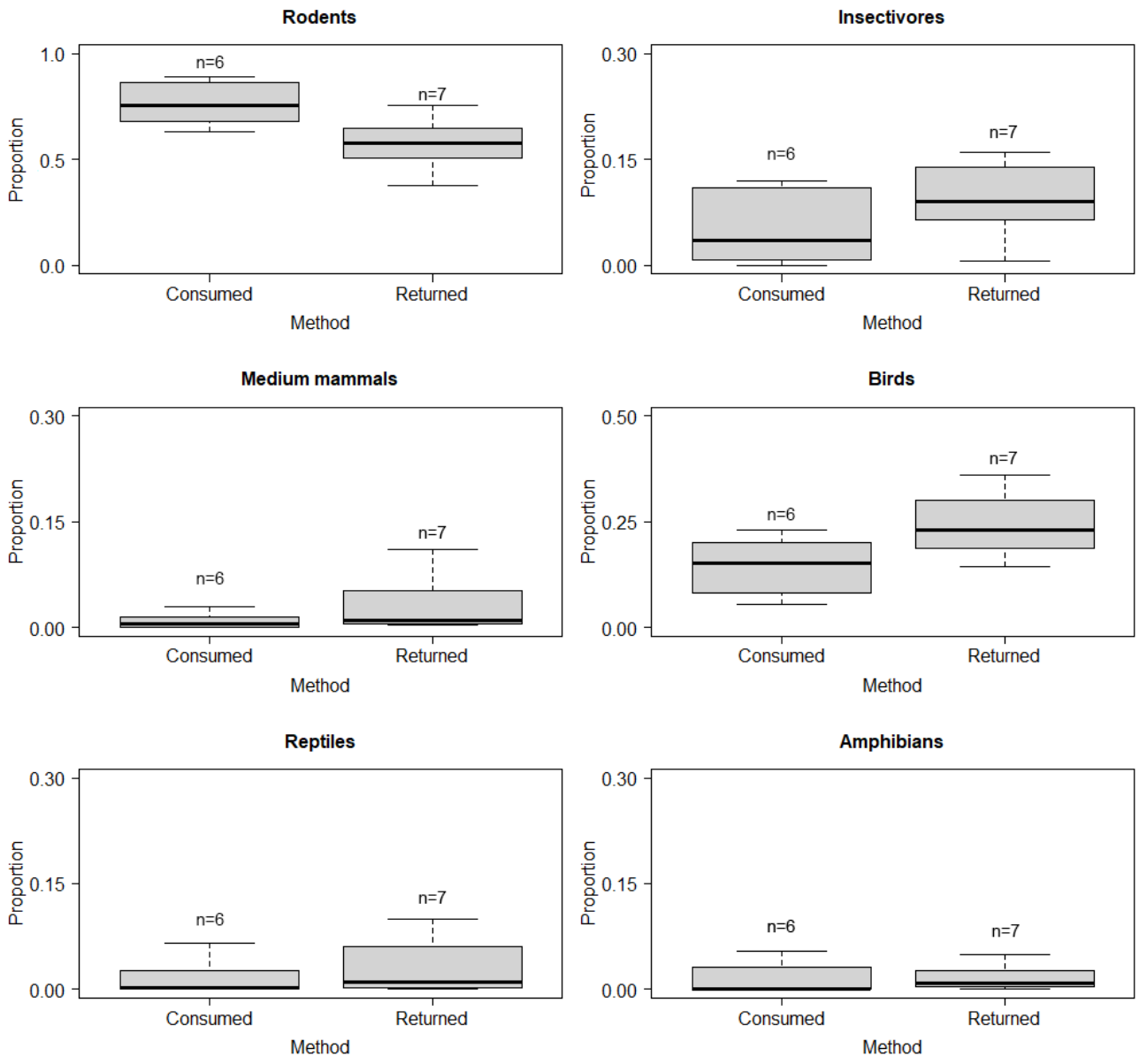


Figure 2. 7. Proportion of total prey returned (questionnaire-based studies) and consumed (scat and stomach studies) for the six main prey groups. Note the differing scales.

2.4 **Discussion**

2.4.1 Prey proportions

In a large majority of studies, the wild diet of cats consists of mostly mammals, followed by birds. However, in some studies (e.g. McGregor *et al.*, 2015; Carrion and Valle, 2018; Hernandez *et al.*, 2018; Woinarski *et al.*, 2018), there is a shift in prey proportions towards reptiles and amphibians. Woinarski *et al.* (2018) and McGregor *et al.* (2015) conducted studies in mainland Australia, where the prey species composition is arguably different compared to areas such as mainland Europe (see 6.3). Many studies have suggested that cats hunt in accordance with prey availability (Churcher and Lawton, 1987; Molsher *et al.*, 1999; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015; Krauze-Gryz *et al.*, 2017; Read *et al.*, 2018). Indeed, 61 articles (including some of the focal studies analysed here) were found to contain prey species lists and within those studies, 782 prey species were either caught, returned, or eaten by cats, illustrating their generalist nature (Appendix 2. 3).

The PCA and cluster analysis found a distinct cluster containing those studies which found a higher proportion of amphibians and reptiles than the majority (cluster two), with one study even recording zero mammals (Bruce *et al.*, 2019), whereas cluster one contained research which points to mammals and birds being the main component of a cat's diet. Cluster one was more representative of the sample presented here, containing 58 studies.

2.4.2 Data collection methods used

The PCA suggests that the methods used in such studies may influence the proportions of prey reported. In Australia, Woinarski *et al.* (2018), analysing stomach contents, found reptiles to be the most predated group (by feral cats) while McGregor *et al.* (2015), utilising collar-mounted video cameras, showed that 43.8% of prey caught were amphibians (also by feral cats). As not all

captures are eaten, it may be that amphibians are more commonly caught than is evident from prey return and stomach and scat analysis studies. Hernandez *et al.* (2018) also used video cameras on an island in Georgia, USA and likewise found amphibians to be the highest predated group. In contrast, return studies in the same country (although different states and on the mainland) show mammals to constitute the highest proportion of total prey (Mitchell and Beck, 1992; Kays and DeWan, 2004). Generally, a lower proportion of mammals was recorded using video than any other method. This may be partly due to mammals making up a smaller percentage of all vertebrates captured, at least in the five video studies, two of which took place in Australia and New Zealand, one on a USA island, one in mainland USA, and one in South Africa. Furthermore, mammals may be more likely to be returned or consumed than discarded. This may also suggest that video studies in some way impede the cats' ability to hunt mammals, although this is unlikely as they are best suited to capturing ground-dwelling prey (Leyhausen, 1979) and the cameras are generally of small proportions and weight (Bruce *et al.*, 2019; Seymour *et al.*, 2020). Similarly, video capture studies also report a lower proportion of birds caught, than are reported in owner questionnaires, which may be due to detectability bias (which is further explored in section 2.4.5).

However, as both the returned and consumed studies concur that mammals are quite consistently the highest predated taxon, it is perhaps likely that the low mammal figures reported in video studies is due to their location and the availability of this taxon. In addition, some models of video camera may emit a light (to indicate recording mode), potentially acting as a warning for small mammals at night. When video studies were removed, the method of data collection used was not found to be a statistically important variable and was therefore deemed unsuitable for model inclusion. This highlights the large effect that these five video studies have on the wider dataset.

The PCA and cluster analysis also showed a high correlation between the video studies which have high amphibian and reptile counts, suggesting that where a cat's diet is high in reptiles, it is also high in amphibians. Seven consumption studies were also included in this cluster, five of

which took place in Australia, highlighting the differences in faunal composition in different locations.

2.4.3 Islands, mainland, and Australasian studies

Study location influenced the proportions of both mammals and reptiles reported. For mammals, proportions reported in Australia and New Zealand were lower than those in mainland areas elsewhere in the world. This can be explained, in part, by the faunal composition of Australasia, with New Zealand having no native terrestrial mammals (IUCN, 2020). The difference between island studies and those in Australasia could be classed as 'borderline' important (as the credible interval is close to the threshold for importance), again with Australasian studies reporting lower proportions of mammals. Similarly to New Zealand, islands typically have few native mammals, although they are often largely inhabited by invasive mammals such as rabbits and rat species, providing ample food resources for cats (Fitzgerald *et al.*, 1991; Tidemann *et al.*, 1994; Nogales and Medina, 1996; Pontier *et al.*, 2002; Bonnaud *et al.*, 2007; Matias and Catry, 2008; Shionosaki *et al.*, 2015). Indeed, a similar review of the diet of the generalist and opportunistic red fox (*Vulpes vulpes*) found that in Australia, small mammals constituted a smaller proportion of total diet than anywhere else in the world, yet reptiles made up a larger proportion (Castañeda *et al.*, 2022).

Reptile data showed no difference between mainland and island proportions, yet important differences were again found between Australasia and mainland study sites elsewhere in the world. However, unlike mammals, Australasian reptile proportions were higher than both island (the effect being 'borderline' important) and mainland locations elsewhere in the world. This may be attributed to the composition of species, where Australia is home to 1218 herptile species (Cogger, 2018), whereas the UK has only 13 native species (Inns, 2009). The removal of video studies from the dataset did not have a great effect on location, as the removed studies were conducted in Australasia, mainland, and island sites.

2.4.4 Feral and owned cats

Prior to the removal of video studies, cat type was included in the beta-regression models for both amphibians and birds. Feral individuals had higher proportions of amphibians in their diets than owned cats. However, the cluster analysis (including video) showed that there was no distinction between feral and owned cats, with an even spread throughout.

Once re-analysed without the inclusion of video data, cat type also became an important factor included in the mammal model. While feral individuals appear to have a greater proportion of mammals in their diet, the statistical importance of this result is somewhat borderline. The strongest difference between feral and owned cats concerns the proportion of birds in the diet, with owned individuals consuming or returning higher proportions of birds. Due to the relationship between methods and cat type, owned individuals are almost always (29 out of 32 records, excluding video studies) monitored using return questionnaires. Therefore, the higher proportion of birds strongly suggests a bias in detectability of species by cat owners, with bird records perhaps being closer to the true capture rate than mammals, for example, as the evidence of bird capture is more easily visible.

2.4.5 Detectability and palatability

The palatability and detectability of different prey categories is an important, yet often overlooked, consideration. It is widely thought that insectivores are unpalatable to cats (Toner, 1956; Turner and Bateson, 2000; Krauze-Gryz *et al.*, 2012; Kauhala *et al.*, 2015). Indeed, Kauhala *et al.* (2015) found that insectivores and reptiles are more commonly brought home by younger cats, suggesting that with age and experience, cats learn that these species are less palatable.

Here, the mammal category was further divided into three sub-groupings (rodents, insectivores, and medium sized mammals) for studies conducted in Europe on mainland sites, as the location

of studies has been found here to influence the results of dietary research. This found significant differences between eaten and returned rodents, with a higher proportion being consumed (scat and stomach analyses), suggesting that rodents are highly palatable and frequently appear in the consumed diet of feral cats (Fitzgerald *et al.*, 1991; Biró *et al.*, 2005; Bonnaud *et al.*, 2007; Krauze-Gryz *et al.*, 2012), as well as pet cats (Piontek *et al.*, 2021). In contrast, a higher proportion of insectivores and birds are returned (questionnaire studies) than consumed, although this finding is not statistically significant. Although lacking in significance (perhaps due to a low sample size), there appears to be a different pattern emerging between returned and consumed insectivores and birds. The inclusion of further studies would improve the reliability of these findings and allow for a clearer interpretation of the patterns observed.

This analysis, as well as the analysis on the entire dataset, suggests that birds have a higher detectability (to cat owners) than mammals, with feathers often visible at the kill or consumption site. It may be the case that birds are rarely eaten whole, particularly larger species, leaving a visible area of discarded feathers. However, it could also be that birds are more commonly caught in urban and sub-urban areas where return studies typically take place. Since owner questionnaires are the most convenient and commonly employed method to monitor predation by owned cats, a certain multiplier is often applied to estimate total predation by cats (accounting for prey undetected by owners, e.g. Kays and DeWan, 2004). It is important to appreciate that owner questionnaires are likely to underestimate the proportion of rodents killed due to their lower detectability (if eaten whole), while overestimating the proportion of insectivores (like shrews and bats) and possibly amphibians, due to their low palatability, and bird species due to their very high detectability. These latter taxa are those deemed as being of highest concern with regards to cat predation compared to mammals in most regions (van Heezik *et al.*, 2010; Woinarski *et al.*, 2017). Therefore, a single, universal multiplication factor is not appropriate for these studies and those attempting to estimate total predation by cats should be aware of, and account for, these inherent biases, something that has not been considered so far. Palatability and detectability, as well as multiplication factors, will be discussed further in Chapters 3 and 4.

2.5 **Conclusions**

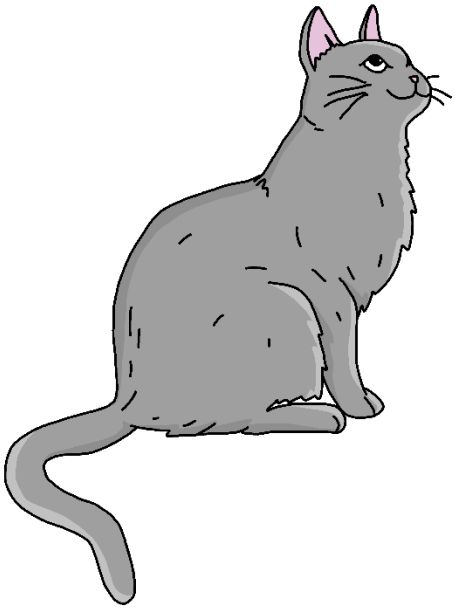
This meta-analysis identifies several areas for concern and further research in the field of cat predation. When planning dietary research, it is important to note the large impacts that methods can have on the results reported. Owner questionnaires are open to misidentification of prey and detectability bias, as described above, and (like scat and stomach analyses) do not provide evidence of all that is caught by the cat. Video capture studies may be more reliable. However, due to the low number of video studies conducted so far, conclusions based on this method should still be considered preliminary, as other impacting factors (such as location) may have affected the reported proportions of prey taxa.

The location of the study is important and cats' diet in one part of the world is not necessarily comparable to that in another area. Since many studies have found that cats hunt in accordance with prey availability (Churcher and Lawton, 1987; Molsher *et al.*, 1999; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015; Krauze-Gryz *et al.*, 2017; Read *et al.*, 2018), differing faunal compositions and availability can have an important effect on the prey types recorded. Studies in Australia and New Zealand generally report a higher proportion of amphibians and reptiles, and a lower proportion of mammals than elsewhere in the world.

Finally, cats appear to consume a greater proportion of rodents than are reported in return surveys, perhaps indicating high palatability of this taxon. In contrast, bird and insectivore proportions are lower in consumption studies (although not significantly so), which may indicate a bias in detectability for birds and distastefulness of insectivores. Thus, applying a single multiplication factor to all prey categories (for extrapolation purposes), total predation of insectivores and birds may be overestimated, while that of rodents may be underestimated. Future studies should therefore take these considerations of location, type of cat, method of data collection, and prey type more consistently and carefully into account before attempting extrapolations. This will be further explored and discussed in Chapters 3 and 4.

Chapter 3

Predation survey



Hannah Lockwood

3.1 **Introduction**

3.1.1 Cats in the UK

There are around 11.1 million pet cats in the UK (PDSA, 2022), with an estimated 2.5 million cats acquired since the beginning of the COVID-19 pandemic (PDSA, 2022). In the UK, in 1995 there were approximately 1 million feral, unowned cats (with no newer information available, Harris *et al.*, 1995). This, along with the pet population estimate, suggests that feral cats may make up 8.3% of all cats in the UK. In contrast, feral cats in countries such as Canada are a larger issue, constituting 25% of all domestic cats (Blancher, 2013). In the USA it is estimated that feral individuals make up an even higher proportion (up to around 47%, Loss *et al.*, 2013). Of the owned cats in the UK, up to 97% have access to outdoor space, unsupervised (Sims *et al.*, 2008). However, estimates regarding the percentage of cats being kept solely indoors vary widely in the UK, being as high as 26.1% in a recent study (Finka *et al.*, 2019; see also Foreman-Worsley *et al.*, 2021). Owned cat density is roughly positively correlated with human density, and pet cats occur in far greater numbers than would be supported in a natural system (Finka *et al.*, 2019; see also Foreman-Worsley *et al.*, 2021). As cats are known to hunt wild prey in addition to having access to anthropogenic food, this has led to cats being cited as one of the most destructive invasive species in the world (Doherty *et al.*, 2016). However, since a large majority of cats in the UK are owned, most are not entirely reliant on wild food sources and thus are not as damaging as feral individuals (Loss *et al.*, 2013).

3.1.2 Cats' wild diet

While cats are surely capable of having deleterious effects on local wildlife populations (Doherty *et al.*, 2016), the degree to which each individual pet cat hunts can vary considerably. The majority of cats are reported to take few or no prey at all (Churcher and Lawton, 1987; Morgan

et al., 2009; van Heezik *et al.*, 2010), whereas a number of 'super predators' are found to increase the mean, often far surpassing the median (van Heezik *et al.*, 2010).

Not only is there variability between individual cats, but predation differs by location around the world (see Chapter 2 for analyses). Cats are generalist predators and are known to hunt in accordance with prey availability (Churcher and Lawton, 1987; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015). In order to estimate the scale of the impact that domestic cats are having on wildlife populations, it is first important to establish how many wild prey items are caught within a study area.

The diet of cats has previously been studied in four ways: the examination of scat samples (Molsher *et al.*, 1999; Pontier *et al.*, 2002; Krauze-Gryz *et al.*, 2012), examination of stomach and gut contents (Tidemann *et al.*, 1994; Paltridge *et al.*, 1997; Brickner-Braun *et al.*, 2007), owner questionnaires (Kays and DeWan, 2004; Baker *et al.*, 2005; Thomas *et al.*, 2012; McDonald *et al.*, 2015), and through new video technology (Hernandez *et al.*, 2018; Bruce *et al.*, 2019, see Chapter 2 for details). While stomach and gut analyses are usually only systematically applied to feral cats, scat analysis can be applied to both feral and owned individuals. However, this can be fraught with potential methodological error. As the range of pet cats can overlap considerably, cats often bury their faeces to hide the scent, whereas wild and feral individuals often leave it in the open (Gorman and Trowbridge, 1989). Therefore, those found in the open are more likely to belong to feral individuals or are in areas with low territory overlap, biasing the results. To combat this issue, Piontek *et al.* (2021) used cat litter trays in gardens as a way of collecting samples, assuming that only pet cats would use them. Owner-targeted questionnaires and video analysis can both easily be applied to pet cats and the use of video technology in such studies is becoming increasingly common to determine what and how much pet cats hunt (Bruce *et al.*, 2019; Seymour *et al.*, 2020, see Chapter 2).

3.1.3 Prey returned

Each of the approaches used to study the diet of domestic cats allow (to some extent) researchers to determine the proportions of species (or taxa) recorded. Questionnaires in particular have the advantage that life stage and sex of prey can be more easily determined than in video footage or stomach content analysis, which can be used to assess whether predation on certain populations is unsustainable. For example, losses of breeding adults can be more damaging to a population than that of juveniles or senescent individuals (Begon *et al.*, 2006; Hoy *et al.*, 2015). Brown rats (*Rattus norvegicus*) predated by cats are commonly juveniles (Fitzgerald *et al.*, 1991), as adults are particularly aggressive and not as easy to subdue (Leyhausen, 1979). Similarly, where larger prey such as the European rabbit (*Oryctolagus cuniculus*) are returned, the majority have been found to be juveniles (Flux, 2007).

Whether prey are returned alive or dead can also be more easily recorded using questionnaires, although these data can be obtained using video footage also. Where this has been reported, the majority of prey items have been returned dead (Baker *et al.*, 2005; Thomas *et al.*, 2012). If a particular species is consistently found to be returned alive more often than dead, there is a greater chance that many predation events on that species do not ultimately lead to death. This does, however, also depend on the injuries already sustained and what the cat owners decide to do with live individuals (i.e. release, send to a rescue centre, or humanely kill).

Questionnaires can also be used to collect palatability data, recording whether each prey item was whole, part-eaten, or fully eaten by the study cats. These data can be useful when extrapolating, as unpalatable species are likely to be over-represented in a questionnaire-based dataset (see Chapter 2 for details). For example, it is rather commonly suggested that shrews and other insectivores are unpalatable to cats, being relatively frequently caught but rarely eaten (Leyhausen, 1979; Krauze-Gryz *et al.*, 2012; Kauhala *et al.*, 2015). However, many highly palatable individuals (such as rodents, see Chapter 2) may remain undetected in these surveys, as they may be eaten whole without the owners' knowledge.

3.1.4 Influencing factors

There are many factors which may affect a cat's propensity to hunt wild prey. Some are controllable such as wearing a belled collar or bib (Calver *et al.*, 2007; Gordon *et al.*, 2010), while others may include the cat's age (Woods *et al.*, 2003; Bruce *et al.*, 2019), sex, or body condition (Woods *et al.*, 2003). It is therefore important to observe factors which may increase the likelihood of being a 'super predator' cat, allowing for targeted intervention.

As owned cats largely rely on anthropogenic food sources, the quality and quantity of this food may influence the need or desire to hunt. For example, in Chile, cats are fed mostly household scraps and hunt more often as food provision is reduced (Silva-Rodriguez and Sieving, 2011). Further to this, Cecchetti *et al.* (2021) found that a fed diet high in meat protein and free of grain reduced predation of both mammals and birds. It is also widely accepted that the use of bell and bibs can reduce prey returned home, particularly for avian species (Ruxton *et al.*, 2002; Calver *et al.*, 2007; Gordon *et al.*, 2010; Pemberton and Ruxton, 2020), although Morgan *et al.* (2009) found no effect. Neutering may also help to decrease the number of prey caught (Robertson, 1998). However, since such a high proportion of owned cats are now routinely neutered (Barratt, 1998; Kauhala *et al.*, 2015), sample sizes are often low for entire cats and statistical tests may therefore lack the power required to detect patterns. The provision of bird food in a garden has also been found to affect prey return rates, with a decrease in the number of birds returned where feeders are present (Woods *et al.*, 2003). However, this perhaps indicated correlation rather than causation, since encouraging prey species into the home range of a pet cat is unlikely to directly cause a reduction in predation. It is hypothesised by Woods *et al.* (2003) that this reduction may be due to either the enhanced vigilance of birds at feeders when in a large group, or perhaps more likely, that only owners whose cats rarely predate on birds were likely to provide bird food.

Another potential influencer of predation is the time of day that cats are free to roam. In Australia, there are a number of cat curfews in place in different areas, which either restrict cats to daytime-only outdoor access or act as a 24 hour ban on free-roaming cats (Moreland City

Council, 2022). However, rather than reducing overall effects of cat predation on all taxa, restricting night-time access to the outdoors is likely to simply alter the proportions of taxa affected (Legge *et al.*, 2020). For example, diurnal species are more available to cats during the day, whereas the opposite is true of nocturnal individuals (Barratt, 1997; Barratt, 1998). Legge *et al.* (2020) suggest that the effectiveness of curfews and 24-hour bans is likely correlated with government investment and ability to police such bylaws. While the effectiveness of curfews has not yet been assessed (Williams *et al.*, 2020), if targeted correctly, they could be a useful tool in reducing predation on the most vulnerable species. Where cats have uncontrolled outdoor access (for example via a cat flap), prey proportions returned are perhaps likely to differ from those of cats without cat flap access, since their outdoor time is not determined by their owners' behavioural patterns (for example, work schedules). Similarly, the number of prey caught may be related to the amount of time spent outdoors, since prolonged periods of outdoor time allow for a greater number of hunting opportunities (Barratt, 1998). These are useful examples of how owners may be able to influence the number of prey caught, while other factors may be less easily controlled.

Although Woods *et al.* (2003) found that thinner cats returned a greater number of birds than overweight individuals, no effect was seen on the return of mammalian prey. This may be because those of a slimmer body condition are more agile and capable of hunting birds, but mammals are relatively easy prey to catch, even for overweight individuals. There appears to be a general consensus that the cats' sex does not influence prey returns (van Heezik *et al.*, 2010; Kutt, 2011; Tschanz *et al.*, 2011; Loyd *et al.*, 2013; Kauhala *et al.*, 2015; McDonald *et al.*, 2015). However, age has been found to influence the number of prey returned home, with elderly cats generally returning fewer than younger individuals (Flux, 2007; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Bruce *et al.*, 2019). As well as affecting the cat's total predation, age appears to alter the proportion of prey returned home. For example, as cats grow older, they may lack the agility required to capture birds and compensate by predating on a larger proportion of small mammals (Kauhala *et al.*, 2015).

As the availability of prey varies by season (with many species breeding in the spring, Hume *et al.*, 2016; Couzens *et al.*, 2017), predation by cats can, too, be expected to differ. It is therefore

important to monitor prey caught over a full year or multiple years. Those studies which investigate predation over one or two seasons (for example, Woods *et al.*, 2003) can provide a biased view of annual predation and are unsuitable for extrapolation. A review of previous literature, including factors which influence predation, provides further detail in Chapter 1.

3.1.5 Owner perception

As some of the influencing factors can be controlled, reducing cat predation ultimately has to start with the cats' owners and their perceptions of what is caught and how often it is caught, balanced with their own views on the cat's freedom to roam. It could be argued that studies where owners are engaged in reporting wild prey returns may increase their awareness and understanding of the potential ecological problems associated with cat predation. McDonald *et al.* (2015) studied these owner perceptions in more detail and found that 98% of cat owners (in the UK) disagree with keeping their cats in at all times. The same study found that 60% disagreed that cats are harmful to wildlife, including statements such as 'it's nature'. It is clear that cat owners in the UK are not fully aware of the potential effect of predation. However, while cat owners were unable to accurately predict the amount of prey which would be returned by their cat over a four-month period, return rates were overestimated rather than underestimated (McDonald *et al.*, 2015).

Since the data collected in questionnaire studies comes directly from the cat owners themselves, it is important that researchers understand the issues of unreliability and inconsistent reporting. Most cat owners are unlikely to be trained ecologists and therefore will perhaps make mistakes regarding identification, sex, and age of prey. In order to combat this issue, some studies required the cat owners to store dead prey items for later identification by the researchers (for example, Baker *et al.*, 2008). Since this is not possible with larger, more widespread studies, data may be verified by photographic evidence of prey. There may, too, be inconsistencies in records from cat owners, where interest in data collection wanes over time or participants do not find the time to submit data. There are a number of previous studies which rely on cat owner recollection over a

substantial period, which is fraught with potential problems. For example, a survey by Robertson (1998) required participants to report on the prey returns over the previous 12 months. The accuracy of such reports is likely greater where cats rarely predate, since these events will be significant and memorable. However, for those cats which return high numbers of prey, it is perhaps unlikely that owners are able to accurately recall numbers, potentially leading to under- or over-estimation. To combat this issue, data may be submitted at regular intervals over the collection period, with reminders sent to participants. Regular contact with and prompting of cat owners to submit data may also help to maintain their interest in the project. It is also a possibility that cat owners deliberately under-report particular prey in questionnaire studies, in an attempt to bias the results, such that cats are not portrayed in a negative light. Although this is a potentially serious issue, it can perhaps be assumed that this misreporting is rare and will not have a notable influence, particularly where the cat sample is especially high.

3.1.6 Aims and hypotheses

Currently, there are few British studies which monitor cat predation on a large scale. While studies such as Woods *et al.* (2003) monitored a large cat population, returns were only recorded over two seasons. Here, a UK-wide, long-term online survey was conducted in order (i) to quantify the average number of vertebrate prey returned home by cats in the UK and (ii) to examine the factors which may influence such predation rates. It can be hypothesised (based on the results from Chapter 2) that the cats in this study will predate largely on mammals, as they are widely available and cats are well adapted to capture them (Leyhausen, 1979). Birds returned home are expected to be lower than the number of mammals, due to their predator escape response of taking flight. Since many studies have reported no effect of sex, it is expected that this will not influence predatory behaviour (Barratt, 1998; Gillies and Clout, 2003; Loyd *et al.*, 2013; Kauhala *et al.*, 2015). It is expected that younger cats (Gillies and Clout, 2003) and those of a slimmer body condition will return a greater number of prey (Woods *et al.*, 2003). Those wearing a belled collar are expected to return fewer prey than those without, which may be particularly apparent for

avian prey (Calver *et al.*, 2007; Gordon *et al.*, 2010). The majority of prey returned are expected to be dead, following previous studies (Baker *et al.*, 2005; Thomas *et al.*, 2012) and most brown rat and rabbit returns are likely to be juveniles (Fitzgerald *et al.*, 1991; Flux, 2007). Since insectivores appear to be unpalatable (Leyhausen, 1979; Krauze-Gryz *et al.*, 2012; Kauhala *et al.*, 2015), it is expected that most individuals will be returned whole and intact.

Overall prey return rates are expected to increase in the spring and summer when prey are more active and available, before declining over autumn and reaching a low in the winter (Thomas *et al.*, 2012). Since prey activity is also dependent on the time of day, diurnal species (such as garden birds) are likely to be caught during the day, whereas mammal returns are expected to be higher during the night (Barratt, 1997; Barratt, 1998). Similarly, cats which have unrestricted access to the outdoors via a cat flap and those which spend a greater amount of time outdoors are expected to return a higher number of prey, as they are perhaps more likely to encounter prey (Barratt, 1998).

3.2 **Methods**

3.2.1 What the cat dragged in

In order to attract a large sample of cat owners from across the UK, a website was produced (www.whatthecatdraggedin.org, which is no longer live) and marketed through online social media channels (Facebook and Twitter), email mailing lists, radio interviews (17 local radio stations), advertisements in The Mammal Society's quarterly magazine (Mammal News), and an interview with New Scientist magazine (Liverpool, 2020). Registration was open to new cats from May 2018 to May 2021 and data were collected from June 2018 until December 2021. The data analysed here also include two cats for which prey return data were collected from 2014 and 2017. Any cat owner residing in the UK (Great Britain and Northern Ireland), whose cat had access to the outdoors, was encouraged to sign up.

Cats were first registered online using a questionnaire. This asked a variety of questions about the cat, including age, sex, body condition (using imagery, see Appendix 3. 1), time spent outdoors, whether a belled collar was worn, neutering status, and whether food was provided to wild birds. This also asked for an approximation of how many prey items were returned in an average month, dividing the year into two seasons (summer and winter; answers were given in categories, see Appendix 3. 2 for all questions). Participants were then sent a joining pack via email, including a Microsoft Excel 'cat diary' document, and help guide. Participants were also provided with a mammal identification guide in the form of a PDF and URL (see Appendices 3.3 - 3.5 for example illustrations), along with a link to the Royal Society for the Protection of Birds (RSPB) bird identification portal online (RSPB, 2022). This helped to improve the accuracy of identification and was of particular importance where photographs were not submitted to accompany prey records.

Each month (for typically 12 months from joining date), participants were emailed to request data submission through an online portal system. This required cat owners to fill in details of their cat's prey returns, including species identification, date and time of detection, whether the animal was returned whole and intact or had been partly consumed, and any additional notes (including, for example, age or sex of prey). Where identification to species level was not possible, or owners were not confident in their identification, they were asked to categorise prey (for example, as 'small mammal', 'mouse' or 'bird'). Participants were also asked to take a photograph of each prey return (where possible) and send these along with the cat diary to confirm species identification and age of the individual. From September 2018, i.e. after the first three months of data collection, until the end of the data period (December 2021), participants were asked to give a little more detail regarding prey returns. They were asked whether the animal was alive or dead when returned, and what eventually happened to that individual, for example, whether it was handed to a wildlife rescue centre, released, or killed by the owner themselves (humanely, where injured). Due to this slight change in data collection, it was not possible to carry out these calculations regarding dead and live prey for the entire dataset.

3.2.2 Data preparation

Where a prey item was returned to a multiple-cat household and the owner could not say with any certainty which cat returned the item, the prey was randomly assigned to one individual (based on a random number generator). This practice was necessary for 3.6% of all data month values.

If, for any reason, a cat was not permitted to roam outdoors for a period of time (e.g. time spent in a boarding cattery), the prey data value was calculated accounting for the proportion of the month for which this condition applied. For example, where a cat spent 7 days out of 30 in a cattery, the prey total for that month was divided by 0.767 (the remaining 23 days divided by 30). Therefore, in this case, if 3 prey were returned home, but 7 days were spent in a cattery (in a month of 30 days), this would give an estimated monthly return total of 3.91 prey. However, as data were required to be in whole counts (for analysis), this figure was then rounded up (if decimal was >0.2) or down (if decimal was ≤0.2), leaving this example with a total figure (for this 30-day month) of 4 prey items. Setting these parameters for rounding up or down allowed the results produced here to offer a worst-case estimate of predation on different taxa. Overall, 8.81% of data values were rounded, either up or down, although this was minimal throughout national COVID-19 lockdowns.

The date of each prey return was recorded, and from this, data were categorised by season: winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November). The year was altered so that each season contained months of the same data collection year. For example, where December 2019, January 2020, and February 2020 formed one winter season, December's year was altered to 2020. The age of cats was recorded in three-year categories at the time of registration. This was then further categorised into four groups: 'kitten' (< 1 year), 'young adult' (1 - 6 years), 'old adult' (7 - 12 years), and 'old' (≥ 13 years). Age was also altered where individuals had been registered with the project for more than two years (it is assumed that their age increased by one three-year category after two full years of data recording). Prey were included for analysis, regardless of

whether they were returned dead or alive, as it was assumed that even live, released individuals were potentially fatally injured.

The time of day of each prey return was recorded by cat owners. Where there was uncertainty regarding capture time, this was given as an approximation (for example, 'caught overnight'). For prey where a precise time was given, this was transformed to give 'hour of day' (for example, 13:42 became 13). Hour of day was then grouped into three-hour categories for analysis, beginning with 00:00 - 03:00.

3.2.3 Formal analysis

Due to a very large number of zeros in the data and the overall very low return rates, reptiles and amphibians were not included in the formal analyses. Similarly, invertebrates were occasionally recorded, but not consistently, and they are therefore excluded from analyses.

Bayesian Generalised Linear Mixed Models (GLMMs) were used to analyse the effects of each variable on the number of mammals and birds returned home by cats in a month. Model selection involved comparing four different error structures to determine which was most suitable. These models were: Poisson, zero-inflated Poisson, zero-altered Poisson (hurdle model), and a negative binomial model. After comparison, the Poisson model was found to be over dispersed and thus the data did not follow a Poisson distribution. The hurdle model assumes that there are no false zeroes, but as detectability of returned prey may vary due to taxon or location of return (indoors or outdoors), this was also unsuitable. On comparing the zero-inflated Poisson and negative binomial models and conducting out of sample predictions (where 10% of data are dropped and then predicted) for each, the negative binomial approach was found to be most suited to the dataset and was therefore used here. The final model used 25,000 iterations with a burn-in of 1,600 iterations (thinning rate of five and three chains), Hence the total number of iterations used was 3 x (25,000 – 1,600) / 5 = 14,040 iterations.

The independent variables tested were: taxon, sex, age, body condition, neutering status, whether a cat flap was present, whether a bell was worn, bird food provision, season, and year. The dependent variables were the count of mammals and birds, respectively, tested in separate models. Due to the length of time taken for each of these models to run, and the computer memory requirements, statistically important variables (for final model inclusion) were identified in two stages. This involved assessing the suitability of one half of the variables (plus interactions with prey taxon), followed by the remaining half (plus interactions with prey taxon). Those variables which were found to be statistically important were selected for inclusion in the final model. The selection of each subset of variables grouped in this process was random and this was conducted again with a different selection, having no impact on the final variable selection. All variables were tested with and without a possible interaction with taxon. Individual cat ID was included as a random factor.

Time of day that prey were returned was analysed using χ^2 goodness of fit tests on both mammals and birds, comparing the observed counts with those expected (if prey were returned in equal quantities per hour). A Wilcoxon rank sum test was used to compare the time spent outdoors by each cat, as estimated by the cats' owners, in the summer and winter periods, since data were non-parametric, but did not violate the homogeneity assumption of the test (square root-transformed data, Appendix 3. 6). Spearman's rank correlation tests were then used to determine whether a relationship existed between the time an individual spent outdoors (as reported by their owner) and the average prey caught per month by each individual, as the time spent outdoors was not normally distributed. One cat was excluded from 'time outdoors' tests, as no data were provided. The eaten status (whether eaten/part eaten or whole) of shrews was then tested using a χ^2 contingency table and compared against that of mammals overall. For both the summer (April- September) and winter periods (October- March), one-sample Wilcoxon rank sum tests were used, due to non-normality of the data, to assess how much the difference between the estimated prey (by owners) and the actual mean for each cat differed from zero, where a zero value would indicate an accurate owner estimate. To compare patterns in the number of prey of different taxa returned in the current study with that of Woods *et al.* (2003), a χ^2

contingency table was used (on data from April to August, in line with the methods of Woods *et al.* (2003)).

While χ^2, Spearman's rank, and Wilcoxon tests were frequentist analyses, all GLMM analyses were conducted in a Bayesian framework, as the R packages available for zero-inflated mixed models in a frequentist context are very limited. Analyses were completed using R version 4.0.2 and R Studio version 1.0.153 (R Core Team, 2016; R Studio Team, 2020), utilising the package 'R2jags' (Su and Yajima, 2020) and BUGS code from Zuur and Ieno (2016).

3.3 **Results**

In total, 1007 cats were registered onto the project. However, predation data were collected for just 553 cats (possibly due to emails going into 'junk' folders). Cats were located across the UK (with the exception of Northern Ireland), with higher densities in areas with a larger human population (around London for example, Figure 3. 1). The number of data months for each cat ranged from only one month to a full 43 months, giving a total of 4674 data months for all cats (sample sizes are found in Table 3. 1). While for the majority of these months zero prey were recorded (2987 months = 64%), prey returns ranged up to 61 in a single month for one cat. All prey species records can be found in Appendix 3. 7.

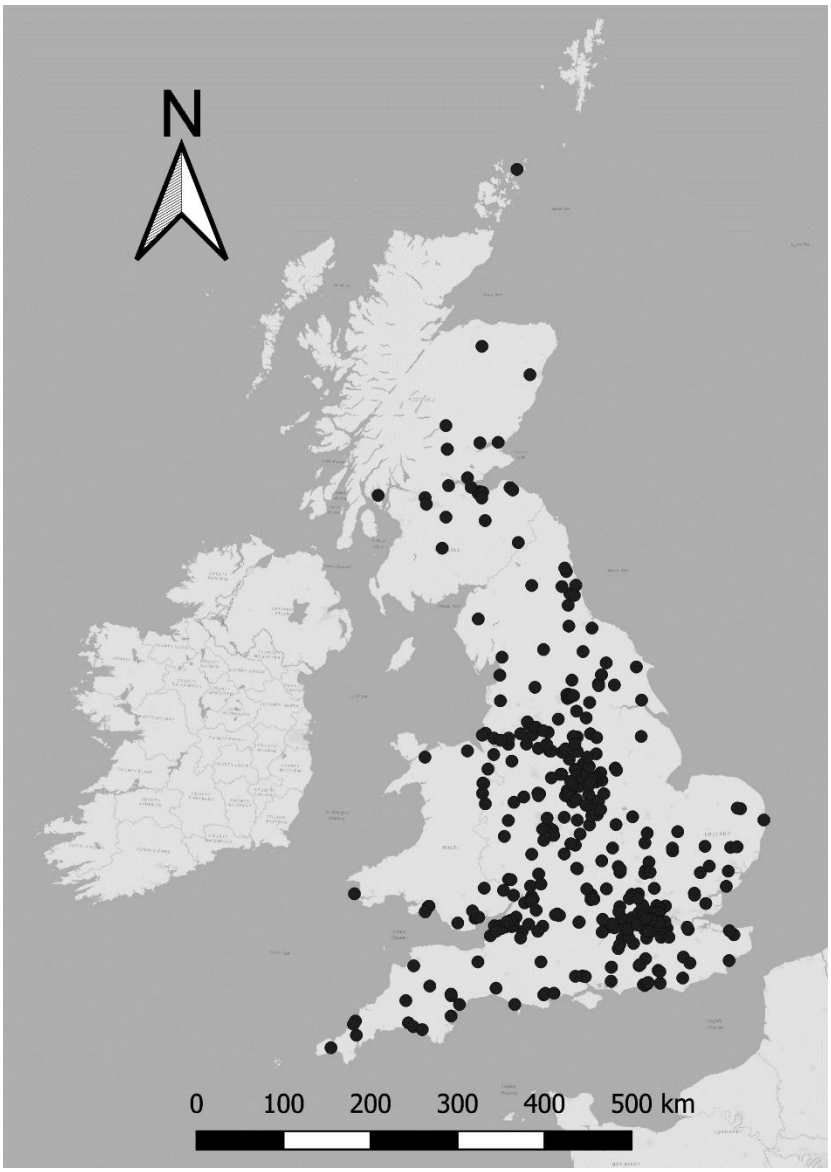


Figure 3. 1. Locations of 553 cats, for which prey return data were collected.

Table 3. 1. Number of cats in each specified category, along with the number of 'data months', and total number of mammals and birds returned. Data displayed are adjusted (rounded up or down), as detailed in section 3.2.2. Number of cats in the age categories do not total 553 (actual number of individuals), as some changed category over the study period.

Category	No. of cats	Data months	Prey: mammals	Prey: birds
Sex				
Male	284	2566	3913	753
Female	269	2108	2194	408
Age				
Kitten	14	95	216	45
Young adult	312	2319	3447	821
Old adult	182	1742	2336	278
Old	53	518	108	17
Body condition				
A	104	790	1375	321
B	291	2334	2996	573
C	141	1349	1624	243
D	17	201	112	24
Bell?				
Yes	147	1252	1605	435
No	406	3422	4502	726
Neutered?				
Yes	541	4584	6063	1152
No	12	90	44	9
Cat flap?				
Yes	413	3703	5102	971
No	140	971	1005	190
Bird food?				
Yes	286	2494	3217	597
No	267	2180	2890	564
Season				
Winter	408	1177	779	137
Spring	374	1096	1540	278
Summer	390	1156	2124	549
Autumn	426	1245	1664	197
Year				
2018	199	597	757	190
2019	162	988	1120	255
2020	223	655	999	107
2021	305	2330	3069	554

3.3.1 Prey proportions and extrapolation

After rounding up the prey data (where cats were restricted to the indoors for a portion of a given month or owners were unable to record), a total of 7322 prey were estimated to be returned by 553 cats across a 4674 data month period, producing a monthly estimate of 1.57 prey per month, per cat with outdoor access in the UK. However, most cats (58.23%) returned a mean of ≤ 0.5 prey per month (≤ 6 prey returned annually).

As discussed in Chapter 2, different prey taxa may be returned or detected (and therefore recorded) in varying proportions. The majority of prey species returned home in this study were mammals (83.21%), followed by birds (16.03%), and a comparatively small number of amphibians (0.61%) and reptiles (0.14%). Per cat (per month), this equates to 1.31 mammals, 0.25 birds, 0.009 amphibians, and 0.002 reptiles. In total, it can be estimated that outdoor-roaming pet cats in the UK return between 154.5 million and 203.5 million prey per year, based on an assumed population of 11.1 million individuals (PDSA, 2022), 73.9% to 97% of which have access to the outdoors (Table 3.2, Sims *et al.*, 2008; Finka *et al.*, 2019).

Table 3. 2. Estimated prey returns per month and per year for all pet cats in the UK with outdoor access. There are two estimates: one for 8.2 million cats (based on an estimated 11.1 million pet cats, 73.9% of which are outdoor, Finka *et al.*, 2019; PDSA, 2022) and the second for 10.8 million cats (based on an estimated 11.1 million pet cats, 97% of which are outdoor, Sims *et al.*, 2008). Note that this only relates to returned prey.

Prey group	Prey per month, per cat	Prey per year	
		8.2 million cats	10.8 million cats
Mammals	**1.31**	**128,904,000**	**169,776,000**
Muridae sp.	0.59	58,056,000	76,464,000
Cricetidae sp.	0.32	31,488,000	41,472,000
Soricidae sp.	0.08	7,872,000	10,368,000
Chiroptera sp.	0.002	196,800	259,200
Birds	**0.25**	**24,600,000**	**32,400,000**
Reptiles	**0.002**	**196,800**	**259,200**
Amphibians	**0.009**	**885,600**	**1,166,400**
All vertebrate prey	**1.57**	**154,488,000**	**203,472,000**

While mean monthly values varied (between 0.59 and 3.79 per cat), most monthly medians were zero (with just five exceptions out of 47 project months). These higher medians appear to be largely due to a lower sample size for some months (minimum n = 16) compared to others (maximum n = 218), as well as season. This rather strongly shows that the majority of cats do not return any prey during a given month.

3.3.2 Prey species of concern

Of the 7012 prey returned during the study period, 15 (0.21% of total prey returned) were reported to be European Protected Species: nine bats and six hazel dormice (*Muscardinus avellanarius*). However, it should be noted that only one hazel dormouse was confirmed with a photograph and wood mice (*Apodemus sylvaticus*) were misidentified as hazel dormice on three occasions (Appendix 3. 8**Error! Reference source not found.**). Mammalian species listed as

endangered in the UK (by Mathews and Harrower, 2020) were not recorded (such as the water vole, *Arvicola amphibius,* and grey long-eared bat, *Plecotus austriacus*). Of the 70 bird species on the UK's red list (Stanbury *et al.*, 2021), five were reported here, totalling 241 individuals (3.44% of total prey returned), with house sparrows (*Passer domesticus*) being the most frequently recorded (207 individuals).

However, all of the five prey-sized mammalian groups commonly perceived as problematic 'pests' (mice, brown rats *Rattus norvegicus*, grey squirrels *Sciurus carolinensis*, rabbits *Oryctolagus cuniculus*, and moles *Talpa europaea*, Baker *et al.*, 2020), were recorded here. These groups totalled 3107 individuals (44.4% of total prey returned), potentially more if 'small mammals' were assumed to be mice (additional 897 individuals) and if voles were considered along with mice to be pests (additional 1434 individuals).

3.3.3 Influencing factors

For the analysis to determine factors which may influence predation, the final model described here included (apart from taxon) six factors: sex, age, body condition score, whether a cat flap was installed, season, and year, some of which showed an interaction effect with taxon. Whether a belled collar was worn, bird food provision, and neutering status were not selected for inclusion in this model (see Appendices 3.9 and 3.10 for numerical and graphical outputs, respectively).

There was an important difference between males and females in the number of prey returned home, with males returning a greater amount (Table 3. 3, Figure 3. 2). However, there was no discernible interaction with taxon here. When comparing young adult cats (1 - 6 years) with kittens (< 1 year) and old adult cats (7 - 12 years), a difference was found between taxa, with birds being less affected by age than mammals (i.e. there was a sharper decrease in mammal returns with increasing cat age, Figure 3. 2). Overall, for age, the numeric outputs show a difference between almost all groups (Table 3. 3).

Cats of body condition ‘A’ (see Appendix 3. 1 for illustration) were found to return a greater quantity of prey than all other categories. However, no interaction was found with taxon returned. Having a cat flap installed had a stronger effect on mammals returned than birds and overall, for those cats who had access to a cat flap, a greater number of prey were recorded per month (Table 3. 3, Figure 3. 2).

An interaction effect was found in the majority of season combinations (except for those between winter and spring, and spring and summer). Overall, bird returns were less affected by seasonal changes than mammal returns, which showed a more pronounced increase in the spring and summer (Figure 3. 2). A greater number of prey were returned in the summer months than in any other season, followed by spring (Table 3. 3).

While the mean number of mammals returned per month peaked in 2020, the same year yielded the lowest bird return rates (Figure 3. 2). Overall, there were a greater number of prey returned per cat, per month in 2018 than in any other year (Table 3. 3). On assessment of the raw data, there was a notable increase in prey returns from April 2020 (at the beginning of the COVID-19 pandemic), which returned to ‘normal’ levels in the autumn of the same year. The mean number of mammals returned for April 2020 was over twice that of the same month in 2019 (2019 mean = 1.14, 2020 mean = 2.49), whereas bird returns remained at a similar level (Figure 3. 3).

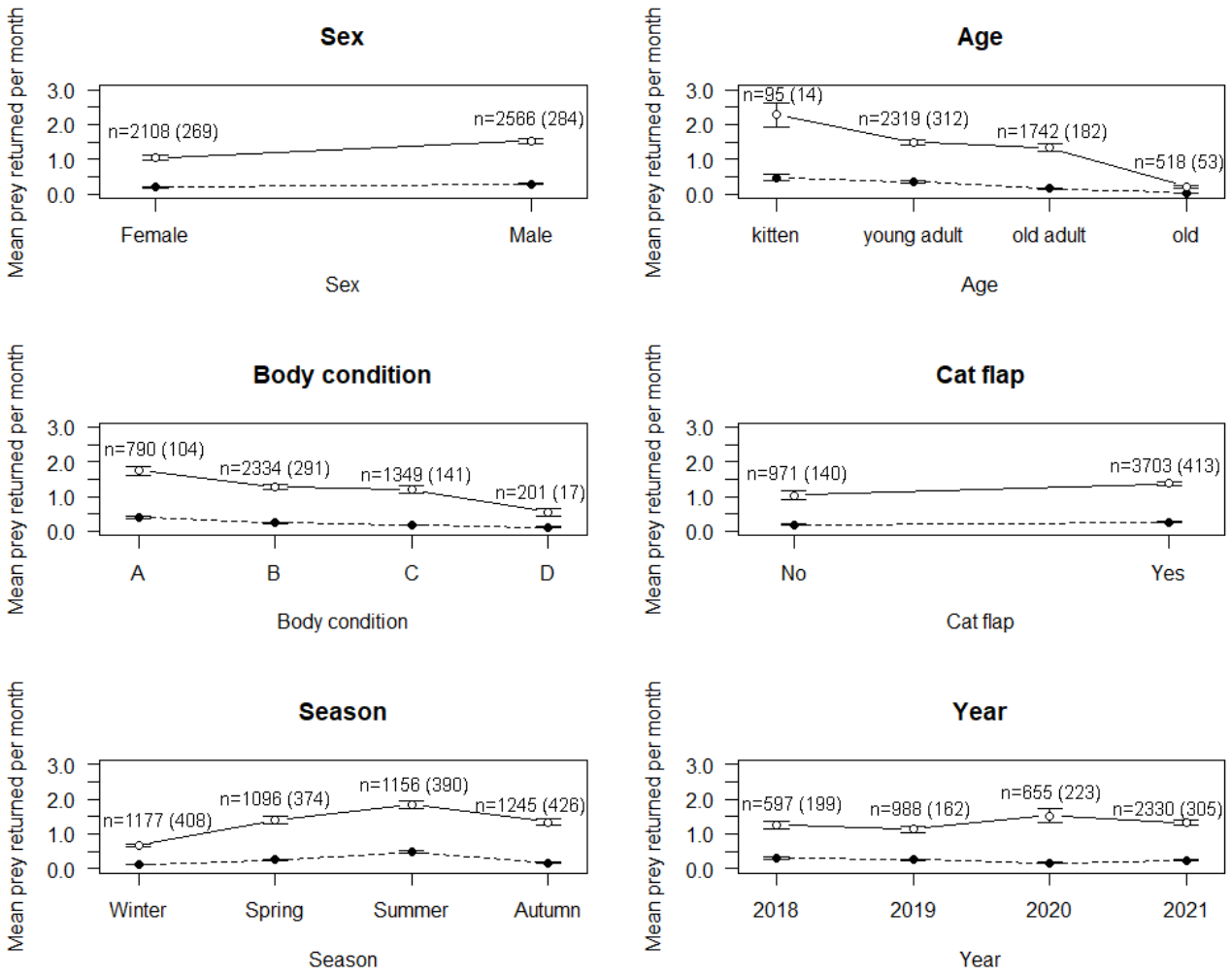


Figure 3. 2. Interaction plots showing the variation in mean prey returned (per month) by different groups of cats for both mammals and birds, along with Standard Error (SE) bars. Solid line with open circles represents mammals, and broken line with filled circles indicates birds. Sample sizes given represent the number of recording months for which there are data in each category, followed by the number of cats in parentheses.

Table 3. 3. Numerical outputs of Bayesian negative binomial GLMM, giving posterior mean (P mean), standard error (SE), and the 2.5% and 97.5% credible intervals. Where credible intervals do not cross zero, a statistically important result is observed (given in bold).

Variable	P mean	SE	2.5%	97.5%
(Intercept)	-3.96	0.7	-5.0	-2.8
Taxon: Birds < Mammals	**0.92**	**0.3**	**0.3**	**1.6**
Sex: Female < Male	**0.73**	**0.2**	**0.3**	**1.1**
Age: Kitten < Young adult	**1.75**	**0.4**	**0.8**	**2.4**
Kitten = Old adult	0.69	0.4	-0.2	1.3
Kitten = Old	-0.66	0.5	-1.8	0.1
Young adult > Old adult	**-0.89**	**0.3**	**-1.4**	**-0.5**
Young adult > Old	**-1.71**	**0.9**	**-3.1**	**-0.1**
Old adult > Old	**-1.25**	**0.3**	**-1.9**	**-0.6**
Body condition: A > B	**-0.76**	**0.3**	**-1.3**	**-0.3**
A > C	**-1.14**	**0.3**	**-1.7**	**-0.6**
A > D	**-1.41**	**0.6**	**-2.6**	**-0.3**
B = C	-0.51	0.3	-1.1	0.2
B = D	-0.59	0.5	-1.9	0.3
C = D	-0.63	0.6	-1.6	0.6
Cat flap: No < Yes	**0.76**	**0.3**	**0.3**	**1.3**
Season: Winter < Spring	**0.76**	**0.1**	**0.5**	**1.0**
Winter < Summer	**1.39**	**0.1**	**1.2**	**1.6**
Winter = Autumn	0.09	0.1	-0.2	0.4
Spring < Summer	**0.51**	**0.2**	**0.2**	**0.8**
Spring > Autumn	**-0.82**	**0.2**	**-1.2**	**-0.5**
Summer > Autumn	**-1.38**	**0.2**	**-1.7**	**-1.1**
Year: 2018 > 2019	**-0.43**	**0.1**	**-0.7**	**-0.2**
2018 > 2020	**-0.59**	**0.2**	**-0.9**	**-0.2**
2018 > 2021	**-0.58**	**0.2**	**-0.9**	**-0.3**
2019 = 2020	-0.26	0.2	-0.6	0.2
2019 = 2021	-0.23	0.2	-0.6	0.1
2020 = 2021	-0.03	0.2	-0.3	0.3
Taxon * Sex: Female - Male	-0.08	0.1	-0.3	0.1
Taxon * Age: Kitten - Young adult	-0.14	0.3	-0.7	0.3
Kitten - Old adult	0.28	0.3	-0.2	0.7
Kitten - Old	0.15	0.4	-0.5	0.9
Young adult - Old adult	**0.43**	**0.1**	**0.2**	**0.6**
Young adult - Old	0.02	0.4	-0.6	0.8
Old adult - Old	-0.18	0.2	-0.7	0.3

Taxon * Body condition: A - B	-0.01	0.1	-0.2	0.2
A - C	0.17	0.1	-0.1	0.4
A - D	-0.17	0.3	-0.7	0.3
B - C	0.09	0.1	-0.2	0.4
B - D	-0.42	0.4	-1.1	0.3
C - D	-0.26	0.2	-0.8	0.2
Taxon * Cat flap: No - Yes	**0.38**	**0.1**	**0.1**	**0.6**
Taxon * Season: Winter - Spring	-0.08	0.2	-0.4	0.2
Winter - Summer	**-0.39**	**0.1**	**-0.7**	**-0.1**
Winter - Autumn	**0.52**	**0.2**	**0.2**	**0.8**
Spring - Summer	-0.16	0.2	-0.5	0.2
Spring - Autumn	**0.77**	**0.3**	**0.4**	**1.2**
Summer - Autumn	**1.01**	**0.2**	**0.7**	**1.3**
Taxon * Year: 2018 - 2019	0.18	0.1	-0.1	0.5
2018 - 2020	**0.75**	**0.2**	**0.4**	**1.1**
2018 - 2021	**0.59**	**0.1**	**0.4**	**0.9**
2019 - 2020	**0.63**	**0.2**	**0.3**	**0.9**
2019 - 2021	**0.44**	**0.1**	**0.2**	**0.7**
2020 - 2021	-0.09	0.2	-0.5	0.2

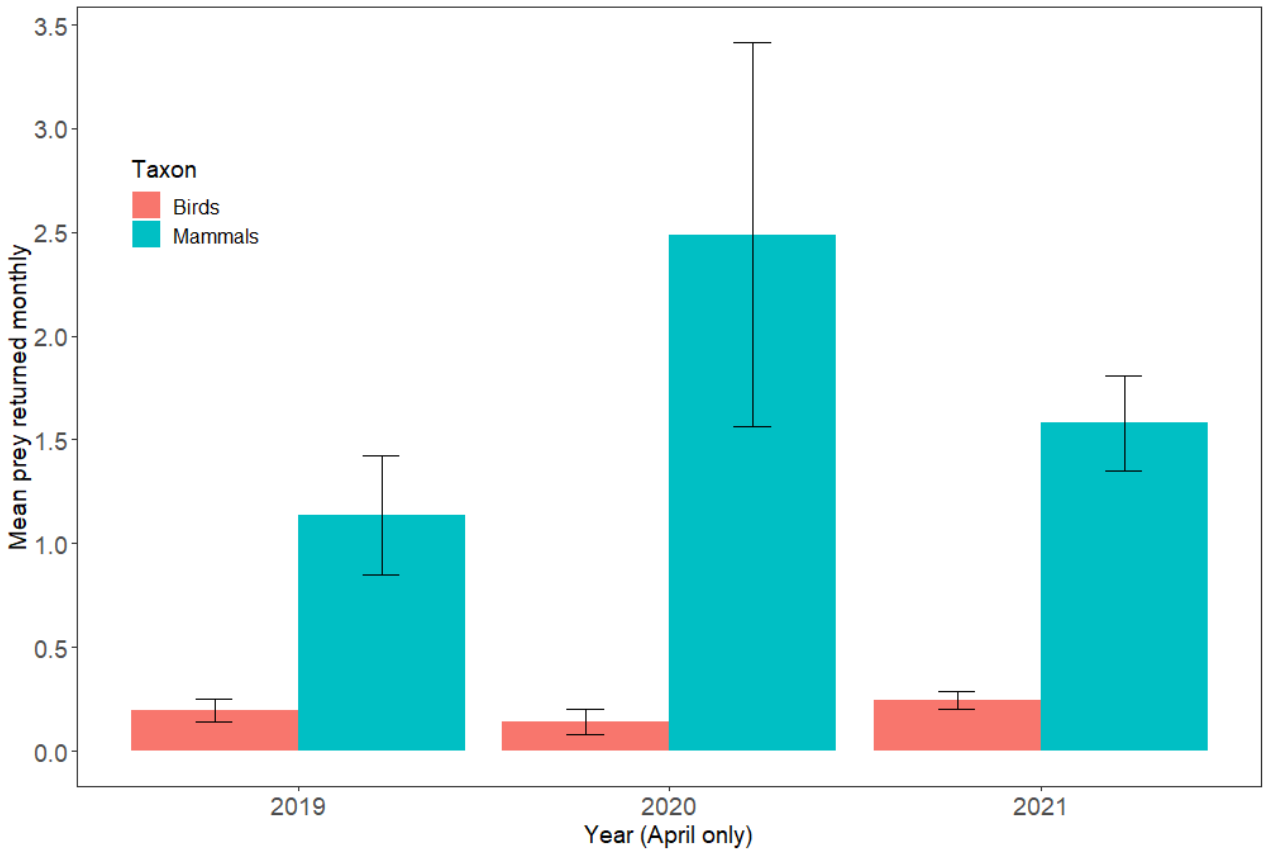


Figure 3. 3. Comparison of mean mammal and bird returns during April 2019, 2020, and 2021, per cat (bars represent Standard Error).

3.3.4 Time of day

There were 3598 mammals and 696 birds returned, for which accurate time data were provided. Both mammal ($\chi^2 = 288.26$, df = 7, $p < 0.001$) and bird data ($\chi^2 = 298.05$, df = 7, $p < 0.001$) showed significant patterns when grouped into three-hour categories (Appendix 3. 11). Bird captures were most frequent during the day, whereas mammal captures followed a more crepuscular pattern, roughly peaking at dawn and dusk (Figure 3. 4).

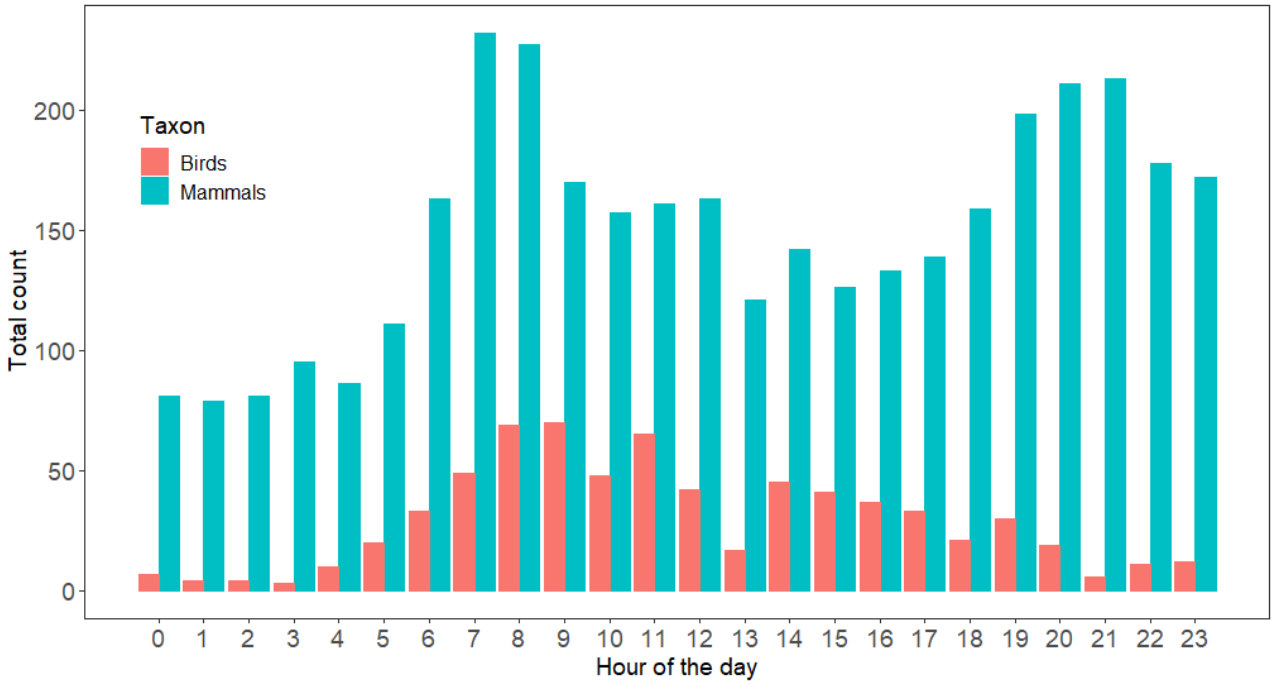


Figure 3. 4. Total count of birds (n = 696) and mammals (n = 3598) returned, by hour of the day.

3.3.5 Time spent outside

Owners estimated that their cat(s) spent significantly longer outside in the summer than the winter (Wilcoxon rank sum test: W = 215419, n = 552, $p < 0.001$), being out for up to 24 hours in the summer (Appendix 3. 12). Cats were estimated to spend a mean of 9.7 hours outdoors in the summer, compared to only 5.8 hours in the winter. Time spent outdoors was significantly positively correlated with mean prey per month (per cat) in both the summer (Spearman's Rank test: $r_s = 0.22$, n = 552, $p < 0.001$) and winter periods (Spearman's Rank test: $r_s = 0.33$, n = 552, $p < 0.001$), where summer was April - September and winter was October - March. Dividing prey to assess mammals and birds individually found that in the summer, both mammal (Spearman's Rank test: $r_s = 0.22$, n = 552, $p < 0.001$) and bird returns (Spearman's Rank test: $r_s = 0.16$, n = 552, $p < 0.001$) were significantly positively (although weakly) associated with the time spent outdoors. Similarly, in the winter period, mammal returns were significantly positively correlated, but weakly, with time spent outdoors (Spearman's Rank test: $r_s = 0.31$, n = 552, $p < 0.001$), as were those of birds (Spearman's Rank test: $r_s = 0.28$, n = 552, $p < 0.001$, Figure 3. 5).

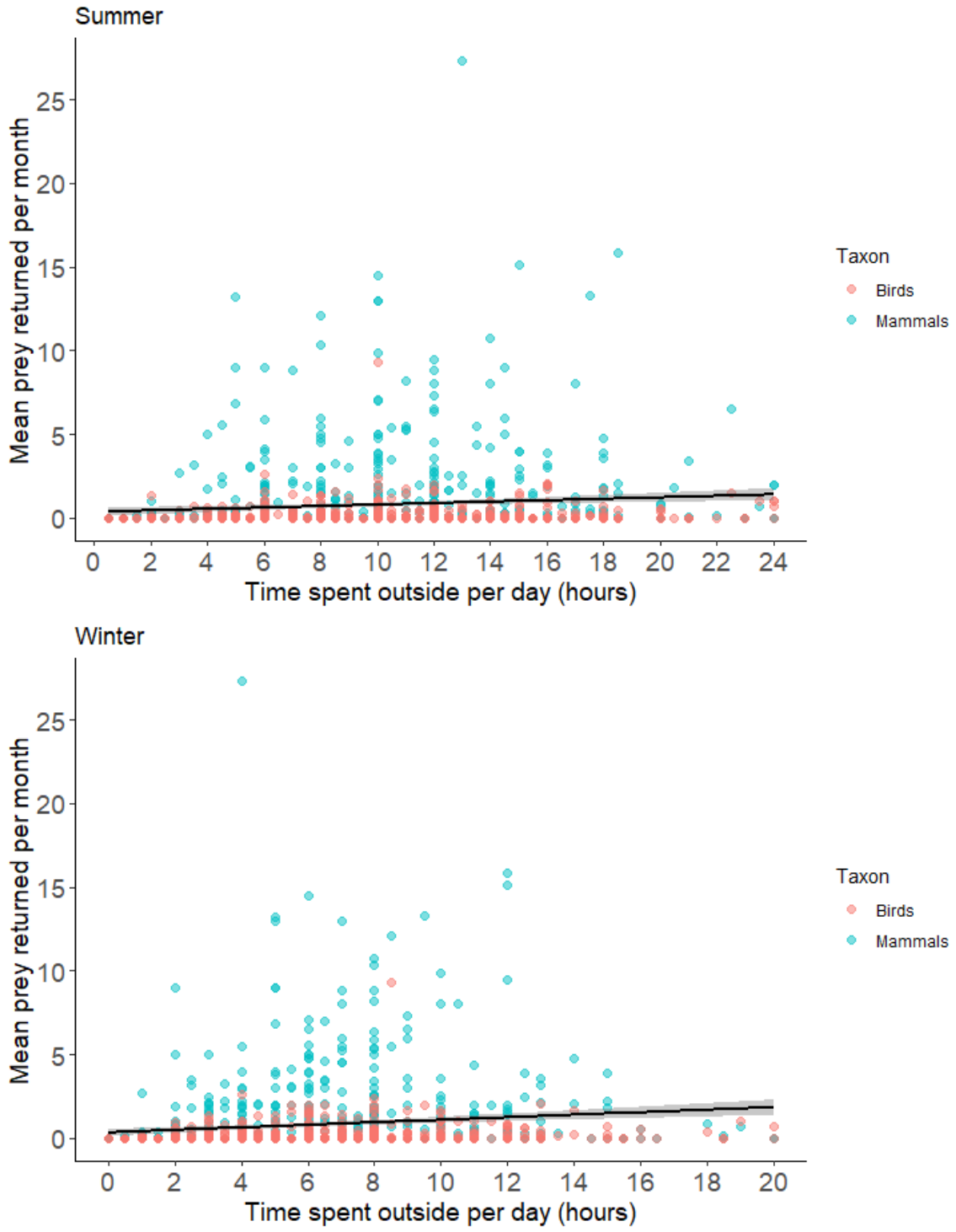


Figure 3. 5. The relationship between the time spent outside per day and the mean prey returned per month, per cat in both the summer (top) and winter months (bottom). Regression line is in black, SE is the area in grey.

3.3.6 'Super predators' and specialists

A small number of cats were identified as 'super predators' which predated (or at least returned prey) in quantities far exceeding the mean. While most cats returned an average of between zero and 0.99 prey per month, a very small number (n = 15) were found to return a mean of 10 prey items or over each month, including three returning more than 15 prey per month (Figure 3. 6). One cat in particular, 'Cally', returned the highest monthly prey figures of all 553 cats in the study, returning 61 prey in a single month (mean of 27.85 prey per month). While most cats returned a mean of ≤6 prey per year, this varied greatly between individuals, ranging up to 333.6 prey (by Cally, the vast majority being mammals). If the cat sample monitored here is representative of the wider population, there are an estimated 222,220 super predator individuals in the UK, returning ≥10 prey per month (based on a population of 8.2 million outdoor pet cats, see section 3.3.1).

Although cats largely returned mammalian prey, some appeared to be bird specialists. One such specialist was 'Joshua'. Joshua was a participant of the project for seven months and returned home 70 prey in this time, 65 of which were birds (92.86%).

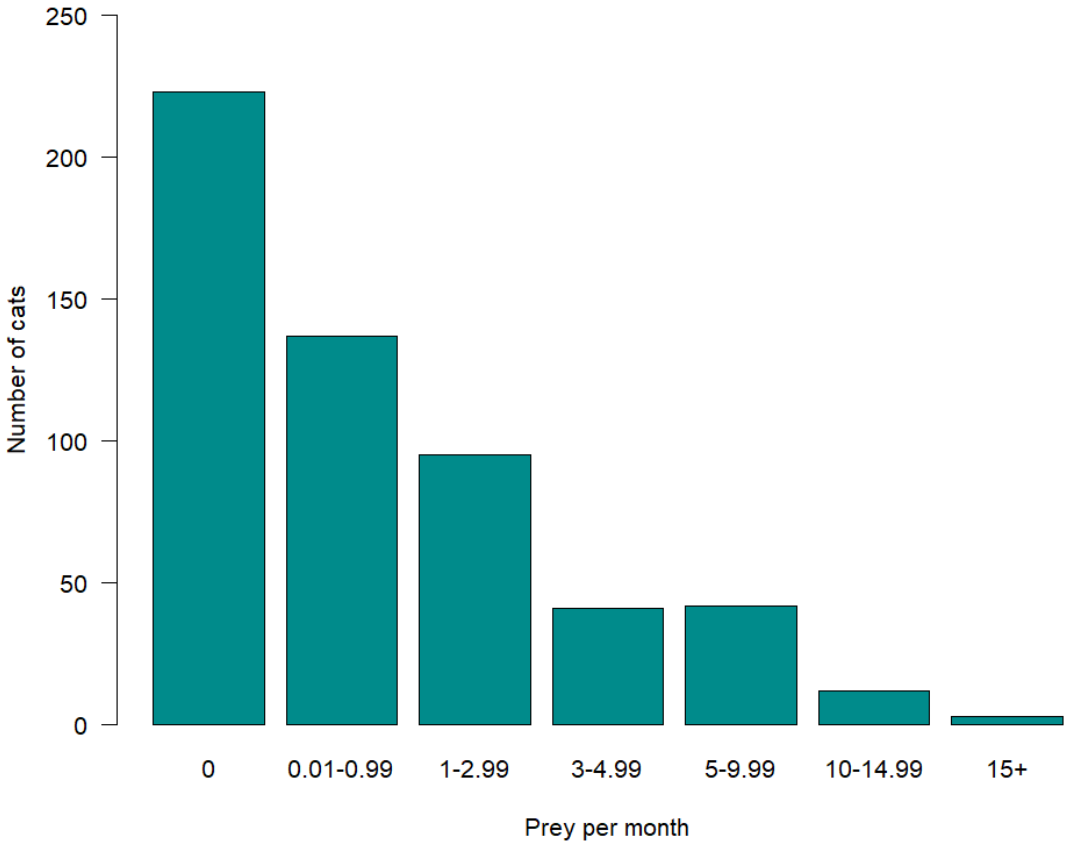


Figure 3. 6. The mean number of prey animals returned each month, and the number of cats returning each category.

3.3.7 Live and dead prey returns

The proportion returned alive was highest for amphibians (80.56%, Table 3. 4), followed by reptiles (75%), mammals (20.39%), and birds (14.26%). There were a number of comments in the 'notes' section of the data collection forms, stating that individuals were released despite obvious injury. As an example, one stated that a small mammal was 'just about alive', suggesting that this individual would not survive for long after release. One bird had 'lost its tail feathers and [was] unable to fly', and yet it was released. Of those returned home alive (n = 1280), most were released (79.14%) or escaped outdoors (10.31%). A very small number were sent to be cared for at a rescue centre (0.86%), and 2.42% were humanely killed by the cat owner (where injured; for the remaining 7.27%, the fate was unknown).

Table 3. 4. The number of live and dead prey returned by cats between September 2018 and December 2021, given as total numbers and percentages for all taxa.

Taxon	No. dead	No. alive	Total no.	% dead	% alive
Mammals	4327	1108	5435	79.61	20.39
Birds	824	137	961	85.74	14.26
Reptiles	2	6	8	25.00	75.00
Amphibians	7	29	36	19.44	80.56

3.3.8 Life stage and sex of prey

Of the 5835 mammals recorded here, 613 were judged to be either adults or juveniles, by an identification photograph or by the cat owners themselves. Of these, 64.17% were noted as juveniles (Table 3. 5). Similarly, of 505 bird prey items that had been aged, 61.58% were juveniles. Interestingly, of the 228 brown rats (*Rattus norvegicus*) recorded, 106 were aged by participants (likely by size) and of these, 83% were reported to be juveniles (Table 3. 5). One cat (named

'Hector') had a tendency to return many European rabbits (*Oryctolagus cuniculus*), particularly throughout the spring to summer period, and was responsible for 44.2% of all European rabbit records. Ninety-eight of the 217 rabbit records had been assigned an age, of which 94.9% were listed as juveniles.

Table 3. 5. The percentage of prey which were assigned an age category and, of these, the percentage which were identified a juveniles and adults. Key mammalian families are represented here, along with two species. Bird species given were commonly found in the predation diet of domestic cats.

Prey	Total	% categorised by age	% juvenile	% adult
All mammals	5835	10.51	64.17	35.83
Muridae spp.	2865	11.27	73.37	26.63
Cricetidae spp.	1434	9.62	43.48	56.52
Soricidae spp.	379	12.93	4.08	95.92
Brown rat	228	46.50	83.00	17.00
European rabbit	217	45.16	94.90	5.10
All birds	1124	44.93	61.58	38.42
House sparrow	207	36.71	56.58	43.42
Robin	100	54.00	77.78	22.22
Blackbird	102	73.53	53.33	46.67
Blue tit	75	56.00	45.24	54.76
Dunnock	72	50.00	75.00	25.00

Prey sex was recorded occasionally, where participants were confident in their assessment. Of the 415 mammals and birds that were classed as adults, 218 were recorded as male or female (52.53%). Of these adult individuals, 57.81% of mammals were male (42.19% female), and 43.33% of birds were male (56.67% female). For birds, 93.76% of those for which sex was recorded were sexually dimorphic species (Table 3. 6).

Table 3. 6. The bird species for which sex was recorded and whether each of these species exhibits sexual dimorphism. The total number of each species which was sexed is given, along with the percentage of total sexed birds.

Species	Sexually dimorphic?	Number sexed	% of total sexed
Blackbird	Y	36	37.50
House sparrow	Y	34	35.42
Chaffinch	Y	15	15.63
Bullfinch	Y	4	4.17
Greenfinch	N	4	4.17
Dunnock	N	1	1.04
Mallard	Y	1	1.04
Wren	N	1	1.04

3.3.9 Unpalatability

A total of 379 shrews were recorded throughout the data collection period (6.5% of all mammals, 5.4% of prey overall). The majority (n = 310) were returned dead and, of these, 96.8% were reported to be 'whole and intact'. The remaining 3.2% were noted as being 'eaten' or 'part-eaten' (Figure 3. 7, Table 3. 7). This is far lower than for mammals overall (40.4% eaten and part-eaten, $\chi^2 = 168.82$, df = 1, $p < 0.001$).

Figure 3. 7. ‘Part-eaten’ shrew species, submitted by a project participant.

Of the 950 birds returned dead, most were whole (66.95%). However, in the case of both reptiles and amphibians, the majority were returned alive and most of the dead individuals were either eaten or part-eaten. In fact, 100% of dead reptiles were found part-eaten (all of which were slow worms, *Anguis fragilis*, Table 3. 7).

Table 3. 7. The percentage of prey which were returned dead and, of these, the percentage which were whole, part-eaten, or completely eaten. The whole, part-eaten, and eaten percentages do not always total 100%, as some participants did not give these data. Each taxon is represented, and mammals are further divided, giving three key families.

Prey	Total	% returned dead	% whole	% part-eaten	% eaten
All mammals	5835	78.61	59.59	16.29	24.01
Muridae spp.	2865	69.18	68.11	19.88	11.76
Cricetidae spp.	1434	84.10	78.86	15.34	5.64
Soricidae spp.	379	81.79	96.77	2.58	0.32
All birds	1124	84.70	66.91	12.29	20.69
All amphibians	43	27.91	25.00	58.33	0.00
All reptiles	10	25.00	0.00	100.00	0.00

The owner of Hector (the rabbit specialist cat) remarked that a number of the European rabbit individuals returned also appeared to have a quite obvious case of myxomatosis (though no photos of these individuals were received). Although many were juveniles and appeared healthy, 'large mature rabbits, which are uneaten' showed prominent symptoms of this disease (quote from Hector's owner, Phillips, 2021).

3.3.10 Misidentification and reliability of data

Of the 7012 total predation records obtained, 46.37% were submitted alongside a photograph, allowing species identification to be confirmed. Of those records with photographs, 7.12% were found to be misidentified by the cat owner (see Appendix 3. 8). Eighteen species were misidentified, the majority being mammals, and the most misidentified prey group were vole species. These individuals were often reported as mice, but were occasionally identified as a different vole species (for example, field voles *Microtus agrestis* were confused with bank voles *Myodes glareolus*). It may be reasonable to assume, therefore, that a similar proportion of all remaining records (without photographic confirmation) were also misreported in similar ratios.

Although 1007 cats were registered to the project, data were only received for 54.92% (n = 553) of these. For the 553 cats included here, submission effort by cat owners was highly variable, with participation ranging from just one month to 47 months of data recording (mean of 8.45 and median of nine months per cat). Indeed, only one month of data was submitted for 17.54% of cats (usually the first month of the requested 12 month data collection period).

3.3.11 Owner predictions

Owner predictions regarding how many prey animals would be returned were found to be overestimates by most owners, in both the Summer months (In this case, April-September, mean overestimate of 2.7 prey), and Winter (October-March, mean overestimate of 1.9 prey). The trend of actual return rates follows that of the owner predictions (observed rates increase with increasing owner estimates), although owners often overestimate. Indeed, the difference between estimated and actual mean monthly value (owner estimate minus actual mean) differed significantly from zero for both the summer (Wilcoxon rank sum test: $V = 54288$, n = 455, $p < 0.001$, Figure 3. 8) and winter period (Wilcoxon rank sum test: $V = 45274$, n = 467, $p < 0.001$, Figure 3. 8).

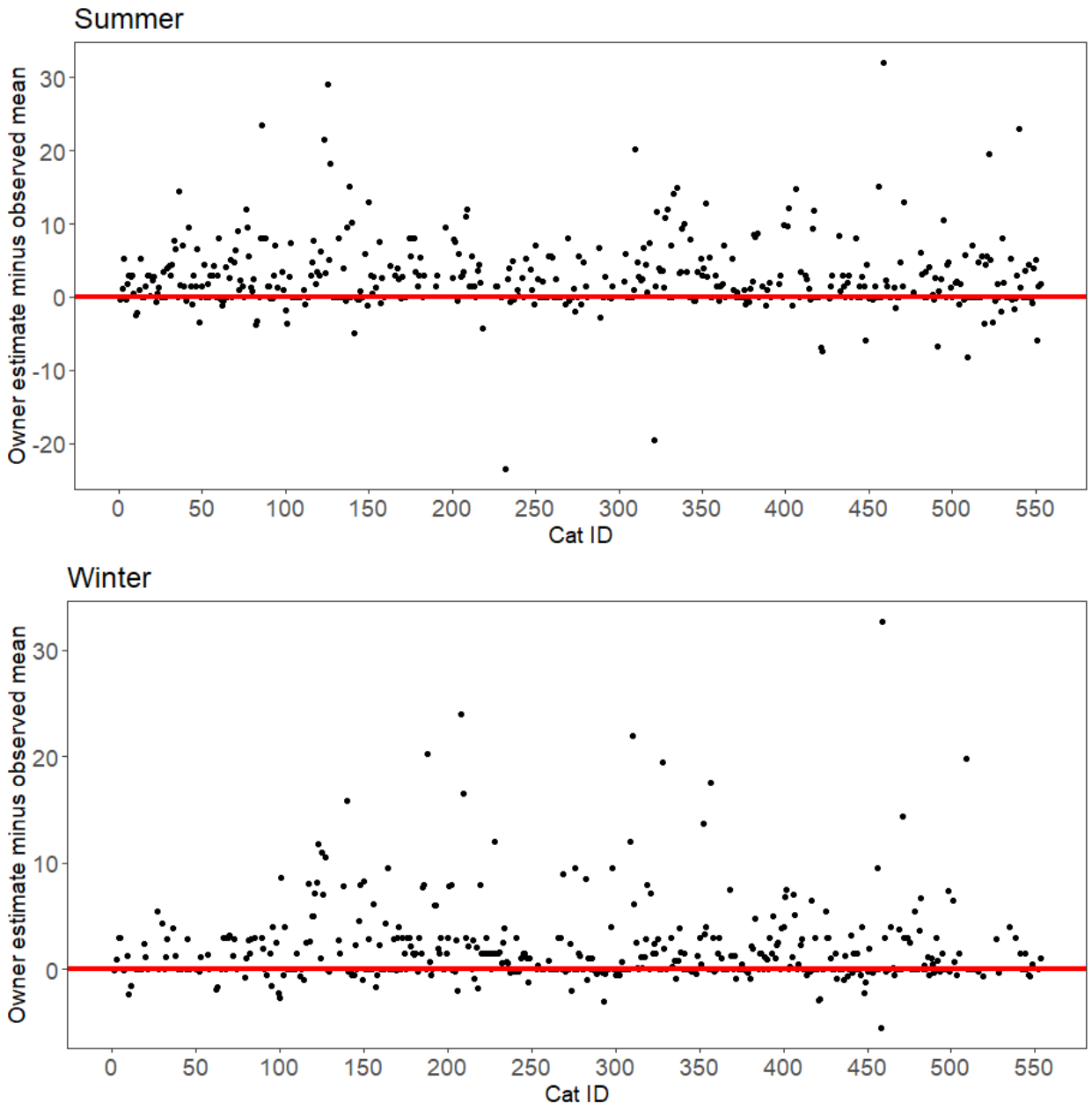


Figure 3. 8. The difference between predicted (by owners) prey per month and observed monthly means (predicted values minus observed means) for each cat in both summer and winter periods. Zero (i.e. no difference) is denoted by a red line. Points above the red line indicate an overestimate, and those below, an underestimate by cat owners.

3.3.12 Changes over time

Data collection was carried out over 20 years after that of Woods *et al.* (2003) in a similar location (across the UK) and on a similarly large sample, but spanning more seasons. Comparison of a select few species (and families), over comparable seasons (April-August) shows that overall, the current study and that of Woods *et al.* (2003) follow different patterns ($\chi^2 = 200.29$, df = 3, $p < 0.001$, when including all mammals, murids, insectivores, and all birds). A greater proportion of mammals is represented in this current study, and a lower proportion of birds (Table 3. 8). Predation on shrews appears to have reduced over time, while that of rodents has increased. As for birds, robins (*Erithacus rubecula*), wrens (*Troglodytes troglodytes*), dunnocks (*Prunella modularis*), and wood pigeons (*Columba palumbus*) all increased in relative proportion, whereas house sparrows, blue tits (*Cyanistes caeruleus*) and blackbirds (*Turdus merula*) reduced (Table 3. 8**Error! Reference source not found.**).

Table 3. 8. A selection of prey percentages recorded by the current study and Woods *et al.* (2003), for comparison. Mammals were mainly divided by family, and birds are species commonly found in UK gardens. As Woods *et al.* (2003) collected data between April and August (inclusive), data presented here (from the current study) are from the same months only.

	Current study		**Woods et al. (2003)**	
Prey	**N**	**%**	**N**	**%**
All mammals	**3172**	**80.22**	**9852**	**70.49**
Muridae spp.	1442	36.47	4360	31.19
Cricetidae spp.	802	20.28	1969	14.09
Soricidae spp.	257	6.50	1753	12.54
European rabbit	180	4.55	1242	8.89
Chiroptera spp.	8	0.20	30	0.21
All birds	**745**	**18.84**	**3387**	**24.23**
House sparrow	161	4.07	961	6.88
Blue tit	55	1.39	344	2.46
Wood pigeon	33	0.83	0	0.00
Dunnock	51	1.29	34	0.24
Wren	32	0.81	105	0.75
Blackbird	68	1.72	316	2.26
Robin	71	1.80	142	1.02

3.4 **Discussion**

3.4.1 Prey proportions

The proportions of returns for each taxon seen here are consistent with the vast majority of previous studies (see Chapter 2), with mammals being the top predated (or at least, returned) group, followed by birds, and herptiles. While for any taxon, mean monthly values varied greatly, the medians were almost consistently zero, strongly indicating that most cats do not return any prey during a given month (zero prey for 62.05% of data months).

Here, mammals constituted 83.2% of prey returned, whereas in all previous owner questionnaire studies in the UK, this group made up a mean of 72.1% (Churcher and Lawton, 1987; Carss, 1995; Howes, 2002; Ruxton *et al.*, 2002; Woods *et al.*, 2003; Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012; McDonald *et al.*, 2015) and 63.9% worldwide (see Chapter 2 Table 2. 3 for references). Birds in the present study formed 16% of all prey returned, which is lower than previous UK studies (24.2%) and those conducted around the world (24.7%). In contrast, herptiles here constituted 0.8% of prey brought home, but the UK mean from previous studies is slightly higher (3.7%), and the worldwide mean is higher still (11.1%). The minimal prey return data for herptiles strongly suggests that these taxa make up a very small proportion of prey caught by cats in the UK, which may be a reflection of prey population declines in the time since previous studies were conducted. While there is some evidence to suggest that reptile and amphibian populations are declining in the UK (Foster *et al.*, 2021), robust monitoring has not yet been undertaken (although an ongoing PhD by Rebecca Turner at the University of Kent aims to assess population trends).

Here, it was estimated that cats return an average of 1.57 prey per cat per month, or 18.84 prey per cat per year. This figure is substantially higher than estimates from recent UK research (5.2 prey per cat per year, Pirie *et al.*, 2022). This difference in estimates may be due to the relatively small geographic range of study and lower sample monitored by Pirie *et al.* (2022, n = 79). However, the finding of the current study is comparable to that of Woods *et al.* (2003), estimating that cats in the UK returned 2.04 prey per month (here, it is estimated at 1.57). Since Woods *et al.* (2003) only monitored prey returns in the spring and summer (five months), predation would have been higher and not representative of a full year (see sections 3.3.3 and 3.4.4).

3.4.2 Prey species of concern

A large percentage (44.4%) of prey recorded here are commonly classified as mammalian pests (Baker *et al.*, 2020) and a very small number (0.21%) were European Protected Species (EPSs). This suggests that in the UK, the majority of prey returned home by cats are of low conservation

concern. It perhaps also confirms that cats will hunt in accordance with prey availability (Churcher and Lawton, 1987; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015), hunting a greater number of species which are more widely available.

Predation by cats is often cited as one of the main reasons that bat species require rescue centre treatment and cats are commonly thought to be a leading source of mortality (Ancillotto *et al.*, 2013; Salinas-Ramos *et al.*, 2021). However, bat populations in the UK appear to be stable or increasing, although little is known about the population sizes of a number of species (Mathews *et al.*, 2018). This lack of declining bat population data, together with the consistently low proportions of bats returned by cats (Woods *et al.*, 2003; Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012), may suggest that predation pressure by domestic cats is negligible, since species appear to remain unaffected, at the population level.

While the majority of bird species on the UK's Red List (Stanbury *et al.*, 2021) are not commonly found in urban and suburban gardens (Holden and Cleeves, 2014), a small number are, and five of the 70 species of concern were recorded here. House sparrows were the most frequently returned bird species here, a species which also appears on the Red List in the UK due to a long-term decline (>50% since 1969) in the breeding population (Stanbury *et al.*, 2021). Churcher and Lawton (1987) found that cats were responsible for 30% of house sparrow deaths in an English village. From 1995 to 2020, populations of house sparrows in the UK remained stable overall, with a relatively large decline in England (-13%), but increased populations in Wales (96%), Scotland (56%), and Northern Ireland (40%, Harris *et al.*, 2022). Although the decline in England is of concern, increasing populations elsewhere in the UK suggest that this may be due to changes in resource availability, rather than predation pressures from domestic cats. The causes of the decline of house sparrows in urban areas are not yet understood, although parasite burden (Dadam *et al.*, 2019) and reduced availability of invertebrates have been investigated (Peach *et al.*, 2015). Declining populations in rural locations are thought to be due to changes in agricultural practices and nesting availability (Woodward *et al.*, 2018). Whether cats may be contributing to the decline of some bird species will be investigated further in Chapter 5.

3.4.3 Sex and age of cats

There was an important difference between the predatory habits of male and female cats, although a similar pattern was apparent regarding both mammal and bird prey. This result suggests that males return a greater number of prey than females, with taxa returned in similar proportions. Although the majority of research indicates that there is no discernible difference in predation between sexes (Barratt, 1998; Gillies and Clout, 2003; Morgan *et al.*, 2009; Tschanz *et al.*, 2011; Loyd *et al.*, 2013; Kauhala *et al.*, 2015; Hernandez *et al.*, 2018), the sample sizes tested here were relatively large and balanced (males n = 2566 data months from 284 cats, females n = 2108 data months from 269 cats), which improves reliability of such a result. This finding may be linked to the range size and roaming distance of male and female cats. As males are known to have larger ranges (Liberg *et al.*, 2000), it may be likely that their roaming areas contain a greater number of small mammal burrows, for example, therefore providing them with greater hunting opportunities. While Robertson (1998) found that in an Australian city, neutered individuals returned a greater amount of prey, in the present study neutering status was not included in the final model. This is perhaps due to the low power, resulting from a particularly low sample size for unneutered cats (n = 12, 2.17% of all cats studied). This is a comparable proportion to Thomas *et al.* (2012), finding that 4% of study cats were unneutered (in the UK). Furthermore, most cat owners in the UK (62%) agree that all cats should be neutered (McDonald *et al.*, 2015).

The age of the cats in this study also proved to be an important variable, influencing predation rates. Kittens (aged <1 year) had the highest monthly mean prey return value, although it should be noted that the sample size for this particular group was relatively low (n = 14 cats, n = 95 data months). Additionally, as a more precise age was not requested (only categories), it is likely that many (if not all) individuals in the 'kitten' group were over four months old, as they should be at least this age before being granted outdoor access (Jones, 2020). As cats increased in age, prey returns reduced for both mammals and birds. A similar result has been found previously (Barratt, 1998; Howes, 2002; Flux, 2007; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Bruce *et al.*, 2019),

although some have found no pattern between cat age and prey return rates (Robertson, 1998; Tschanz *et al.*, 2011). The two previous studies which did not observe an effect of age were conducted in very different areas (an isolated town in Switzerland, Robertson, 1998; Tschanz *et al.*, 2011, and a metropolitan area of Australia). While one used a relatively small sample of cats (n = 32, Tschanz *et al.*, 2011), the other was based on owner recollection and simply whether each cat had returned prey in the previous 12 months (i.e. the number of prey returned was not tested, Robertson, 1998). Given a larger sample size, it is possible that variables (including age) which were not found to be of importance, may become significant. Furthermore, the methods used by Robertson (1998, i.e. simply looking at predators and non-predators) are rather different from the majority which assess the number of prey returned. Therefore, the results of this study (Robertson, 1998) are not directly comparable to most others.

Here, there was a slightly different pattern apparent for each taxon, showing that the variation between groups was greater for mammal returns than birds. This difference between age groups suggests that kittens hunt many more mammalian prey than birds, perhaps as they are easier to catch and require less skill and practice (Leyhausen, 1979). However, the kitten group also had the highest mean bird returns of all age groups. Indeed, Leyhausen (1979) suggests that many individuals 'give up' hunting birds as they grow older and develop greater hunting experience, as bird predation often requires greater skill. In the 'old' age category (aged ≥13 years), the difference between mammal and bird returns was smaller, suggesting a large reduction in mammal predation, and a moderate slowing in bird predation as cats grow older. This is in contrast to previous results, which have found a greater reduction in bird returns with increasing cat age (Gillies and Clout, 2003; Kauhala *et al.*, 2015). However, since the number of bird returns recorded here was particularly low (only 16% of total vertebrate prey, mean = 0.25 birds per cat, per month), the mean birds returned per month could not possibly fall by the same amount as mammals. The mean did reduce by a larger magnitude, however (15.7 times lower mean between kittens and old cats for birds, and 10.8 times lower for mammals). Additionally, since the sample sizes for both kittens and old cats were substantially lower than for the remaining two age categories (n = 14 and n = 53 cats, respectively), the disparity between these two groupings is perhaps to be expected. In order to increase reliability of this particular result, a

greater number of old cats and kittens would need to be included in the study, although this may bias the overall results, since the sample would not be representative of the population.

3.4.4 Seasonal and annual differences

Important differences were apparent in prey returns between seasons, along with large differences in taxa returned each season. For both taxa, prey returns were highest in the summer months (June - August), followed by spring (March - May), autumn (September - November), and winter (December - February). These differences between the seasons are greater for mammals, than for birds, indicating that bird prey returns are not as strongly affected by season as mammal returns.

While some previous research on feral cats in Australia has found no evidence of seasonal changes in predation (Hutchings, 2003), a number of studies (also on feral cats in Australia) have identified significant patterns (Molsher *et al.*, 1999; Kutt, 2011; Palmas *et al.*, 2017; Woinarski *et al.*, 2018). A similar seasonal pattern has also been found in pet cats in the UK (Howes, 2002). It may be expected that predation would follow the breeding patterns of prey species, as cats are known to predate in accordance with prey availability (Churcher and Lawton, 1987; Barratt, 1997; Molsher *et al.*, 1999; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015). These seasonal variations may therefore be explained by the annual activity patterns of prey. Since commonly caught bird species (such as house sparrows) may have between one and three clutches of offspring a year, the timing of which is dictated by season (Holden and Cleeves, 2014), one might expect larger increases of birds in the spring and summer months. However, bird return rates varied less by season than those of mammalian species (although bird records were also highest during the spring and summer). Interestingly, mammal returns could be expected to fluctuate less than birds by season, due to high productivity (particularly of rodent species) and many litters throughout the year (Merritt, 2010; Couzens *et al.*, 2017). In Australia, pet cats were found to spend more time outdoors in the summer than in the winter, and generally more time outdoors during the day than the night (Robertson, 1998). A number of studies have also found that the amount of

time spent outside can influence predation (Barratt, 1998; Robertson, 1998; McDonald *et al.*, 2015). Therefore, given that cats will actively hunt mammals (waiting patiently to pounce), but appear to opportunistically hunt birds (Leyhausen, 1979), it may be that spending less time outdoors in the winter (see section 3.4.6) leads to a reduction in time spent hunting mammals, yet birds are still as available (or unavailable) as in the summer months.

Overall, a greater number of prey were recorded (per month, per cat) during 2018 compared to 2019, 2020, and 2021. As the main project (excluding the two long-term cats from 2014 onwards) began in June 2018 and sample sizes were relatively low at the start, the mean values appear skewed by 'super predator' cats for the first two months. The increase in prey returns from April 2020 (at the beginning of the COVID-19 pandemic) may have been due to National 'lockdowns' which resulted in people staying at home throughout the day, potentially increasing prey detection.

Interestingly, there was an interaction effect between year and taxon, as although returns of mammals increased from 2019 to 2020 and then declined slightly in 2021, the opposite was true of bird returns. This may be explained by either the natural 'boom and bust' cycles experienced by some small mammal species, or a change in detection of different taxa by cat owners. Since every few years, some mammal populations experience large fluctuations in size (boom and bust, Merritt, 2010; Andreassen *et al.*, 2021), it may simply be that this was reflected in the prey records of cats monitored here. However, a reduction in bird predation (although only slight) was unexpected. If indeed mammalian prey were more abundant during 2020, cats may have focussed their attention on these species, as their hunting strategy is best adapted to small mammals (Leyhausen, 1979). Therefore, the reduction of bird prey recorded may simply be a product of increased mammal availability. Previous research has shown that during 'bust' years, cats predate on a wider range of species, but in 'boom' periods, mammal predation can double (Yip *et al.*, 2015; Andreassen *et al.*, 2021). However, assuming that mammal availability was roughly the same from 2019 to 2020, this increase in records would suggest that detection of this taxon increased. However, the same pattern is not observed in birds, perhaps suggesting that they are detected and recorded at the same level, whether cat owners are spending all day at home or not.

3.4.5 Other explanatory variables

Where a cat flap was available to cats, more prey were returned than in households that lacked this access to and from the outdoors. It may be that cat flaps increase the number of prey that are detected by owners, whereas those left outside the house may be scavenged or otherwise go unnoticed and unrecorded. It is also likely that the implementation of a cat flap will influence the total time a cat spends outdoors, along with the time of day outdoors. For example, those without cat flaps will likely be either locked inside or outside for the duration of the night, whereas those with cat flap access are able to roam freely. This may have an effect on the proportions of different prey taxa returned (see section 3.4.6). Although both mammals and birds followed a similar pattern in that returns were higher for both when a cat flap was present, having unlimited access to and from the outdoors (via a cat flap) affected mammalian prey returns more strongly, whereas it did not appear to have as large an effect on bird returns. Although this may be linked with the time of day that cats with or without cat flap access are able to roam outdoors (section 3.4.6), it may also be due to the higher detectability of birds (whether outdoors or indoors), as feathers are often more visible and less likely to be overlooked than mammal remains (for example, a tail). For mammals, it appears that cats with cat flaps were returning prey to the inside of the house, increasing detectability by owners. This variable has not been investigated in previous literature, despite its clear influence. If the presence of a cat flap does indeed lead to an increase in mammalian predation (rather than an increase in detection), this suggests that cats with free access to and from the outdoors spend more time out at night than those without cat flaps.

There was an important difference between cats in the ‘A’ category for body condition and all remaining categories. ‘A’ category cats (those which are lean or underweight) returned the most prey per month. Prey return rates reduced with each successive body condition category (B-D) for both taxa, with ‘D’ category individuals returning the least prey per month. The condition score of an individual is likely related to its fed diet (Silva-Rodriguez and Sieving, 2011), although it can be a result of illness (Bellows *et al.*, 2016), neutering status (Scott *et al.*, 2002), or age

(Crawford *et al.*, 2020). However, body condition may be related to predation in a number of ways. Cats which are fed less at home, may have a greater motivation to hunt, and therefore return a greater number of prey. Biben (1979) found that the probability of a cat killing its prey is reduced for those which are well-fed. Similarly, Cecchetti *et al.* (2021) found that a diet high in meat protein cat reduce the number of prey returned. However, there is evidence to suggest that cats will hunt regardless of hunger (at least to some extent, Adamec, 1976; Leyhausen, 1979; Turner and Bateson, 2000). If cats are indeed supplementing their diet with wild prey, they are perhaps less likely to be particularly thin (Silva-Rodriguez and Sieving, 2011). In addition to this aspect, cats which are of a leaner condition may be more agile and able to hunt with greater success, although research is lacking in this area. Furthermore, all of the 'kitten' age cats monitored here were registered as being of either 'A' or 'B' body condition (thinner and leaner). It is likely that as these cats develop into adults, some will become larger (22.1% of young adults were in category 'C' or 'D'). Therefore, age and body condition effects may be linked. Indeed, Smit *et al.* (2022) found that with age, body condition score increased, as physical activity decreased.

No difference was found in prey returns between cats wearing a bell and those not wearing a bell. This result is in contrast to many previous studies (Ruxton *et al.*, 2002; Nelson *et al.*, 2005; Gordon *et al.*, 2010), which have consistently found a reduction in both mammal and bird returns, although Morgan *et al.* (2009) observed no significant effect and Woods *et al.* (2003) found a reduction in mammalian prey, but not in birds. The studies which found that bells reduce all prey returns had a paired design, where the same sample of cats were monitored with and without a bell (Ruxton *et al.*, 2002; Nelson *et al.*, 2005; Gordon *et al.*, 2010). Therefore, those which did not usually wear a belled collar (all cats in the case of Ruxton *et al.*, 2002) were not used to it and certainly not used to stalking prey successfully with its presence. It is perhaps therefore likely that, given time, individuals become acclimatised to this novel addition and their hunting behaviours then continue as before. These trials monitored cats with a belled collar for a period of four to six weeks (Ruxton *et al.*, 2002; Nelson *et al.*, 2005; Gordon *et al.*, 2010). Although the methods were robust to variation in location and season (by monitoring different groups of cats with and without bells at different times), the trial period remained quite short (Ruxton *et al.*,

2002; Nelson *et al.*, 2005; Gordon *et al.*, 2010). However, studies which take a cross-sectional view of this issue (comparing cats which wear bells to cats which do not) tend to use a longer data collection period (up to 12 months, Morgan *et al.*, 2009). Interestingly, few cross-sectional prey return surveys investigate the effect of a belled collar, perhaps as there are many variables which cannot be controlled in such a study (for example, fed diet, location, prey availability, season, and age). Woods *et al.* (2003) did find an effect of wearing a bell, although it was not found to reduce bird returns. This may simply be due to relatively few bird return data, but may also be because birds rely more heavily on visual (and sometimes olfactory) cues than auditory ones to identify threats (Roth *et al.*, 2008; Arteaga-Torres *et al.*, 2020). In addition, it is suggested by Woods *et al.* (2003) that perhaps cats which wear a bell, wear it because they were previously very successful hunters. However, this may not be the sole reason for fitting a belled collar, as one participant stated that their cat wore a collar (which came with an attached bell) to hold their contact details and identification information. Bells may potentially be very useful in reducing predation, but for species of greatest concern (particularly birds), this may not be a helpful measure.

Both neutering status and the provision of bird food in the garden were not significant and therefore not included in the final model. Since only 2.17% of cats monitored here were not neutered, samples were highly unbalanced and data on unneutered individuals are insufficient and not particularly reliable. This figure is similar to that of Barratt (1998) and Kauhala *et al.* (2015), where 1.9% and 5% of cats were unneutered, respectively. Interestingly, Robertson (1998) found neutered cats to predate more frequently than entire pet cats in Australia, although sample sizes are not known. Bird food provision was found to be significantly related to predation by Woods *et al.* (2003), finding that where birds were fed, predation was reduced. This is likely because owners of prolific predators do not wish to attract birds to their garden. Feeders can also reduce the overall foraging time of birds, thus reducing the time an individual is exposed to predation threats (Jansson *et al.*, 1981). Observing predation at feeders by cats and birds of prey in the USA, Dunn and Tessaglia (1994) suggest that it is unlikely that providing food for birds causes greater mortality than would be found in a natural setting.

Anecdotal information from one bird-specialist cat's owner suggest that while play and a high protein diet may reduce predation in the short term (as found by Cecchetti *et al.*, 2021), these effects may wear off over time. A similar, temporary result was seen when a Feliway pheromone diffuser was used in the house, which is claimed to reduce anxiety and aggression in cats (Feliway, 2022). Although only a temporary effect in this case, this may warrant further study into the use of pheromone diffusers to reduce predation by cats.

3.4.6 Time of day

A significant pattern was found in the timing of prey captures for both mammals and birds, showing relatively high frequency of bird captures throughout the day, and peaks in mammal captures around dawn and dusk. This is an area which has not previously been explored, although some research has been conducted on the peak activity times of cats. For example, Morgan *et al.* (2009) found that roaming activity did not vary by time of day in New Zealand, although Elizondo and Loss (2016) saw higher activity during the night hours in the USA.

One measure aiming to reduce cat predation is curfews, which are being implemented in Australia in particular. For example, in Victoria, 27 of 79 councils have an overnight ban on free-roaming cats, and a further ten have a 24 hour ban, where cats are not permitted to roam outdoors at all (Moreland City Council, 2022). While the 24-hour curfew will undoubtedly have an effect on predation (owners can be fined if their cat is found roaming), the dusk-dawn curfews may have limited benefits in the UK and countries with similar faunal compositions, since the majority of prey here (in particular, birds) have been returned during the day. As birds are generally of greater conservation concern in the UK (although bats and other uncommonly caught mammals are also), an overnight curfew for cats would likely prove ineffective for commonly caught bird species such as house sparrows. One study in the UK did look into the effect of keeping cats indoors at night, finding that this led to a significant reduction in mammal returns, although birds were unaffected (Woods *et al.*, 2003). This finding agrees with the results presented here, as birds are more commonly caught during the day. Therefore, overnight curfews

would effectively reduce predation on species commonly considered pests, such as mice and rats, while not effectively reducing predation on birds (Baker *et al.*, 2020).

3.4.7 Time spent outside

As in previous research (Robertson, 1998), it was estimated here (by owners) that cats spent more time outdoors in the summer months, when the weather is more favourable and dry. It was apparent that there was a significant positive relationship between the number of hours spent outside and the mean prey returned home monthly, a finding which is in line with other studies (Barratt, 1998; Robertson, 1998; McDonald *et al.*, 2015). Correlations were weak, yet significantly positive in all cases. This weakness is likely due to most cats spending up to 12 hours outdoors per day, leaving few data representing longer periods. Including more cats which spend >12 hours outdoors daily may improve the strength of this pattern, but would introduce bias, as it would not be representative of pet cats in the UK.

3.4.8 'Super predators' and specialists

While most cats return fewer than one prey item per month (with a median of zero), a small minority return ten or more prey per month (including winter months). A number of previous studies found a similar pattern (Barratt, 1998; Baker *et al.*, 2005; Morgan *et al.*, 2009; van Heezik *et al.*, 2010; Thomas *et al.*, 2012; Kauhala *et al.*, 2015), showing that most pet cats return few prey, if any. Indeed, video-based studies also found that few cats predated during the data collection period (70.91% did not predate, Loyd *et al.*, 2013; 37.93% did not predate, Hernandez *et al.*, 2018). However, in questionnaire studies at least, the mean is increased due to the predation of a relatively small number of individuals. One such 'super predator' was 'Cally', a female cat residing in the rural Dumfries and Galloway area of Scotland, who returned a total of 362 prey items over a 13-month period (98.1% mammals, 1.9% birds). Although not looked into

here, a number of studies have found a difference in predation rates of each taxon between urban and rural locations (Mitchell and Beck, 1992; Barratt, 1997; Krauze-Gryz *et al.*, 2017). Cally was categorised as an 'old adult' cat (aged 7-12 years), was of body condition 'C' (larger cat, see Appendix 3. 1), and did not have use of a cat flap. Overall, the data suggest that a cat such as Cally would not be expected to return the highest numbers of prey. However, living in a rural area may mean that she had access to large prey populations. As rural cats (living in low densities) have been found to have larger home ranges (Churcher and Lawton, 1987; van Heezik *et al.*, 2010), this may also be a factor contributing to such high return figures. Ultimately, it is apparent that there is a high amount of variation between cats (returning between zero and 61 prey per month), some of which can be expected regardless of factors such as age, sex, and body condition.

This variation is also apparent in the proportions of prey returned, with some cats appearing to specialise in mammals and others in birds. While there is evidence to suggest that cats are better adapted to hunting terrestrial mammalian prey (Leyhausen, 1979), a small number monitored here returned mostly birds (for example, Joshua, for whom birds constituted 92.86% of total returns). Both super predators and specialist cats can potentially have a relatively large individual impact on local prey. It is therefore important that recommendations to reduce predation target owners of these individuals, in particular (since most cats return ≤0.5 prey per month).

3.4.9 Live and dead prey returns

The majority of prey were returned dead (80.12%), although proportions varied by taxon (from 19.44% of amphibians to 85.74% of birds). The proportions of mammals and birds that were returned dead or living was similar to those reported in previous studies, with the majority being dead (Baker *et al.*, 2005; Thomas *et al.*, 2012). This may be because, in order to be successfully returned home, birds and mammals need to be in some way subdued, as they may otherwise escape (and are killed, as a result). In contrast, the opposite was true for herptiles, with most individuals being returned alive. However, Thomas *et al.* (2012) reported that amphibians follow

a similar pattern to that of mammals and birds, finding that most are returned dead (54%). Sample sizes for amphibians were low, relative to mammals and birds (50 and 36, in Thomas *et al.*, 2012 and the current study, respectively), and therefore reliability is somewhat questionable.

3.4.10 Life stage and sex of prey

A similar proportion of mammals and birds were identified as being juveniles (64.17% and 61.58%, respectively), which may be a reflection of the availability of prey throughout the study period. A five-year study into the demographics of a British passerine (bullfinch, *Pyrrhula pyrrhula*) found that at its peak (October), the population contained over three times as many juveniles than adults (using mist nets, Newton, 1999). This study suggests that juveniles can make up around 78.5% of the total population (in the Autumn, Newton, 1999), and therefore, the results found here add further evidence to the suggestion that cats hunt in accordance with what is available (Churcher and Lawton, 1987; Molsher *et al.*, 1999; Loyd *et al.*, 2013; Kitts-Morgan *et al.*, 2015; Yip *et al.*, 2015).

However, as juvenile birds are generally dimorphic from adults, at least until their post-juvenile moult, and are therefore quite easy to identify as such, age may have been more frequently noted for young individuals. Age was not explicitly requested on data entry forms, and therefore, many participants may have assumed that this information was not useful (or were not certain). This could have led to many people only recording age when reporting an obvious juvenile. As a result, young birds (and mammals) may be over-represented in the data, and it would therefore be incorrect to assume that the entire dataset follows these proportions. Although these data are not typically given for the majority of dietary research, one study in the USA reported that only 12.5% of bird returns were juveniles (Kays and DeWan, 2004). While the total sample size was very low (n = 8 birds), all dead prey items were identified by researchers, rather than cat owners (Kays and DeWan, 2004). Interestingly, monitoring returns was conducted over just three months (May-July) when birds are beginning to fledge, so higher proportions of bird captures may be

expected to be juveniles (Kays and DeWan, 2004). Given the small sample of birds, any interpretation of this result should be conducted with caution.

Of the mammal returns, it was apparent throughout data collation that many brown rats and European rabbits were reported to be juveniles, so this was examined further. The high proportion of brown rat juveniles may be considered representative, as adults are known to be very aggressive and are therefore less likely to be caught (Fitzgerald *et al.*, 1991). Brown rats can also be relatively easily aged by size, which may have increased participants' ability to accurately collect these data. Of the European rabbits reported, just under half (45.16%) were assigned an age, largely because many were not returned whole (and therefore could not be easily assigned an age). The high number of juveniles in this sample appears to represent availability, as a large increase in rabbit records was observed in spring and summer months (when juveniles are plentiful). Indeed, Flux (2007) found that 97.14% of European rabbits returned home were juveniles (in New Zealand), comparable to the 94.9% found here.

Of the mammalian adults returned, the majority may be expected to be males, as females are less active during breeding seasons (Andersson and Erlinge, 1977). Adult mammal prey were indeed predominantly males, although only by a slight margin. Birds were also only slightly unbalanced, with the majority being female. For birds, it can be assumed that individuals are sexed on plumage differences, rather than a prominent brood patch, for example (as this would require greater knowledge of bird anatomy). This means that potentially only sexually dimorphic species were differentiated with confidence. Indeed, of those birds for which sex was recorded, 93.76% exhibited sexual dimorphism. Mammals, however, would have to be sexed based on genitals, as they are generally monomorphic in size and pelage (Lu *et al.*, 2014). As testicles are more obvious during breeding seasons, it is perhaps likely that those males for which sex was recorded, were breeding adults (Gurnell and Flowerdew, 2019; McCleery *et al.*, 2021). In females, prominent nipples suggest that an individual currently has (or very recently had) a litter, reliant on milk (Gurnell and Flowerdew, 2019; McCleery *et al.*, 2021). Again, it is easier to determine sex in females during the breeding season. Therefore, in the case of mammals, it may be assumed that the majority (if not all) of individuals for which sex was recorded, were breeding adults. Although it is sometimes possible to sex juvenile mammals, these data may be less reliable as

male and female genitals can look very similar when young (or outside of breeding seasons, Gurnell and Flowerdew, 2019).

The removal of breeding adults can have a larger impact on prey populations than that of juveniles or senescent individuals (Begon *et al.*, 2006; Hoy *et al.*, 2015). Similarly, particularly in the case of mammals, extensive losses of females would likely impact the population more than male losses, as females are generally vital to the success of a litter, whereas males are not always (Begon *et al.*, 2006). In the case of birds, however, males and females can play similar roles in ensuring the successful fledging of their brood (Cockburn, 2006). Therefore, any adult losses (either male or female, of optimal breeding age) to the bird population could potentially limit reproductive success.

3.4.11 Unpalatability

Another factor recorded regarding the prey returned (along with age, sex, and whether or not the animal was alive) was whether the individual was eaten, part-eaten, or left whole by the cat. Here, the high proportion of shrews observed being returned 'whole and intact' (96.8%) provides further evidence to suggest that insectivores are generally unpalatable to cats (as suggested by Toner, 1956; Leyhausen, 1979; Turner and Bateson, 2000; Krauze-Gryz *et al.*, 2012; Kauhala *et al.*, 2015). This may lead to a higher proportion of total predated shrews (total captures) being recorded in return-questionnaire studies, than other (more palatable) small mammals. This strongly suggests (along with the analyses in Chapter 2) that it would be inappropriate to extrapolate these data (in order to reach a figure for total predation) using the same multiplication factors as for more palatable taxa. For example, where Kays and DeWan (2004) estimated that cats return 30% of prey killed, all returned taxa were multiplied by 3.3 (see Chapter 1 for further details). Here, the data suggest that, for insectivores, this multiplication factor should be far lower than that of rodents for example, as rodents are eaten in much higher proportions. Similarly, as birds are perhaps more detectable than small mammals (as suggested

in section 3.4.5 and Chapter 2), these prey should also be multiplied by a lower figure than rodents.

As reported by one of the project's participants, a number of European rabbit adults appeared to have myxomatosis (all of which were uneaten). This provides anecdotal evidence that individuals which are infected with the myxoma virus may be somewhat unpalatable to cats, and they may recognise that these individuals are best left unconsumed. However, a study into the diet of wildcats (*Felis silvestris*) in Scotland found that young rabbits were heavily predated during the spring and summer months (when availability is high), but wildcats later showed a preference for adult rabbits infected with myxomatosis in the autumn and winter months (Corbett, 1979). Although a study on wildcats rather than domestic cats, this suggests that (for European rabbits, at least) cats largely hunt individuals of reduced fitness, or juveniles (Corbett, 1979).

3.4.12 Misidentification and reliability of data

Almost half of the prey records were submitted alongside a photograph, which were then used to assess the reliability of such data from members of the public. While only a small percentage were misidentified (7.12%), this spanned a range of species (n = 18). Owners had some problems identifying and distinguishing relatively common species, a finding similar to previous studies (Lepczyk *et al.*, 2004; Baker *et al.*, 2008), despite providing identification guidance online and through a printable PDF. This could perhaps be expected in countries which have a particularly rich diversity of fauna, but UK species are arguably simpler to identify (at least to family level). However, voles were mistaken for mice quite frequently, as were shrews. Due to the recent progression of technology and the popularity of smart phones, the proportion of prey which were misidentified by cat owners here may be rather lower than that seen in earlier studies (particularly those conducted over 10 years previous, for example Woods *et al.*, 2003; Baker *et al.*, 2005), as identification information is more readily available and instantly accessible. However, misidentification rate is rarely monitored by researchers and it is therefore difficult to make comparisons with previous literature.

Misidentification can be a problem with citizen science studies such as this, as there is a heavy reliance on the records submitted. Such research relies on assumptions regarding the participants' identification skills, honesty, vigilance, and rigour. Of course, vigilance and detection of prey is likely to vary depending on the cat owners' routines and patterns of leaving the house. For example, retired people, or those working from home are more likely to detect prey before it is eaten by the cat or scavenged by another animal. This difference is thought to have been observed here where mammal records doubled as the UK experienced national lockdowns due to COVID-19 during the spring and summer of 2020.

Misidentification of prey can cause particular problems where species of conservation concern are over- or under-recorded as a result. For example, here, wood mice were recorded as hazel dormice on three occasions (at least), which is equal to one third of all reports of this species. Indeed, only one hazel dormouse was confirmed with a photograph. As this species is undergoing population declines (Mathews *et al.*, 2018), these reports may have been cause for slight alarm. Extrapolating these low figures (for the hazel dormouse) to estimate total predation by all cats in the UK would lead to an overestimate of 33%. Therefore, the impact would be estimated to be greater than it likely is. However, requesting photographic confirmation has, in this case, proved to be an important consideration in this type of research.

One large unknown factor within this research project is whether cat owners were more or less likely to submit data when their cat had not predated. For example, it may be the case that participants gradually lost interest in the project or they felt that their contribution was not valuable, as their cat was not regularly returning prey. Alternatively, it may be that cats were returning large numbers of prey, therefore increasing the reporting effort of their owner and lowering interest in the study. This is important to consider, as data recorded may not be representative of the larger cat population. While data were only received for 54.92% of the cats registered, it may be assumed that many participants did not receive email correspondences, as a number of people got in contact to say that reminders (amongst other correspondences) were discovered in their 'junk' email folder. Of the 553 cats for which data were successfully obtained, 17.54% (n = 97) were only monitored for one month. Despite efforts to ensure the ease of data submission, whilst gathering detailed records, it appears that interest in the project fluctuated

from month to month for a number of participants. It seems likely, after further email communication with a number of participants, that many of the non-responding cat owners had little to report. Therefore, those cats which regularly return prey are perhaps overrepresented in this sample.

3.4.13 Owner predictions

Owners were found to overestimate prey returns made by their cat(s). A similar result to previous studies (Barratt, 1998; Tschanz *et al.*, 2011; McDonald *et al.*, 2015), this shows that predictions made by owners are not a reliable measure of cat predation. While one study claims that cat owners 'failed to perceive the magnitude of their cats' impacts on wildlife' (McDonald *et al.*, 2015), it is indeed reported in the same study that owners generally overestimate rather than underestimate their cat's prey returns (which is not equivalent to impact or total kill rates). As suggested by Baker *et al.* (2005), predictions made by cat owners may be used to assess bias within the participant sample. Here, since prey were overestimated by owners, it appears that the sample is perhaps more biased towards those whose cats return larger numbers of prey, as owners of active hunters may have been more likely to register. Therefore, the overall estimate produced here (1.57 prey per month per cat) may itself be an overestimate.

Barratt (1998) suggests that owner estimates may be influenced by the time of year that they register to join such a study. For example, owners who complete the registration questionnaire in the summer months may overestimate predation by their cat in the winter, since prey returns are high at the time of signing up. As suggested by McDonald *et al.* (2015), this overestimation may stem from the owners' own views and whether they perceive predatory behaviour to be a positive or negative attribute. Anecdotally, while many owners of cats in the current study did not show either a positive or negative reaction to their cat's hunting activities, it was apparent that a number were concerned where prey return rates were high, yet some owners appeared to have a sense of pride regarding their cat's predatory prowess. This certainly warrants further

investigation, as owner perceptions and views are of key importance to reducing potential impacts of free-roaming pet cats.

3.4.14 Changes over time

There were a number of differences between the prey proportions presented here and those found by Woods *et al.* (2003). This previous study, conducted in 1997, reported house sparrow returns as a higher proportion of total prey than were reported here. Since the UK-wide population of house sparrows has remained stable over this time, this difference is likely due to local availability of prey, as bird predation is proportionally higher in urban areas (Barratt, 1997; Kauhala *et al.*, 2015; Krauze-Gryz *et al.*, 2017). The proportions of dunnocks appear to have increased, which is in line with a national increase of 14% between 1995 and 2020 (Harris *et al.*, 2022).

For mammals, there has been a notable decrease in proportions of shrew species and European rabbits in the data over this 21-24 year period, but an increase in the proportions of rodents reported. Indeed, European rabbits appear to be undergoing a population decline in the UK, and both common and pygmy shrews are noted as 'stable/declining' (Mathews *et al.*, 2018). Rodent populations, however, appear stable, with brown rats increasing slightly (Mathews *et al.*, 2018). This decrease of shrews and rabbits in the cats' diet may be a functional response to a change in availability. Cats are known to be generalist predators which can easily adapt and switch between prey types, according to what is most available (Molsher *et al.*, 1999; Dickman and Newsome, 2015). However, an Australian study found that a large majority of cats (81.9%) caught fewer than five different species in a year, despite prey diversity being quite high (67 species were reported to be returned throughout the study period, Barratt, 1997). This specialist predatory behaviour may lead to declines in some populations, if a preferred species is of conservation concern (Dickman and Newsome, 2015). The current study, however, has found that such species are rare in the prey returns of cats in the UK, with the exception of house sparrows (although comprising only <3% of all prey items, see sections 3.3.2 and 3.4.2). Indeed, many of the prey

species frequently recorded here are commonly regarded as pests by members of the public (Baker *et al.*, 2020).

Of course, the comparison between this study and that of Woods *et al.* (2003) can only be used to give an indication of relative changes in prey proportions over time. It may, however, provide the basis of future research into temporal variation in prey proportions (see Chapter 5 for further analyses).

3.5 **Summary and conclusion**

The most returned taxon were the mammals, followed by birds, amphibians, and reptiles, proportions of which were in line with many previous studies, in particular across Europe (Chapter 2). All variables tested here were found to influence predation. While age, sex, year, and season cannot be controlled by cat owners, there are a number of things that owners could do which may reduce predation. Body condition may be controlled in some individuals (although this can depend on overall health and metabolism) by altering food provision. The 'time of day' analysis indicates that overnight curfews (currently implemented in areas of Australia) would likely not have the desired effect in the UK and other countries with similar prey composition, since birds are more commonly caught during the day. This analysis is important as curfews should reflect the activity times of species of highest conservation concern. Installing a cat flap may affect the number of prey caught, as cats have access to the outdoors at all hours of the day and night. This may also influence the number returned home (or at least, detected), as those with cat flap access are able to deposit prey inside the house during the night. Cats with night-time access to the outdoors (whether through a cat flap or by being locked out) are likely to return greater numbers of small mammals, as their activity follows a crepuscular pattern.

Reducing the amount of time that a cat is permitted outdoor access at certain times of day and particularly in spring and summer will likely reduce predation. Limiting outdoor time may be particularly useful to reduce the number of prey caught and returned by those termed 'super predators'. For bird-specialist cats, limits on day-time outdoor roaming can be expected to

reduce predation impacts. However, for those which hunt predominantly mammals, night curfews could be used. In the case of highly productive, large rodents, such as rats, there is the possibility of mesopredator release effects if cats are removed from the environment (Rayner *et al.*, 2007; Ritchie and Johnson, 2009). This could potentially lead to impacts on some bird populations, directly through predation of chicks and eggs by rats (Jones *et al.*, 2008), if rats are not controlled. It is therefore important to first assess the impacts of domestic cats on small mammal populations, before advising such curfews. If impacts are negligible and populations remain stable with cats existing as a predation pressure, it may not be advisable to attempt to reduce predation on mesopredator species.

It was found that the majority of both mammals and birds were aged as juveniles, although this may be a due to them being perhaps more notable, increasing reports (since age was not explicitly requested survey information). Individuals more likely to be caught by cats appear to be vulnerable in age (juveniles) or condition (illness). Therefore, the potential impact on populations is reduced, as removing young, senescent, or unwell individuals from a population has little effect on reproductive success and breeding productivity of that population (Hoy *et al.*, 2015). However, it is important to note the importance of season when considering the age of avian prey in particular, as predation of older juveniles towards the autumn will likely have a larger impact on the population than losses of those more recently hatched (during the spring and summer).

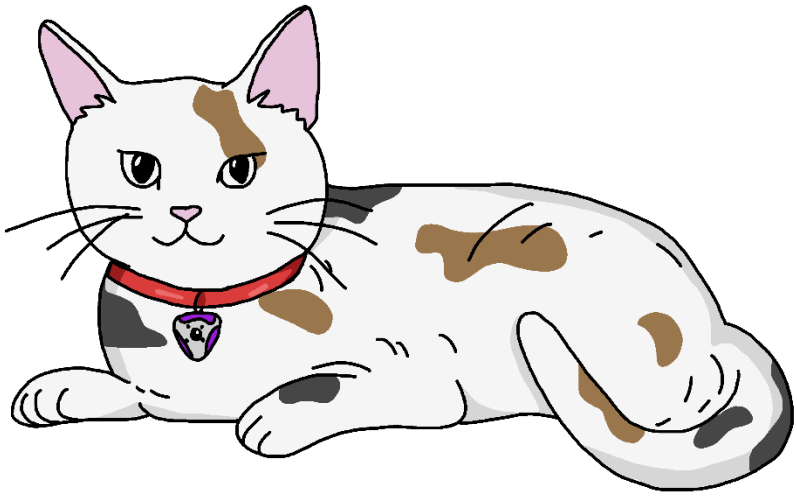
The current study found that cats may return over 150 million prey per year in the UK, derived from an estimated 18.84 prey per cat, per year (and 8.2 million outdoor-going cats). Although mean prey returned per month was 1.57, most cats returned far below this figure (≤0.5 per month, ≤6 per year) and the overall mean is increased by 'super predator' cats which return prey in much greater numbers than the average individual. The estimates presented here may be higher than the true values, although perhaps only marginally. Since cat owners were not randomly targeted in the recruitment phase (e.g. by telephone or post), people who have cats which regularly returned prey may have been more likely to find the website and register. Furthermore, it was assumed here that all live (and rescued) prey subsequently died (both live

and dead prey were included), therefore the figures produced are more likely overestimates than underestimates.

Here, estimated prey returns do not account for discarded, eaten, or otherwise undetected prey. This will be further explored in Chapter 4. It was noted here that only a very small proportion of shrews (3.2%) were reported as being eaten or part-eaten, which adds further evidence supporting the idea that shrews are unpalatable to cats. Therefore, insectivore species should certainly be treated differently when extrapolating to produce a figure of total predation by cats (which includes those unrecorded in questionnaire-based studies).

Chapter 4

Cat cameras



Hannah Lockwood

4.1 **Introduction**

4.1.1 Total prey caught by cats

As discussed in previous chapters, free-roaming outdoor pet cats may have a negative effect on wild fauna (Doherty *et al.*, 2016). However, in order to assess the impact of domestic cats, there must first be a reliable estimate of the number of prey killed in a particular area. While Chapter 3 explored the number and type of prey returned home in the UK, it is very likely that cats do not return all prey captures, as a proportion may be eaten or discarded. It is also worth noting that some returned items may have been scavenged and not caught by the returning cat. Those killed and discarded may later be picked up by a neighbouring cat and returned. Additionally, animals killed by other means (traffic and window collisions, or intentional poisoning) may also be returned home by a cat. For example, anecdotal evidence from the prey return study conducted in Chapter 3 shows that, occasionally, cats may bring home prey that is already in a state of decomposition. Two cats were also noted to have previously carried birds of prey into the house (male sparrowhawk, *Accipiter nisus* and female merlin, *Falco columbarius*), which are likely to have struck a nearby window, rather than being caught by the cats directly.

In order to estimate the total number of prey caught by cats, there must be some observation of the proportion returned home. This has been achieved in previous studies through direct observation (watching and recording cat predation in real time, for example Kays and DeWan, 2004), comparing scat and stomach samples with returned prey (Krauze-Gryz *et al.*, 2012), and more recently, through the use of point-of-view video cameras on cats (Loyd *et al.*, 2013; Bruce *et al.*, 2019; Seymour *et al.*, 2020). So far, estimates of the proportion of prey returned home are widely variable, ranging from 8.8% (estimated by comparing consumed and returned prey in Poland, Krauze-Gryz *et al.*, 2012) to 30% (estimated based on direct observation in the USA, Kays and DeWan, 2004). This means that return data may be multiplied by a factor between 3.33 (Kays and DeWan, 2004) and 11.4 (Krauze-Gryz *et al.*, 2012).

Extrapolating these data relies on the sample being representative of all cats in a given area (in the UK, in this case). A cat's propensity to hunt can be dependent on many factors, including the age (Woods *et al.*, 2003; Bruce *et al.*, 2019), sex, and body condition (Woods *et al.*, 2003) of the individual, as well as extrinsic factors such as fed diet (Cecchetti *et al.*, 2021). Chapter 3 showed that while most cats returned fewer than one prey per month (median = 0), some individuals returned over 10 prey animals in the same time period. One cat returned 61 vertebrate prey in a single month (see Chapter 3 for details). It is therefore important to compare data against a sample deemed to be representative of the local cat population (which will likely vary around the world, Chapter 2).

4.1.2 Extrapolation

Extrapolating data to give an estimate of total predation by cats should be conducted cautiously. As discussed in Chapter 2, the use of a single multiplier for all prey species groups may produce overestimates of insectivores and birds, compared to rodent predation. This is likely due to differences in palatability (the likelihood that a prey item will be eaten) and detectability (the likelihood that prey will be detected by owners) between species groups. For example, where a bird species is predated, there may be very visible evidence (feathers) at the site of capture or consumption. This is then more likely to be recorded by owners in a 'cat diary' questionnaire than some less conspicuous prey remains (such as rodents), and therefore can be overestimated during the extrapolation process. Similarly, shrews which are returned home have been found to be 'whole' and uneaten most of the time (96.8% of shrew returns, see Chapter 3 for details), perhaps indicating low palatability (Leyhausen, 1979). This may mean that return studies are recording closer to 100% of insectivore prey captures than that of other small mammals, again resulting in potential overestimation through extrapolation. In addition, where a single multiplier is used in all extrapolations, it will most strongly represent species which more frequently appear in the cats' diet (mice and voles, see Chapter 3). This could be problematic, as it produces a

multiplier which may greatly inflate and overestimate bird and insectivore captures, while only moderately underestimating rodent prey.

The method of extrapolation can be improved by assigning each prey group a different 'multiplication factor' (number by which prey figures are multiplied to estimate total predation). For example, if cat owners are found to detect 50% of rodents caught, return figures for this prey group would be multiplied by two. However, if 90% of insectivores are detected and reported in return surveys, the figures for this prey group would be multiplied by 1.11.

As discussed in previous chapters, a frequently used multiplication factor is 3.3 (Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012), which is derived from an estimate that cats return 30% of all prey captured (Kays and DeWan, 2004). However, this estimate is based on prey return data of a small sample of pet cats (n = 12) and data of 11 cats that were directly observed outdoors over a decade before the return study was conducted (assumed to be different individuals in each part of the study). Rather than using the proportion of prey returned and detected (of the total caught) to produce a multiplier, Kays and DeWan (2004) first calculated a daily predation rate (using the hourly capture rate multiplied by a cat owner-estimate of time spent outdoors per day), before comparing this to the return data (from 11 years later). This showed the daily predation rate to be 3.3x higher than returned prey. One must exercise caution when interpreting these results, as there are likely differences in habitat, prey availability, and the individual propensity to hunt of the different cat samples (11 years apart). While studies using direct observation of individuals were once useful in the absence of less intrusive methods, the development of cat-point-of-view video cameras (hereafter 'cat cameras') creates an opportunity to reassess predation rates in a more accurate and less time-intensive way, while also avoiding effects of observer presence.

4.1.3 Video cameras

Cat cameras can give a cat's eye view of the surrounding environment and can be used to assess behaviour, including predation (Huck and Watson, 2019). The suggested ideal weight of collar-mounted devices varies among study species, but Coughlin and van Heezik (2015) concluded that for domestic cats, devices should weigh no more than 2% of the cat's body mass. Therefore, devices such as cameras should weigh around 80g or less, based on an average cat body weight of around 4kg (Coughlin and van Heezik, 2015). Most previous video studies have slightly exceeded this guideline (Table 4. 1), using devices of up to 140g in weight. In order to minimise any effects of the cameras' presence, weight and size should be kept as low as possible (Casper, 2009). However, smaller devices have reduced battery life. Thus, in order to achieve a greater sample of footage, study design may call for a slightly larger unit. When working alongside cat owners, studies may request that the cat wears the camera on multiple occasions (for example, Seymour *et al.*, 2020), whereas when studying feral individuals, this would require recapture and is not always a possibility (for example, McGregor *et al.*, 2015). Therefore, in order to maximise recording time per individual subject, larger cameras may be used on feral cats.

Previously, video studies on owned individuals have been conducted in New Zealand, USA, and South Africa, but not yet in Europe (Table 4. 1). Of these, only two studies have simultaneously compared the prey returned home (recorded by cat owners) with the prey observed via video footage (Loyd *et al.*, 2013; Seymour *et al.*, 2020). As found in Chapter 2, location can influence the proportions of prey recorded, as availability varies around the world. Other factors which may differ around the world include owner-fed diet (for example, most cats in Chile are fed household scraps) and parasite burden (as none of the subject cats in the same Chilean study received basic healthcare or preventative treatments, Silva-Rodriguez and Sieving, 2011), both of which may affect an individual's appetite and propensity to hunt. Therefore, research into caught and returned prey should be conducted regionally.

Table 4. 1. Previous video footage studies, their location, camera information, and details regarding the sample sizes.

Reference	Year	Location	Cat type	Camera weight	Battery life (hrs)	Number of cats	Mean recording time per cat (hrs)
Loyd *et al.*	2013	US	Owned	90g	10-12	55	38
McGregor *et al.*	2015	AU	Feral	100-140g	2-8	13	3.9
Hernandez *et al.*	2018	US	Feral	90g	24 (mean)	29	22
Bruce *et al.*	2019	NZ	Owned	90g	10-12	37	4.9
Seymour *et al.*	2020	ZA	Owned	32g	2-2.5	25	36

The amount of footage required to examine the proportion of prey returned, relative to total captures, is dependent on how frequently prey are caught. This can vary widely, depending on the individual cats being monitored. For example, Loyd *et al.* (2013) found that the amount of footage obtained before the first predation was observed was between two hours and 55 hours (mean = 19.3 hours). This variability may be partly due to individual propensity to hunt between cats (as explored in Chapter 3), as well as differences in habitat, prey availability, and opportunity.

4.1.4 Influence of prey size and taxon

In a cat camera study in the USA, prey size was found to influence whether prey were discarded or consumed, with larger prey being more likely to be discarded (Loyd *et al.*, 2013). Despite this finding, no pattern was apparent between prey size and whether the prey was carried home by the cat (Loyd *et al.*, 2013). However, this may be limited by a small sample of captured prey (n = 39).

The prey weight categories used by Loyd *et al.* (2013) are as follows: <5g = small, 5-17g = medium, >17g = large. These categories would group most British rodents into the same category as much larger-bodied prey such as rabbits ('large' prey weighed >17g, Table 4. 2). While this may have

been appropriate to apply to North American prey species, weight categories would need to be adapted for application in the UK. As it has been found that small collar-mounted equipment does not limit the behavioural range of cats (for example, a 32g camera, Seymour *et al.*, 2020) prey of a similar weight are also unlikely to be burdensome to cats. Therefore, weight categories should be adjusted so that camera equipment is not in the largest size category.

Table 4. 2. Commonly returned prey in the UK (as identified in Chapter 3), their weight range, and size category (as defined by Loyd *et al.*, 2013). Each prey species is then compared to the weight of the smallest camera used previously (32g, Seymour *et al.*, 2020). Mammal weights are taken from Couzens *et al.* (2017), and bird weights from BTO (2023b).

Species	Weight range (adult)	Size category (if using categories defined by Loyd *et al.*, 2013)	Size relative to 32g cat camera*
Mammals			
Wood mouse	13-27g	Medium/Large	Smaller
House mouse	12-22g	Medium/Large	Smaller
Brown rat	200-400g	Large	Larger
Bank vole	14-40g	Medium/Large	Similar
Field vole	20-40g	Large	Similar
European rabbit	1200-2000g	Large	Larger
Common shrew	6-12g	Medium	Smaller
Pygmy shrew	2.5-7.5g	Small/Medium	Smaller
Birds			
House sparrow	24-31g	Large	Smaller
Blackbird	87-122g	Large	Larger
Robin	16-23g	Medium/Large	Smaller
Blue tit	10-12g	Medium	Smaller
Dunnock	19-24g	Large	Smaller

*Although 32g was the lightest camera used previously (by Seymour *et al.*, 2020), the cameras used by Loyd *et al.* (2013) weighed 90g.

As well as the number of prey items returned home, prey size may also influence detection rates, as larger-bodied prey cannot be brought through a cat flap as easily as smaller species. Therefore,

even if larger prey items (such as rabbits) are carried home, they may be more likely to be left on the doorstep which leaves them open to being scavenged by other carnivores in the area.

Different taxa may be placed into separate size categories, such that invertebrates will occupy the 'small' prey group and may be treated differently to mammals in the 'medium' group. Indeed, an effect of taxon on whether prey are returned or not has previously been found, with mammals being more frequently returned, relative to invertebrates and reptiles (Seymour *et al.*, 2020). It is therefore important to account for taxon when assessing prey size influence.

4.1.5 Aims and hypotheses

Currently, only three cat camera studies have been conducted on owned domestic cats (Loyd *et al.*, 2013; Bruce *et al.*, 2019; Seymour *et al.*, 2020), none of which monitored cats in Europe. Here, small video cameras (weighing 32g) were used on a sample of cats in the UK, in order to (1) determine the proportion of all prey that are detected (after being returned home), or not detected (e.g. eaten in situ, discarded elsewhere, or otherwise not found by the cats' owner), and to (2) calculate 'multiplication factors' using two different methods. These could then be used to (3) calculate total annual predation in the UK (from the return data in Chapter 3). Multipliers can then be (4) divided according to taxonomic group and (5) methods compared (aims, including secondary aims, and structure of this chapter are described in Figure 4. 1**Error! Reference source not found.**).

Based on previous research in this field, it can be hypothesised that between 8.8% (Krauze-Gryz *et al.*, 2012) and 30% (Kays and DeWan, 2004) of all prey will be returned home. However, this is likely to vary between prey groups, as some taxa may be more commonly eaten (highly palatable), and therefore not detected by cat owners. In New Zealand, Bruce *et al.* (2019) found that none of the prey items recorded on camera were returned home, perhaps as prey caught consisted of invertebrates and reptiles (both of which were commonly consumed). However, in studies where mammal captures are recorded, these prey are more commonly brought home

(e.g. 66% of mammalian prey returned home in South Africa, Seymour *et al.*, 2020). Indeed, prey size has also been found to influence whether an item is consumed or discarded (Loyd *et al.*, 2013). It can also be expected that, of the prey returned home, a proportion will go unnoticed by the owners. In particular, it is likely that less conspicuous prey remains (partially eaten small mammals, for example) may have lower detectability than larger, more obvious remains (such as birds). Due to the variation in detectability and palatability (perhaps also size) of different prey groups, overall, proportions of captured prey of different taxa are likely to differ from those found in the cat diary study (Chapter 3), along with previous return research in Europe (Churcher and Lawton, 1987; Woods *et al.*, 2003; Baker *et al.*, 2005; Baker *et al.*, 2008; Krauze-Gryz *et al.*, 2012; McDonald *et al.*, 2015; Piontek *et al.*, 2021). Specifically, it can be expected that rodents will represent a greater proportion of captures than observed in return surveys (61.58% in Chapter 3, not including unidentified small mammals), and that birds and insectivores will make up a smaller proportion than seen in return studies (16.03% and 5.6%, respectively, in Chapter 3).

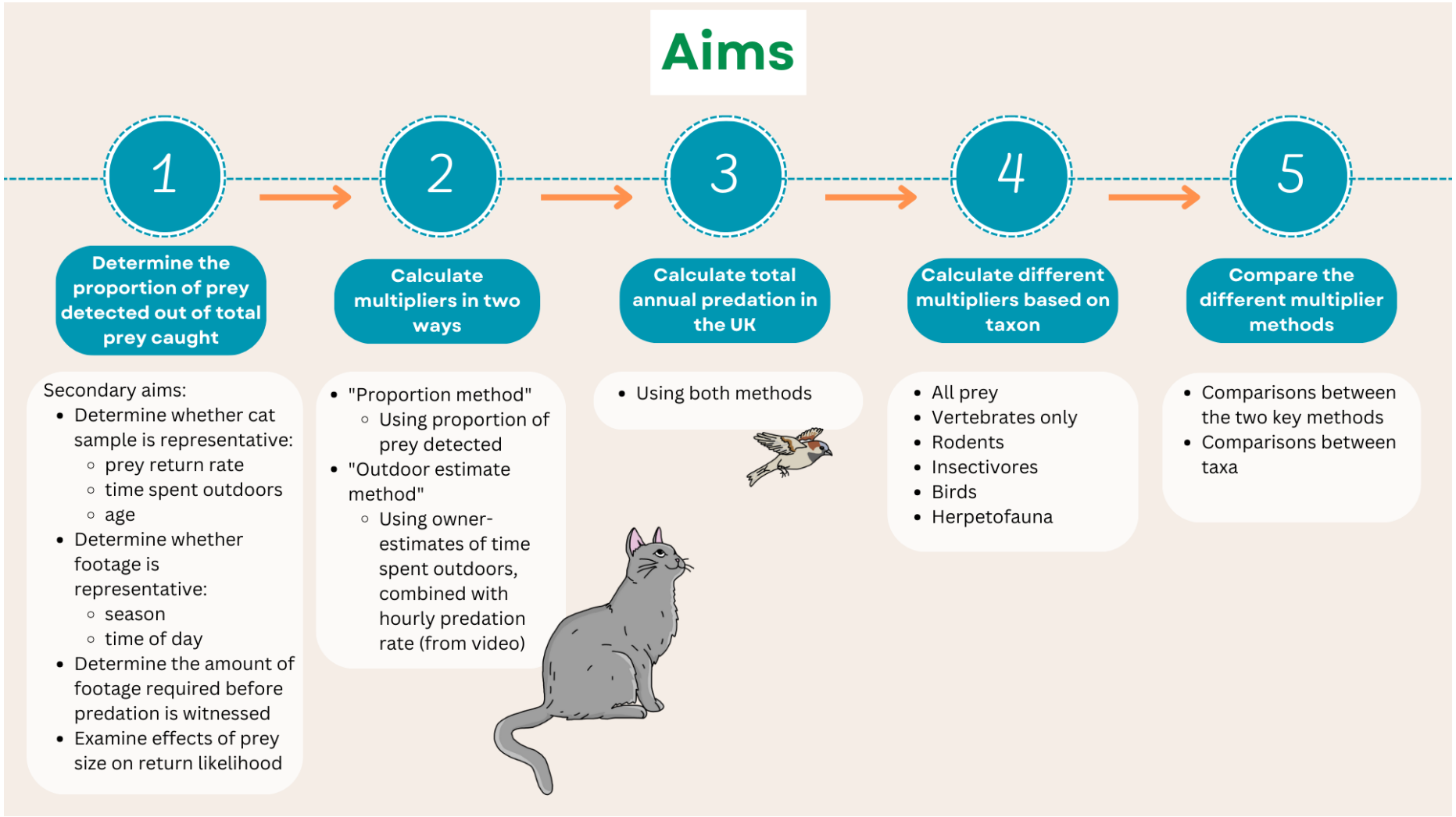


Figure 4. 1. The five key aims and structure of the present study, along with secondary aims.

4.2 **Methods**

4.2.1 Cat cameras

The outdoor lives of 21 pet cats were monitored, however, due to a technical difficulty, outdoor video data were only available for 20 cats (locations shown in Figure 4. 2). Overall, recording covered all four seasons, between September 2010 and September 2021, and all times of day and night. Participating cat owners were asked to record every couple of days, as convenient, for a period of one month (for a number of cats, this period was extended, see Table 4. 4 for details). Cat owners were provided with a camera, full instructions, charging/data cable, and a break-away safety cat collar.

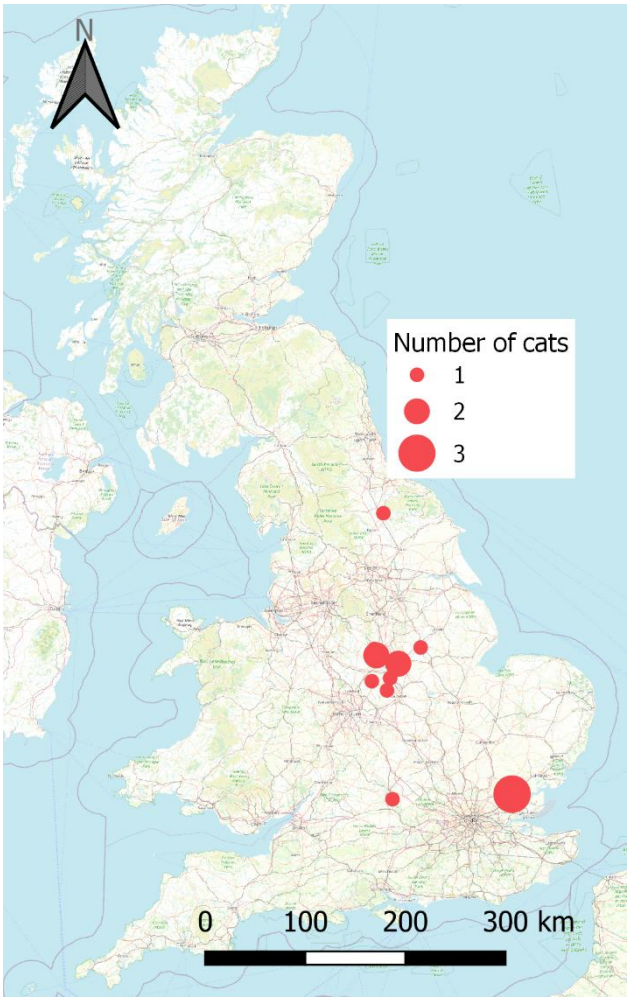


Figure 4. 2. Locations of cats which were selected to wear cat cameras. Point size denotes the number of cats monitored in the same household (not necessarily during the same time period).

The cameras used were commercially available, manufactured by Eyenimal (2022). Cameras were mounted onto a cat's collar using a fastening clip attached to the unit (Figure 4. 3). Weighing just 32g and being 41mm by 44mm by 25mm in size, the camera units were not considered to hinder the movements of the subject cats or impact their behaviour in any way. Based on the assumption that the average British cat weighs around 4kg (the recommended healthy weight, Blue Cross, 2022), a 30g camera is below 1% of the cats' body weight, far below the recommended maximum weight for mammal transmitter equipment (Casper, 2009; Loyd *et al.*, 2013; Coughlin and van Heezik, 2015; Dickinson *et al.*, 2020). Prior to enrolling participant cats,

cameras were first tested on a small sample (personal communication, based on Huck and Watson, 2019; n = 6, Huck, 2022) to ensure that individuals could carry out a range of normal behaviours, including hunting postures, walking, running, pouncing, and cleaning. The same camera system was used by Seymour *et al.* (2020), where the equipment was not found to impact hunting behaviour.

The Eyenimal cameras had an infra-red 'night vision' mode which was automatically enabled in low-light conditions, allowing recording after dusk. There was a small blue light on the units which participants were asked to cover with sticky tack or opaque tape, minimising any 'warning' effect that this may have on prey at night. Recording was continuous (rather than motion-activated) and the internal battery of the Eyenimal camera can record for up to 2.5 hours in this mode (although the battery life can degrade with increased use), with footage stored onto an internal 4GB memory card.

Figure 4. 3. 'Treacle' (left) and 'Alfie' (right), each wearing a collar-mounted camera. Photographs by M. Huck (Treacle) and H. Lockwood (Alfie).

4.2.2 What the cat dragged in

A ‘cat diary’ (prey return survey) was completed by cat owners, giving return data pertaining to 553 individual cats (as described in Chapter 3). This citizen science project was titled ‘What the Cat Dragged in’ and data collection was spread over a 3.5 year period (June 2018 – December 2021). Cat owners reported all prey returned home, whether alive or dead. A subset of these cats was then recruited for the camera study (n = 15). A further six participant cats were recruited and monitored prior to the start of the prey return survey (recruited for the study by Huck and Watson, 2019).

Upon registration to take part in the prey return survey, owners completed a registration questionnaire, offering information regarding their cat’s history and routine (questions are listed in Appendix 3. 2). Here, owners were asked to estimate how long (in hours) their cat typically spent outdoors, splitting the year into two seasons (warm season: April-September, cold season: October-March). These data were later used to evaluate whether cats in the video study subset were representative of the larger sample (Aim 1: secondary aim, Figure 4. 1). In addition, time spent outdoors was further used to estimate the number of prey caught per cat, per day, following the methods of Kays and DeWan (2004, Aim 2), producing a multiplier when compared to return rates (“outdoor estimate method”, Figure 4. 1).

4.2.3 Footage

All camera footage was uploaded to online cloud storage by the cat owners and reviewed by the author. Predation events were recorded, along with the overall recording time to predation for each cat, and the total footage time for each cat. Only footage recorded outdoors was included here. When a predation event was recorded on camera, it was noted whether the prey animal escaped, was returned home by the cat, was eaten, or discarded. If returned home, this was then compared to the cat diary data (see Chapter 3 for details) to see whether it was detected by the

cat owner. If the owner was not actively recording prey returns, individuals were assumed to be detected if it was clear from the footage that owners were aware of the prey capture. Prey were easily identifiable once successfully caught (at least to family level), as prey in the mouth of the cat was clearly in view of the camera (Figure 4. 4). Both invertebrate and vertebrate prey were recorded here, but analyses focussed on vertebrates, allowing for comparison with findings from Chapter 3.

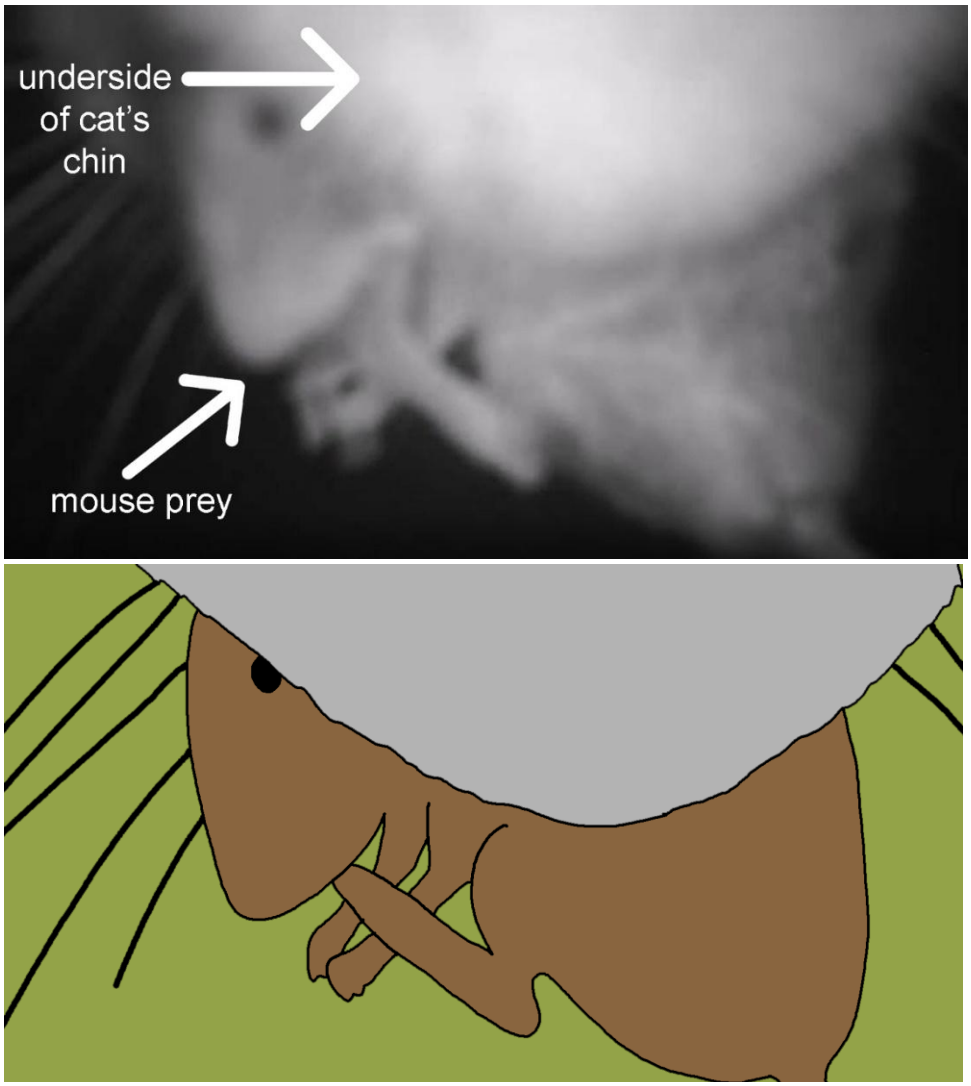


Figure 4. 4. A still taken from camera footage of a mouse capture (top), showing the underside of the cat's chin at the top of the frame and the prey hanging from the cat's mouth. This is shown more clearly as an illustration (bottom).

4.2.4 Analyses

4.2.4.1 Aim 1: determine the proportion of prey detected, relative to total caught

The number of each prey type caught (on video) were assessed, along with prey size, although not formally analysed. The proportion of prey both returned and detected (out of all prey captures observed on video) was determined for each taxon.

In order to ensure that these results were representative of typical cat behaviour, the estimated time spend outdoors, prey return rate, and age of the cat camera sample were tested against the wider survey sample (What the Cat Dragged In, Chapter 3). After initial testing found that data violated normality assumptions (although not homogeneity assumptions, Appendix 4. 1), Wilcoxon rank sum tests were used to establish whether the estimated time that video study cats spent outdoors was representative of the wider study sample. This was conducted for both the warm (April-September) and cold seasons (October-March). The same statistical methods were applied to prey return data to find, again, whether the video sample was representative of the larger survey sample (for normality and homogeneity of variances test results, see Appendix 4. 2**Error! Reference source not found.**). A further Wilcoxon rank sum test was used to compare the age of participating cats for both the camera sample and the wider survey sample.

χ^2 goodness of fit tests were conducted to assess whether the amount of camera footage retrieved was as expected (if data were evenly distributed) for each month, and time of day. The time of day that the cameras were used was divided into four (unequal) time periods (shown in Table 4. 3), which was accounted for in the χ^2 testing. Expected values for each time category were calculated using the following, where v = the total length of all videos and h = length of time category (e.g. evening) in hours:

$$(\mathrm{v} \div 24) \times \mathrm{h}$$

Table 4. 3. Time periods used when analysing the volume of camera footage retrieved, including the specific timings, and length of each period.

Time of day	Hours	Length of period (hours)
Morning	06:00 – 11:59	6
Afternoon	12:00 – 16:59	5
Evening	17:00 – 20:59	4
Night	21:00 – 05:59	9

All formal analyses were conducted using R version 4.3.0 (R Core Team, 2022) and R Studio (R Studio Team, 2020). Graphical plots were created using the R package ggplot2 (Wickham, 2016).

4.2.4.2 Aims 2 & 3: calculate multipliers in two ways and calculate total annual predation in the UK

The number and proportion of prey returned (and detected by the cats' owners), were calculated and used to generate a multiplication factor, by which return data can be multiplied to estimate total predation. This was done using the following calculation, to first find the total annual prey returned home, and then to multiply those returned data by the factor generated from video footage:

$$\mathrm{T} = ((((\mathrm{Pr} \div \mathrm{Mo}) \div C) \times 12) \times Pop) \times (100 \div x)$$

Where:

$\mathrm{T}=$	Total annual predation in the UK
$\mathrm{Pr}=$	Total prey (or prey group) returned in Chapter 3
$\mathrm{Mo}=$	Number of months of return survey (Chapter 3)
$\mathrm{C}=$	Number of return survey cats (Chapter 3)
$\mathrm{Pop}=$	The estimated UK outdoor cat population
$x=$	the percentage of prey (or prey group) returned home (video)

The second method used to calculate the multiplication factor is adapted from Kays and DeWan (2004). The mean estimated daily time spent outdoors by cats (estimated by owners) was used, from survey data collected in the wider 'What the Cat Dragged in' project, to extrapolate prey captures. Annual predation rates were calculated by multiplying the mean time spent outdoors (estimated by cat owners) per day by the number of vertebrate prey caught per hour of video recording (to give a daily rate). This was then further multiplied by 365 to give an annual rate (Figure 4. 5), and again by the outdoor cat population of 8.2 million for a national figure. When national vertebrate predation rate was divided by the national vertebrate return rate of 154.5 million (Chapter 3), this generated a multiplier.

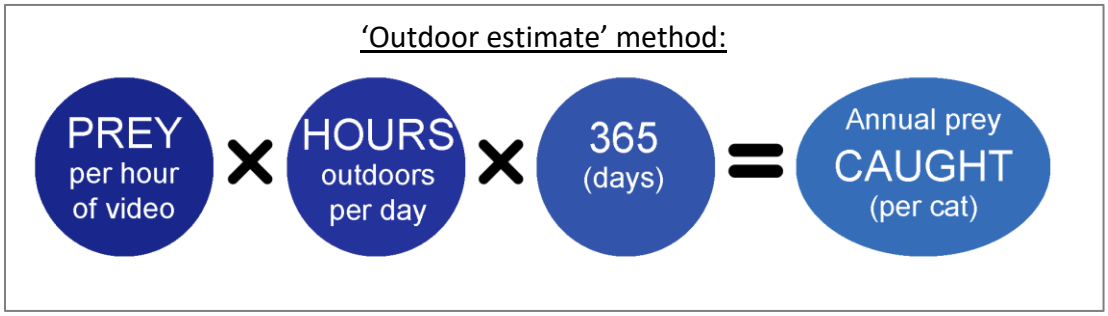


Figure 4. 5. Calculation used to estimate the total annual predation of cats in the UK (per cat). This is then multiplied by an estimate of the total cat population (which has outdoor access) in the UK. Method adapted from Kays and DeWan (2004).

4.2.4.3 Aims 4 & 5: calculate different multipliers based on taxon and compare different multiplier methods

The calculations for both multiplier methods were performed for different taxonomic groupings, where sample sizes of caught prey (on video) were sufficient to calculate the proportion of prey returned home. The resulting multipliers were then compared with those produced by previous studies.

4.3 **Results**

4.3.1 Overview and cat demographics: representativeness of sample

Total outdoor camera recording time for all cats was 157 hours 34 minutes (157.58 hours), but ranged from 0.06 hours to 51.72 hours per cat (mean = 7.88 hours, Table 4. 4). The male to female sex ratio for all cats was 1:1 (Table 4. 4). The majority of cats monitored using cameras were aged six years and under (77.78%, Table 4. 4), and the camera study cats were not significantly younger than the wider survey sample (Wilcoxon rank sum test: n = 984, 13, W = 4824.5, p = 0.1164).

Table 4. 4. The age and sex of each cat that participated in the video study, along with the mean number of hours spend outdoors daily, the number of hours of camera footage recorded outdoors, and the time period in which each cat was monitored. As some individuals were monitored over a number of years, the age category may have changed during data collection. An * denotes those cats who are known to have moved from one age category to another during this time. For some cats, outdoor estimates were not reported by the owners (marked as NA). Data are then summarised for age category (median), sex (as a ratio), hours outdoors (mean), and hours of outdoor footage (mean), comparing the video study cats with the wider study sample, described in Chapter 3.

Cat name	**Age (at first registration) in years**	**Sex**	**Hours spent outdoors per 24 hours[1]**	**Hours of outdoor footage**	**Period monitored**
Benji	1-3	Male	14.25	11.36	Jul - Aug 2020
Joey	1-3	Female	3.75	1.47	Aug 2020
Titch	4-6	Male	13	9.25	Aug 2020
Rascal	1-3	Male	12	1.49	Nov 2020
Domino	7-9	Female	10.5	0.88	Nov 2020
Ling	1-3	Male	5	3.07	Nov 2020
Simba	1-3	Male	11.5	0.38	Nov 2020
Darling	1-3	Female	10.5	8.17	Aug - Sep 2021
Rocky	4-6*	Male	NA	31.32	Feb 2017 - Apr 2019
Treacle	1-3*	Female	9	51.72	May 2015 - Jul 2018
Leyhausen	1-3	Male	9.5	19.24	Apr 2019 - Jul 2020
Crystal	7-9	Female	14.5	0.86	Aug 2020
Magic	16+	Female	8	0.08	Aug 2020
Poppy	4-6	Female	12.5	1.26	Aug - Sep 2020
Esme	7-9	Female	NA	0.06	Oct 2016
Ivan	4-6	Male	NA	3.67	Oct - Nov 2016
Jet	4-6	Male	NA	5.82	Nov - Dec 2016
Loki	1-3	Female	NA	3.16	Oct - Nov 2016
Nala	4-6	Female	NA	1.46	Oct 2016
Sooty	7-9	Male	NA	2.84	Sep 2010
Average (video cats)	4-6 (median category)	1:1 (ratio F:M)	10.31 (mean)	7.88 (mean)	-
Average (wider study sample)	4-6 (median category)	1:1.09 (ratio F:M)	8 (mean)	-	-

[1.] Time spent outdoors is based on owner estimates and is not an absolute measure.

While overall, owners in the 'What the Cat Dragged in' survey (Chapter 3) estimated that their cat spent a mean of 8 hours per day outdoors (mean = 9.95 hours April-September, mean = 6.05 hours October-March, n = 983 cats), individuals monitored using cat cameras spent an estimated 10.31 hours (mean) outdoors per day (mean = 12.54 hours April-September, mean = 8.08 hours October-March, n = 13 cats, Table 4. 4). Video sample cats were estimated to spend significantly longer outdoors than the wider cat sample in both the warm (Wilcoxon rank sum test: n = 984, 13, W = 8532, p = 0.0374) and cold seasons (Wilcoxon rank sum test: n = 984, 13, W = 8429.5, p = 0.0483).

In addition, the data collected in Chapter 3 show that for all cats monitored throughout the warm season (n = 456, April-September), a mean of 2.08 vertebrate prey were returned home per cat, per month, whereas the subsample used for cat camera monitoring (n = 14) returned 2.68 prey per cat, per month. This difference was not significant (Wilcoxon rank sum test: n = 553, 13, W = 3053, p = 0.4798). Similarly, in the cold season (October-March), the video study cats returned an average of 0.65 more vertebrate prey (mean = 1.7) than the entire sample (mean = 1.05), per cat, per month. Again, this difference was not significant (Wilcoxon rank sum test: n = 553, 13, W = 3852.5, p = 0.0943).

4.3.2 Footage retrieved: representativeness of the sample

The number of hours of video footage recorded each month followed a different pattern than expected (χ^2 = 73.35, df = 11, p < 0.001). More video footage was recorded in the summer months, with the most being obtained in July and August, respectively (Figure 4. 6). The mean number of hours of video footage recorded was 13.13 per month (range: 1.61 - 32.11 hours, Figure 4. 6). August and November had the largest sample of cats monitored (n = 9 and n = 8, respectively), while January and February had the fewest (n = 2 for both months, Figure 4. 6). On average, 4.25 cats (mean) were monitored using the cameras each month (range = 2 - 9 individuals). As well as this variation in sampling effort throughout the year, time of day that cameras were active also varied. The volume of video footage obtained during each time

category (as described in Table 4. 3) followed a different pattern than expected (χ^2 = 10.33, df = 3, p = 0.016), with more cats monitored during daytime hours than evening and overnight (Figure 4. 7). However, this does not indicate a greater amount of footage during daytime periods, since the monitoring time is unbalanced between cats. The overnight period (21:00 - 05:59) yielded the greatest amount of footage (56.33 hours, Figure 4. 7), although the majority of this was recorded before midnight (72.99%). More footage was obtained from the morning (06:00 - 11:59) than would be expected if data were evenly distributed throughout the day (Figure 4. 7). In contrast, afternoon footage (12:00 - 16:59) was below the expected number of hours (Figure 4. 7).

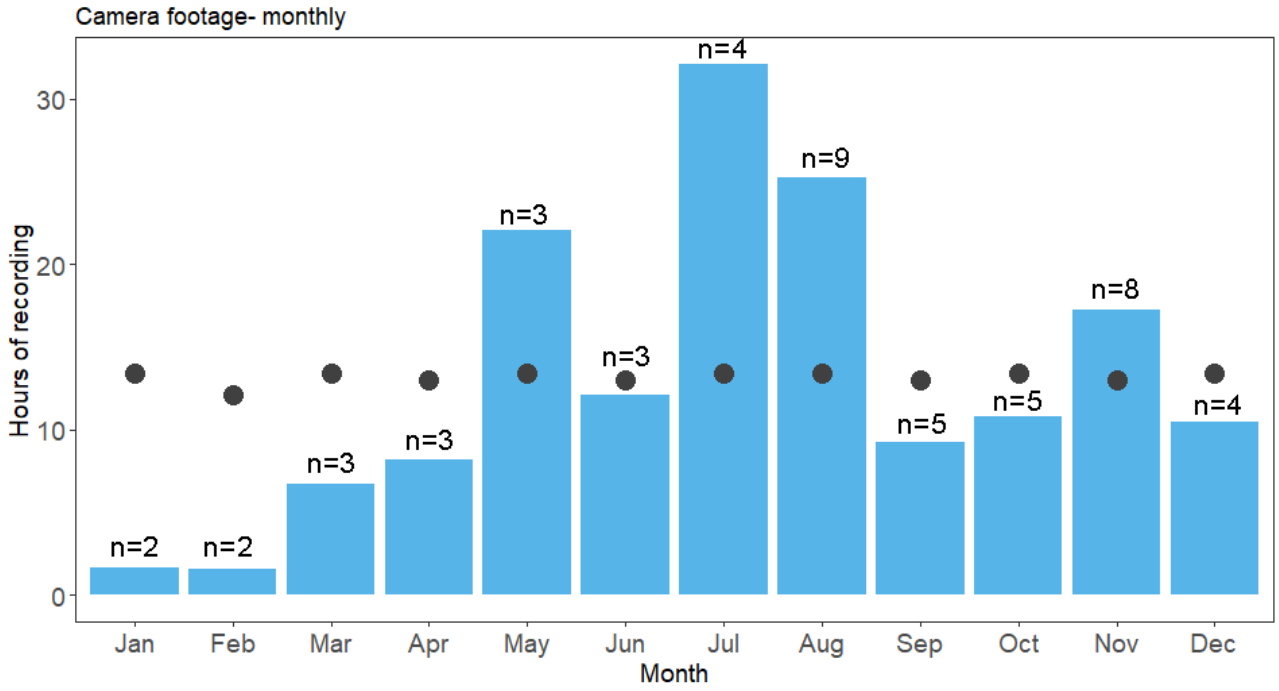


Figure 4. 6. The hours of outdoor camera footage obtained for each month of the year, for all cats (n = 20). The number of cats for which outdoor footage was recorded is given above each bar. Each black point represents the expected recording time, if this were equal for all months (accounting for uneven month lengths). Months for which bars extend above the grey point can be considered over-represented, whereas those below are under-represented.

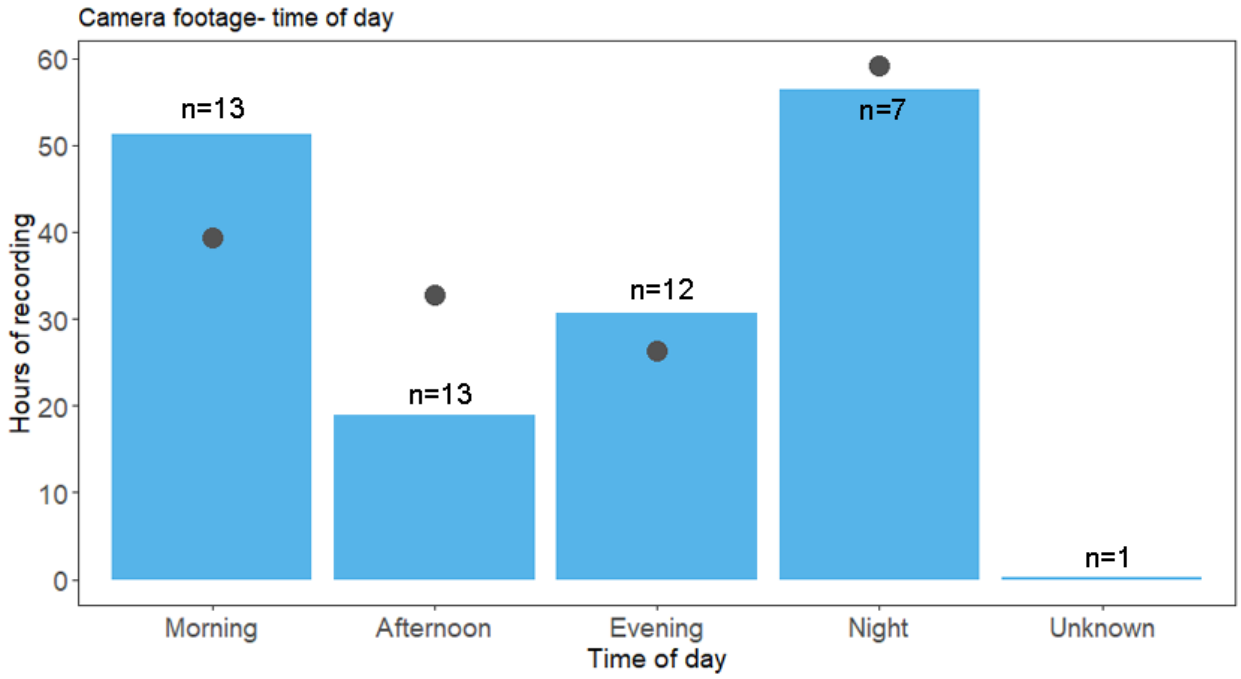


Figure 4. 7. The number of hours of outdoor footage obtained during each of the four time periods within each day. The number of cats for which outdoor footage was recorded is given for each bar. Each black point represents the expected number of recorded hours of footage, if this were equal for each hour of the day. Time periods for which bars extend above the grey point can be considered over-represented, whereas those below are under-represented.

4.3.3 Prey caught

Overall, six of the 20 cats were observed to successfully capture prey on video footage (30% of cats, but only five caught vertebrates), although these six yielded 78.23% of all footage captured (123.28 hours of 157.58 total hours). Fourteen prey items were observed to be captured during 157.58 hours of video recording, giving a mean of 0.09 prey per hour of footage. The recording time required before the first predation was observed, varied by individual, but ranged from 0.51 hours to 19.37 hours (mean = 7.66 hours), for the six cats found to predate whilst wearing a cat camera (Figure 4. 8, Appendix 4. 3).

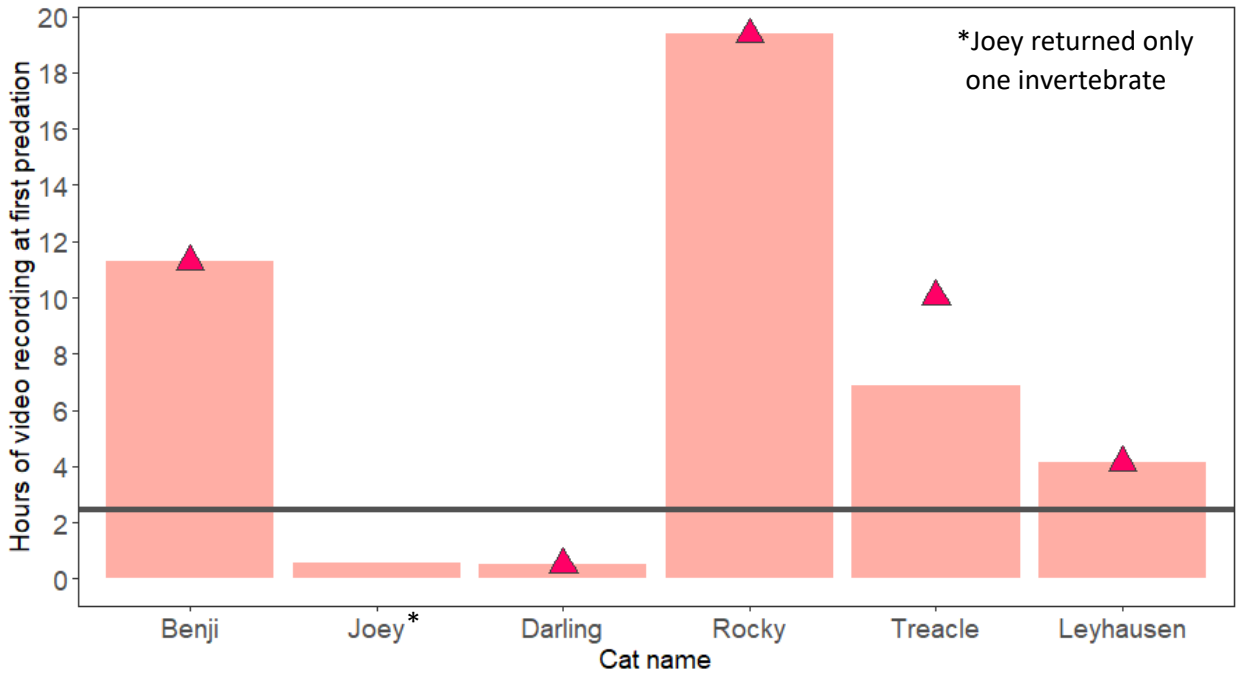


Figure 4. 8. The number of hours of video footage retrieved before the first prey capture was observed for each predating cat. Bars include all data, and triangle points represent the first vertebrate predation ('Joey' did not capture any vertebrates during monitoring, and 'Treacle' caught both invertebrates and vertebrates). The mean recording time for remaining cats (who were not observed to capture prey during recording) is shown by the horizontal line (2.45 hours).

Two cats caught their first vertebrate prey within 4.5 hours of recording ('Darling' and 'Leyhausen', Figures 4. 8 and 4. 9). Less than 10 hours of footage was obtained for each of the cats which were not observed to predate. However, for three out of the five cats with vertebrate captures on video, more than 10 hours of outdoor footage was recorded before the first prey item was caught (Figure 4. 9). For one of these, 'Treacle', more than a further 30 hours of outdoor footage was recorded before a second vertebrate capture was observed (Figure 4. 9).

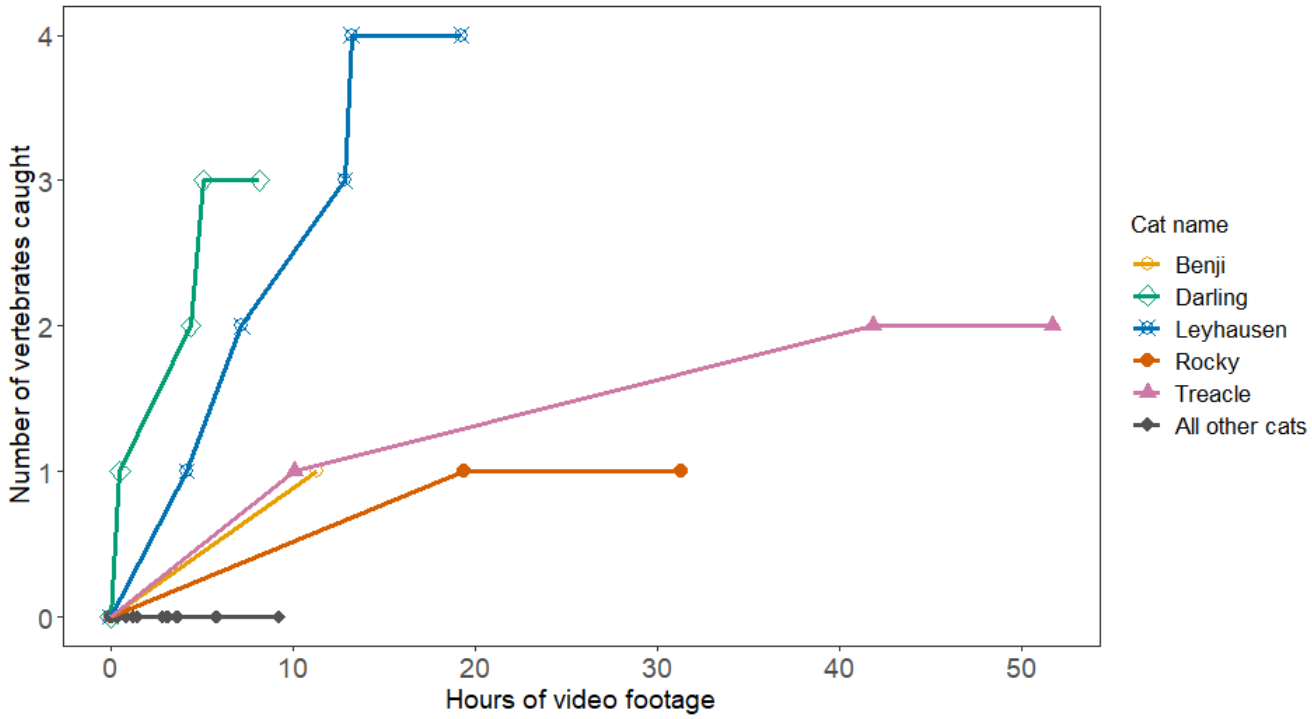


Figure 4. 9. Cumulative number of vertebrates caught by each cat and the total amount of outdoor footage recorded at the point that prey were captured. 'All other cats' represents those which were not found to predate (vertebrates) whilst wearing a cat camera. Where line sections are horizontal, no further prey were caught and the line extends to the end of the recording period for each cat.

Of the prey captures recorded, mammals constituted the majority (n = 10, 71.43%), followed by invertebrates (n = 3, 21.43%), and a single bird (7.14%, Table 4. 5). The most frequently caught prey item was the bank vole (*Myodes glareolus*), constituting over a third of total prey captured on video (Table 4. 5). No data are available for insectivores, although a live shrew was observed on one occasion. Despite the shrew being detected on the footage, and the cat ('Rocky') being most likely aware of its presence, there was no capture attempt made. In addition, a different cat, 'Treacle', observed a hedgehog (*Erinaceus europaeus*) on one occasion, but showed no interest in it. One small mammal captured was not successfully identified from the footage, although it was characteristic in shape and size of an adult or sub-adult rodent (murid or cricetid).

Eleven vertebrate prey were captured by five cats, resulting in a mean of 0.07 vertebrate prey per hour of outdoor recording time (mammal mean = 0.06/h, bird mean = 0.01/h). Of these,

90.91% were small mammals (Table 4. 5). There were insufficient data to formally test the influence of prey size on whether returned home (mean prey per category = 1.75, range: 0 - 8 prey). There was also an apparent problem with the size categories identified, as all invertebrates occupied one category, all mammals were in another, and the single bird in its own category (Table 4. 5, Figure 4. 10).

Table 4. 5. Species caught by six hunting owned cats, as recorded using cat cameras. Results are given as totals and percentages. For comparison with Chapter 3, the percentage of the total returned prey sample from the questionnaire study is given for each species (e.g. bank voles represent 45.45% of vertebrates found on video, but 7.86% of prey returned in Chapter 3). Prey sizes are based on published species weights (for mammals, Couzens *et al.*, 2017; and the blackbird, BTO, 2023a). Size categories are as follows: Small: <5g, Medium: 5-50g, Large: >50g, as adapted from Loyd *et al.* (2013).

Prey	**Prey size**	**Number captured**	**% of all captures**	**% of vertebrate captures**	**% of all prey returned (Chapter 3)**
Mammals					
Mouse (Muridae sp.)	Medium	2	14.29	18.18	12.46
Wood mouse (*Apodemus sylvaticus*)	Medium	1	7.14	9.09	20.62
Vole (Cricetidae sp.)	Medium	1	7.14	9.09	2.90
Bank vole (*Myodes glareolus*)	Medium	5	35.71	45.45	7.86
Unidentified small mammal	Medium	1	7.14	9.09	12.79
Birds					
Blackbird (*Turdus merula*)	Large	1	7.14	9.09	1.45
Invertebrates					
Cockchafer (*Melolontha melolontha*)	Very small	1	7.14	-	-
Fly (Diptera sp.)	Very small	1	7.14	-	-
Butterfly or moth (Lepidoptera sp.)	Very small	1	7.14	-	-
Total		14			

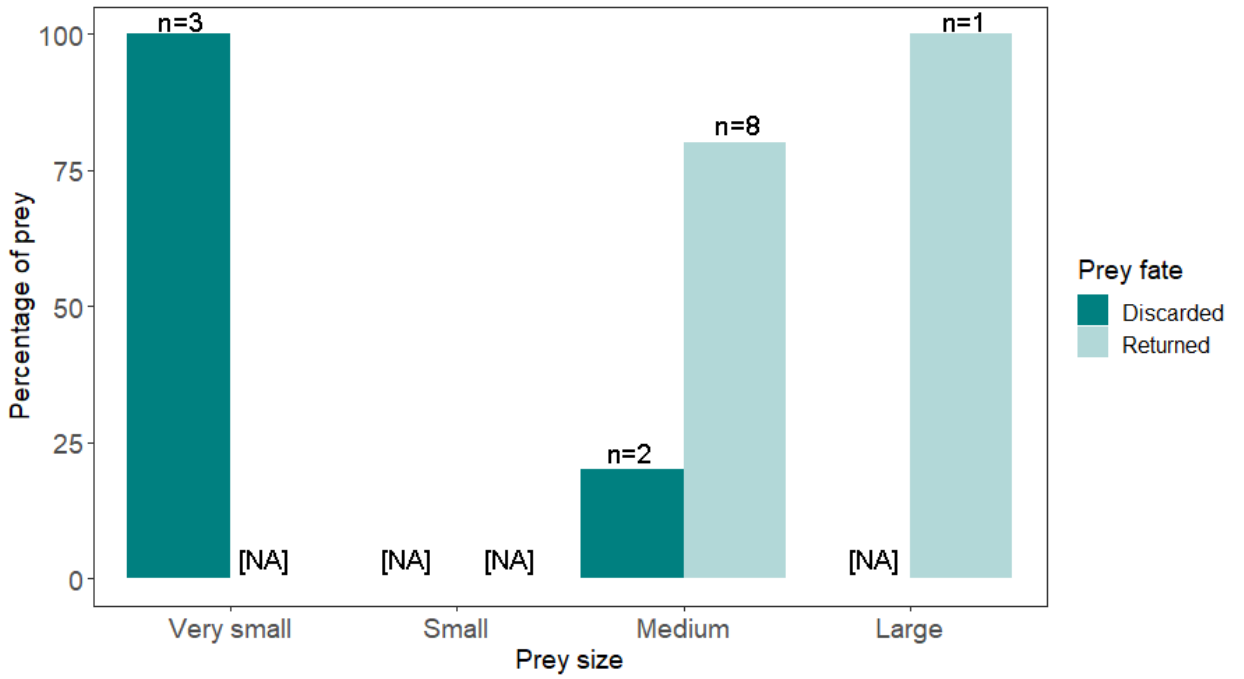


Figure 4. 10. Percentage of each prey size category which were returned and those discarded (none were eaten). Sample sizes are given above each bar and 'NA' denotes instances for which no data were retrieved. It should be noted that all 'very small' species were invertebrates, all 'medium' species were rodents, and the large individual was a blackbird.

4.3.4 Proportions returned and detected: multiplier method 1

Eight out of ten small mammals (80%) were observed to be returned home (20% were discarded or escaped), and at least six were detected and reported by the cats' owners (Table 4. 6). For two of the mammals caught and returned (by 'Darling'), the cat's owner could not recall whether these prey were detected (they were returned to the rear garden in open habitat). Owing to this uncertainty, between 60% and 80% of mammals captured were returned and detected. This gives a multiplication factor of between 1.25 and 1.67 for rodent prey (calculated as 100% / 80% and

100% / 60%, respectively), allowing extrapolation to estimate total predation rates. Only one bird predation was recorded on the footage (which was detected by the owner) and none of the invertebrates (n = 3) were returned home, remaining undetected by owners (although owners were not specifically requested to report invertebrates returned home, see Chapter 3).

Overall, 63.64% of vertebrate prey were detected by the cats' owners and reported in the prey return survey (Table 4. 6). However, if Darling's owner did indeed detect those which they could not recall, vertebrate detection would be 81.82%. This generates a multiplication factor of between 1.22 and 1.57 for vertebrate prey (calculated as 100% / 81.82% and 100% / 63.64%, respectively).

Table 4. 6. The number of mammals and birds captured by each cat, along with the total number returned (as seen on footage), and how many of these were detected and recorded by the owner in the prey return survey during the corresponding time period. A dash (-) denotes zero prey recorded and cases where fewer prey were detected than caught are in bold.

Cat name	Mammals caught	Mammals returned	Mammals detected	Birds caught	Birds returned	Birds detected
Benji	1	1	1	-	-	-
Joey	-	-	-	-	-	-
Titch	-	-	-	-	-	-
Rascal	-	-	-	-	-	-
Domino	-	-	-	-	-	-
Ling	-	-	-	-	-	-
Simba	-	-	-	-	-	-
Darling	3	3	**1***	-	-	-
Rocky	1	1	1	-	-	-
Treacle	2	1	**1**	-	-	-
Leyhausen	3	2	**2**	1	1	1
Crystal	-	-	-	-	-	-
Magic	-	-	-	-	-	-
Poppy	-	-	-	-	-	-
Esme	-	-	-	-	-	-
Ivan	-	-	-	-	-	-
Jet	-	-	-	-	-	-
Loki	-	-	-	-	-	-
Nala	-	-	-	-	-	-
Sooty	-	-	-	-	-	-
Totals	**10**	**8**	**6**	**1**	**1**	**1**

* Darling's owners did not record prey detected during this time, but one vole was observed to be detected on the video

On 27 occasions, prey animals were returned home (and reported in the return survey) on the same day that the camera was worn, although not during the filming period (see Appendix 4. 4 for details). Usually, recording began shortly after prey had been returned (18 out of 27 occasions, Appendix 4. 4).

Only one of the two previous studies which compared the prey observed via video footage with simultaneous record keeping by owners provided sufficiently detailed data on prey species to enable analyses on different taxa (Seymour *et al.*, 2020). While Seymour *et al.* (2020) observed that just 17.7% of all prey were returned home (resulting in a multiplier of 5.65), there was high variance between prey groups, with 60% of rodents and 100% of insectivores being returned, yet none of the invertebrates caught were seen by owners (Table 4. 7). On comparison, the current study also found that rodents were returned in similar proportions, yet no data were available for insectivores (Table 4. 7).

Table 4. 7. Comparison between prey return data for the current study and three previous cat camera studies (data collected by Loyd *et al.*, 2013; Bruce *et al.*, 2019; Seymour *et al.*, 2020; Loyd, 2023, personal communication). The percentage of each prey group that was returned home (and detected), followed by the sample size (n/total caught) in parentheses. NA depicts instances where data were not recorded.

Prey group	**% Returned home (n/total caught)**			
	Current study	**Loyd *et al.* (2013)**	**Seymour *et al.* (2020)**	**Bruce *et al.* (2019)**
Mammals (all)	60 (6/10)*	50 (5/10)	66.67 (10/15)	NA
(Rodents)	60 (6/10)*	55.56 (5/9)	60 (6/10)	NA
(Insectivores)	NA	0 (0/1)	100 (4/4)	NA
Birds	100 (1/1)	40 (2/5)	0 (0/1)	NA
Reptiles	NA	7.14 (1/14)	0 (0/31)	0 (0/3)
Amphibians	NA	50 (1/2)	100 (1/1)	NA
Invertebrates	0 (0/3)	0 (0/8)	0 (0/13)	0 (0/37)

* Conservative estimates, as it is unknown whether all of Darling's prey were detected

4.3.5 Estimates of time spent outdoors: multiplier method 2

In the wider sample of cats (Chapter 3, 'What the Cat Dragged in'), cat owners estimated that their cats spent a mean of eight hours outdoors per day (per 24h period, Table 4. 4). Since the

sample size was rather larger than that observed here in the video study (Chapter 3: n = 985, video study: n = 13), the wider dataset is more representative of the cat population in the UK.

Cats here caught 0.07 vertebrate prey per hour of outdoor video footage. This, multiplied by eight hours of outdoor time equals an estimate of 0.56 prey caught per day (using method 2). Multiplied again by 365 gives 204.4 prey per cat per year, which is 10.85x the number returned home each year (18.84 per cat), far higher than that produced using method 1.

4.3.6 Extrapolation methods

In Chapter 3, it was found that cats returned an estimated 1.57 vertebrate prey per cat, per month. Multiplied by 12 months and then by a figure of 8.2 million owned cats with outdoor access in the UK (based on an estimated 11.1 million cats, 73.9% of which have outdoor access, Finka *et al.*, 2019; PDSA, 2022), this gave a total estimate for vertebrate returns in excess of 150 million, annually (Figure 4. 11):

$$(1.57 \times 12) \times 8200000 = 154{,}488{,}000$$

The population estimate of 8.2 million cats was used here, rather than the higher estimate of 10.2 million (as described in section 3.3.1), since the estimated percentage of cats with outdoor access (73.9%, Finka *et al.*, 2019) is more recent (than the 97% estimate, Sims *et al.*, 2008).

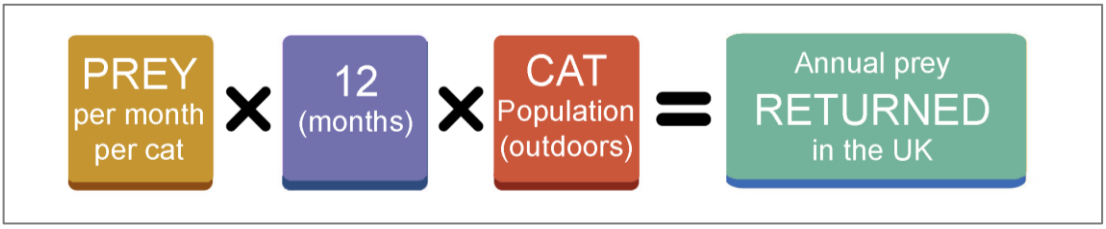


Figure 4. 11. Calculation used to estimate the annual figure for returned prey across the UK. Note that this is not the total predation rate and a multiplication factor is yet to be applied.

When multipliers established here (1.57 and 1.22, both using method 1, section 4.3.4) were applied to the return data of Chapter 3, the resulting estimate of total predation in the UK equates to between 188.4 million and 242.6 million vertebrates per year (Table 4. 8). However, using the alternative method based on video footage and owner-estimated time spent outdoors, this figure was between 6.9 and 8.9 times higher (multiplier of 10.85, using method 2, section 4.3.5), at 1.68 billion vertebrate prey per year (Table 4. 8**Error! Reference source not found.**).

The same methods were applied to rodents only, using adjusted multipliers. This gave an estimate of between 111.9 million and 149.6 million rodent prey per year (using the multiplier method). Using the time spent outdoors (method 2), an estimated 1.44 billion rodents are caught per year in the UK (Table 4. 8). This second estimate is between 9.6 and 12.8 times greater than that generated using the multiplier method. A third method was not able to be applied here, as it compares prey eaten (evident from scat and stomach analyses) with return rates (Krauze-Gryz *et al.*, 2012).

Calculations using previous study data showed a difference between multipliers, when split by taxon (Tables 4.9 and 4.10). For example, the 5.65x multiplier from Seymour *et al.* (2020) represents all taxa, but this can be broken down (from the raw data available) to 4.36x for vertebrates, 1.67x for rodents, and 1x for insectivores, although the insectivore multiplier is based on only four individuals (Table 4. 9).

Table 4. 8. Estimates of annual predation by the UK population of outdoor-going cats, using two different methods. Method (1) used the percentage of prey recorded via cat cameras that was returned home (and detected) to generate a multiplier to be applied to return data (e.g. Seymour *et al.*, 2020). Method (2) multiplied prey per hour of footage by estimated time spent outdoors each day (estimated by cat owners in the wider study, following the methods of Kays and DeWan, 2004). Total predation estimates are based on a population of 8.2 million cats (section 3.3.1).

Prey group	Method	Details	Multiplication factor	Returns/ cat/year	Total prey/cat/ year	Annual UK predation estimate
Vertebrates	(1) Percentage of prey returned (video)	63.64% returned and detected	x1.57*	18.84	29.58	242,556,000
		81.82% returned & detected	x1.22**	18.84	22.98	188,436,000
	(2) Prey per day (based on outdoor estimates)	0.07 prey/h of video, 8h outdoors	x10.85	18.84	204.40	1,676,080,000
Rodents	(1) Percentage of prey returned (video)	60% returned & detected	x1.67*	10.92	18.24	149,568,000
		80% returned & detected	x1.25**	10.92	13.65	111,930,000
	(2) Prey per day (based on outdoor estimates)	0.06 prey/h of video, 8h outdoors	x16.04	10.92	175.2	1,436,640,000

*Conservative estimate, if Darling's prey were **not** all detected (i.e. one of three detected)

** If Darling's prey were all detected (i.e. three of three detected)

Table 4. 9. The multiplication factors (by which return data can be multiplied to estimate total prey captures) used in this study, along with those produced by four other studies and three different methods. Factors represent different taxonomic groups of interest, which were produced from the available data. Where data were not sufficient to draw conclusions (i.e. where data were not presented in sufficient detail or too few prey in one category were recorded), 'NA' is reported. Locations are given as two-letter country codes. The two key results of this study (vertebrates) are highlighted by a green box.

Study[1]	**Study method**	**Extrapolation method**	**Location**	**Multiplication factors**					
				All taxa	**Vertebrates**	**Rodents**	**Insectivores**	**Birds**	**Reptiles**
This study[2]	Video	Proportion of prey returned	UK	x1.56	x1.22	x1.25	NA	NA[4]	NA
This study[3]				x2.00	x1.57	x1.67	NA	NA[4]	NA
Loyd *et al.* (2013)	Video	Proportion of prey returned	US	x4.35	x3.45	x1.80	NA[4]	x2.5	x14
Seymour *et al.* (2020)	Video	Proportion of prey returned	ZA	x5.65	x4.36	x1.67	x1[5]	NA[4]	At least x31[6]
Kays and DeWan (2004)	Direct observation	Estimates of time spent outdoors and kill rate per hour observed	US	x3.33	x3.33	NA	NA	NA	NA
Krauze-Gryz *et al.* (2012)	Scat and stomach	Compared prey caught and eaten to prey returned	PL	x14.6	x11.4	x12.6	x1.05	x13.79	x4.89

[1.] It should be noted that some studies (for example, Loss *et al.*, 2013) also refer to a thesis study by C.A. Fiore, which is reported to have generated a 1.2 multiplier to extrapolate from prey return data. This thesis does not appear to be available online at all now, and the author has not been traced, so it is not included here.
[2.] If Darling's prey were all detected (includes invertebrates)
[3.] Conservative estimate, if only one of Darling's prey were detected (includes invertebrates)
[4.] Data insufficient, see Table 4. 7 for sample sizes
[5.] Based on fewer than 5 individuals
[6.] Zero returned home

Table 4. 10. The multiplication factors of this study, along with the four previous studies (as described in Table 4. 9). Given here are both single multipliers ('one size fits all') to be applied to all prey returned, and a separate vertebrate multiplier calculated from each study, to be applied to vertebrate prey returns only. Annual UK estimates of total prey caught are also given, as calculated for each multiplier.

Study	**Single multiplier**	**Annual UK estimate (all prey)**	**Vertebrate multiplier**	**Annual UK estimate (vertebrates)**
This study	x1.56	241,001,280	x1.22	188,475,360
This study	x2	308,976,000	x1.57	242,546,160
Kays and DeWan (2004)	x3.33	514,445,040	x3.33	514,445,040
Loyd *et al.* (2013)	x4.35	672,022,800	x3.45	532,983,600
Seymour *et al.* (2020)	x5.65	872,857,200	x4.36	673,567,680
Krauze-Gryz *et al.* (2012)	x14.6	2,255,524,800	x11.4	1,761,163,200

4.4 **Discussion**

4.4.1 Overview and cat demographics: representativeness of sample

The current study is the first of its kind (comparison between returned and caught prey) to be conducted in the UK, as the majority of previous work has focussed on the USA (George, 1974; Kays and DeWan, 2004; Loyd *et al.*, 2013), and only the third study worldwide to use these specific video methods to compare prey caught with prey returned (the other two being: Loyd *et al.*, 2013; Seymour *et al.*, 2020).

The length of outdoor footage retrieved here is shorter than most other studies (mean= 7.9 hours per cat here, but 38 hours per cat in Loyd *et al.*, 2013), although more data were collected here than in some (McGregor *et al.*, 2015). This is likely due to the difference in battery capacity, being around two hours here, but up to 12 hours in Loyd *et al.* (2013) and Bruce *et al.* (2019). Because of this comparatively low amount of footage retrieved, there were not sufficient prey captures during this time to robustly and reliably analyse, although they do give an important insight into predatory behaviour in the UK.

Overall, the subsample of cats monitored here using cat cameras spent 26% and 34% more time outdoors throughout the year than the wider group, in the warm and cold seasons, respectively. The differences between the two samples were significant, indicating that the subsample selected for video monitoring was not representative of the wider population. This presents a potential problem, since more time outdoors may indicate higher activity and cats may have encountered a greater number of prey per day. However, this study's chief aim was to find the proportion returned (and detected) out of those caught, and it is not clear whether an unrepresentative sample (in terms of time spent outdoors) may affect the cats' behaviour after prey are caught (i.e. what the cat does with the prey).

While vertebrate returns were 29% and 62% higher (in the warm and cold season, respectively) in the video sample than in the larger cat population, these differences were not significant. These tests of representative data have not been conducted in previous video research, but it is

important to understand whether data are likely under-or over-estimates. One study in the USA monitored a small sample of cats in the same location, 11 years apart (direct observations in 1991, followed by prey diary study in 2002, Kays and DeWan, 2004). The multiplication factor derived from this research (Kays and DeWan, 2004), relied rather strongly on the assumption that the cats were representative of the wider population, as the predation rates observed were assumed to be true of most individuals. It is particularly important to assess how representative a population is when sample sizes are small.

4.4.2 Footage retrieved: representativeness of sample

In addition to representation of the average cat, camera data collected here slightly over-represent certain months, particularly in the summer (July and August). This is largely due to the timing of participant recruitment and of equipment being sent out, as some cat owners had the equipment for only a short number of weeks. August had the highest number of contributing cats, and therefore, over-representation can be expected. Most studies of this kind (comparing return rates with true predation) only record for a limited time or season. For example, Kays and DeWan (2004) studied cats in the USA between May and August (in 1991 and again in 2002), and Seymour *et al.* (2020) recorded video footage in November in South Africa (summer), lacking any data for the colder seasons. Here, data for the winter months were present but still under-represented, with January and February data being collected by just two individuals. While this is partly due to the timing of cat recruitment, for a number of months, some owners were in possession of a camera, yet did not record any footage. This may be a result of many things, such as unexpected circumstances, other commitments, waning interest in the project, or just that people forgot to use it. However, this is speculation and should be formally studied to increase participation and maximise data collection in the future.

The apparent over-representation of the morning period is likely due to the owners' schedules and other commitments, as this may be the most convenient time to deploy the camera. Similarly, the afternoon period was under-represented, conceivably as it spanned common

working hours for many people, therefore participants were perhaps not always able to collect data. Although the amount of footage collected during the night was as expected, it was understandably very rare for owners to deploy the camera after midnight (around three quarters of night recording began before midnight). Since the battery capacity of the cameras was around 2-2.5 hours, this means that very little footage was retrieved between 02:00 and 06:00 (when the morning period commenced). Since mammals are generally caught and returned between dusk and dawn (see Chapter 3), mammals may be under-represented in proportional data, meaning they may constitute a higher proportion than is apparent here. This is unlikely to lead to under-representation of birds, as they are generally caught during the day (Chapter 3). In previous research, nocturnal observations have also been lacking, which has been due to some cats remaining at home overnight (Kays and DeWan, 2004) or camera battery limitations (Seymour *et al.*, 2020). In other studies, cats have not been allowed outdoors without their cat camera being switched on (Loyd *et al.*, 2013), ensuring that all predation events are captured.

4.4.3 Prey caught

Although 30% (n = 6) of cats were observed (on video) to capture prey, these cats were responsible for almost 80% of all footage retrieved, owing to unbalanced recording times between cats.

The amount of video footage required before a predation event was observed varied greatly, from around half an hour to over 19 hours, between individuals. The mean time of 7.66 hours is far lower than that of a previous US study by Loyd *et al.* (2013) where it was found that up to 55 hours of footage were required (mean = 19.3 hours). Furthermore, Loyd *et al.* (2013) reported the time to 'hunting behaviour', rather than successful capture, increasing the disparity between the two study results. This may be due to a difference in habitat and prey availability between one city location in the USA (Loyd *et al.*, 2013) and multiple locations around the UK, since predation rates are variable around the world (Chapter 2) and between urban and rural areas (Mitchell and Beck, 1992; Blancher, 2013; Kauhala *et al.*, 2015; Krauze-Gryz *et al.*, 2017).

Of the prey data recorded here, proportions of taxa were similar to those found in return studies (Chapter 3), as mammals are quite consistently the top predated taxon (however, see Bruce *et al.*, 2019; Seymour *et al.*, 2020). All prey caught here are commonly-occurring native species to the UK. Interestingly, one cat ('Rocky') was observed to notice and watch a shrew without showing any signs of predatory interest in it. As suggested in Chapter 3 (and by Toner, 1956; Leyhausen, 1979; Turner and Bateson, 2000; Krauze-Gryz *et al.*, 2012; Kauhala *et al.*, 2015), insectivores such as shrews appear to be unpalatable to cats, as many remain uneaten in dietary research. Here, it seems that this cat (six years old at the time) may have had an awareness of the shrew's unpalatability and its avoidance may be learned behaviour.

Since cats used in the video research spent overall more time outdoors and returned a greater number of prey per month (although not significantly so) than the wider sample, the results pertaining to prey are likely to be biased towards frequent hunters. For example, the estimates of 0.09 and 0.07 prey captured per hour of outdoor footage (for all prey and vertebrates, respectively) are limited in accuracy, due to small sample size, uneven quantities of footage between individuals, and biases in the selection process of cats for the camera study. As the camera subsample of cats returned 29% and 62% more prey than the wider sample (in the warm and cold season, respectively), these estimates of prey per hour outdoors are potentially overestimated and therefore, any impacts of predation using these figures may be inflated.

Due to low sample size, the prey weights (sizes) were not analysed formally. While there appear to be differences in proportion of each prey size category returned home, these categories are also reflective of taxon. Although previously prey size has been found to have no effect on whether returned home or not (Loyd *et al.*, 2013), differences in the weight of camera equipment used limits the comparability with this study.

There are, however, other factors which may influence whether prey are brought home by cats. For example, there may be an interaction between prey taxon and whether dead or alive. If alive, despite injury, some taxa may be more active and exhibit escape behaviour. Birds, for example, may be more challenging to carry home and through a cat flap than a mammal of similar size, due to beating their wings and the position held in by the cat. Mammals on the other hand are

perhaps more likely to be grasped by the neck and may be more easily subdued. Additionally, the distance from the point of capture to the cat's home could alter how likely it is to return prey. Cats which roam particularly far may be less likely to bring home all prey caught. These are factors which should be considered in future research, given a sufficiently large sample size.

4.4.4 Proportions returned and detected

Eighty percent of mammals caught here (observed on video footage) were returned home, yet not all were necessarily detected. Indeed, between 60% and 80% of caught mammals were both returned and detected, owing to some uncertainty around whether two voles were spotted by the owners of one cat. Detectability (as previously discussed in Chapter 3) is likely to vary between taxa, such that one prey group may be particularly conspicuous (such as birds) and therefore be more likely to be detected and recorded by cat owners, whereas others may be less noticeable due to small body size (undetected in long grass, for example) or likelihood of being eaten with little trace (also affected by taxon palatability). It is important not to assume that all returned prey would also be recorded in a prey return diary (such as that in Chapter 3), as this can lead to under-estimation of less conspicuous prey remains, while producing over-estimates of those easier to detect.

On comparison with previous research, the rodent proportions described here (60-80% returned and detected) are similar to results in both the USA (55.6% returned, Loyd *et al.*, 2013) and South Africa (60% returned, Seymour *et al.*, 2020). While bird data recorded here were not sufficient to draw any reliable conclusions, Loyd *et al.* (2013) found that 40% of avian prey were returned (Loyd, 2023, personal communication). However, it is not clear whether these returned prey (n = 2) were also detected by the cats' owners. Insectivores were returned 80% of the time across the two studies in which they were recorded (Loyd *et al.*, 2013; Seymour *et al.*, 2020), although sample sizes were, again, low (total n = 5). It seems that reptiles are rarely returned home by cats (around 2% across all three studies, Loyd *et al.*, 2013; Bruce *et al.*, 2019; Seymour *et al.*, 2020), but rather, often eaten (73.3% of captures, Loyd *et al.*, 2013; Seymour *et al.*, 2020). However,

reptiles are rarer prey for cats in the UK than in the warmer climates of Georgia, USA and South Africa, where their abundance is likely higher (for example, southern Africa is home to over 300 lizard species, whereas the UK is home to only three, Alexander and Marais, 2007). Invertebrates are also very rarely brought home and detected, with zero returns (out of 61 captures) throughout the four studies (including the present study, Loyd *et al.*, 2013; Bruce *et al.*, 2019; Seymour *et al.*, 2020). This suggests that previous return surveys have vastly underestimated invertebrate predation (if invertebrates were even recorded). However, compared with other threats to flying insect populations (such as pesticide use, Brühl *et al.*, 2021; Møller *et al.*, 2021), predation by cats may have a negligible effect.

4.4.5 Extrapolation methods

Two methods of calculating multiplication factors were applied here. The first used video footage to estimate the proportion of total prey represented by questionnaire studies (i.e. the proportion returned home). The cat camera footage showed that vertebrates were returned and detected 63.64% of the time (multiplication factor of 1.57), whereas overall (including invertebrates), 50% were returned (multiplication factor of two). If the two uncertain prey caught by Darling were detected, return data should be multiplied by 1.22 for vertebrates and 1.56 for all prey. Using similar methods, Seymour *et al.* (2020) and Loyd *et al.* (2013) produced multipliers of 5.65 and 4.35, respectively, for all taxa. The reasons for this difference appear to be largely related to study location and prey availability, as well as differences in how each taxon is dealt with by cats, generally. For example, it is likely that different prey types are returned, eaten, and discarded in varying proportions, such that rodents are likely treated differently to insectivores and to birds. Furthermore, differences in detectability between birds and mammals would also lead to them being reported in different proportions in questionnaire studies. Although finding a multiplier of 5.65 for all taxa, data from Seymour *et al.* (2020) show that the multiplier for rodents only would be 1.67, comparable to that found in the present study. It appears that the 'all taxa' multiplication factor was heavily influenced by a large number of reptiles being caught, all of which were eaten

(Seymour *et al.*, 2020). This illustrates how the most frequently caught taxon can affect the results when producing a 'one size fits all' multiplier, showing that the single multiplier approach is not appropriate when applied to all taxa.

The second method used was adapted from Kays and DeWan (2004), and involved taking cat owner estimates of time spent outdoors and multiplying the mean of these by the hourly predation rate (as observed on video), to give a daily predation rate. This was then compared to the return diary results from Chapter 3 to give a multiplier. This method produced a far larger multiplication factor of 10.85, which would produce a total predation rate 8.9 times larger than the first method. In the original study by Kays and DeWan (2004), a small sample of cats (n = 11) were monitored outdoors by human observers, the presence of whom may have affected the cats' behaviour (despite efforts to reduce this), as well as potentially reducing accuracy of data recording and prey identification, as cats were watched from a distance. The multiplication factor produced by Kays and DeWan (2004) was far lower (3.3) that that generated here (10.85). This is a result of the present study having a higher hourly predation rate (0.07 prey, as opposed to 0.02 prey), as the time spent outdoors was comparable (around 20 minutes difference), as was the monthly return rate (1.57 prey here, as opposed to 1.67 prey, Kays and DeWan, 2004). One possible reason for this difference in hourly predation is that the outdoor observations made here (through cat cameras) consisted of many short recording sessions (due to limited battery life), whereas Kays and DeWan (2004) were able to directly observe cats' behaviour for far longer. It may be that predation events are more likely to be observed early in an outdoor excursion (such that four 2.5 hour sessions on different days may record more predation events than one continuous 10 hour session). The cats in the present study may also have a greater propensity to hunt than the average cat, with vertebrate returns being around 30-60% higher for those cats which were selected to wear the cameras, than the wider sample. It is therefore likely that the 10.85 multiplier is an over-estimate. Furthermore, these estimates rely on cat owners' recollection and guesswork around how long on average their cat spends outdoors per day. This may vary depending on the time of year that they are asked, in a similar way to estimates gathered by Barratt (1998) and Robertson (1998), who relied on owner recall to produce estimates of predation, and is therefore widely unreliable.

Applying these two differently derived multipliers to the return data retrieved in Chapter 3, the annual estimate of predation by cats varies widely, and is between 188.4 million and 1.68 billion vertebrates per year. Due to the clear difference in the resulting estimates and the unreliable assumptions that the second method is based on, it is reasonable to suggest that calculating multiplication factors from proportions returned is the most appropriate method of extrapolation. However, far more data are required before reliable estimates can be drawn, particularly for less frequently caught taxa such as insectivores and birds. One way to increase the amount of data gathered is to improve both the battery and memory storage of cat cameras. The storage capacity is not such a problem, as small microSDUC cards can hold up to 128TB of memory (around 60,000 hours of footage at the current resolution). However, improving the performance of the battery requires a physically larger and heavier unit, such as those used by Loyd *et al.* (2013), Hernandez *et al.* (2018), Bruce *et al.* (2019), and McGregor *et al.* (2015). While these larger units were found to not restrict or alter natural behaviours and movements of the cats monitored, smaller cameras are certainly preferable (Coughlin and van Heezik, 2015). These larger cameras may still have affected the cats' propensity to eat prey or carry it home, for example. Increasing the battery life would mean that recording sessions would be longer and could last throughout the night (thereby not missing the period after around 2am). This could potentially also allow researchers to monitor a full 24 hours' worth of outdoor activity, as was the case for Loyd *et al.* (2013). Further to this, another way of retrieving a greater amount of footage may be to provide participating cat owners with a recording schedule and maintain regular contact to try to ensure that resources are being used efficiently.

On comparing taxon-specific data from multiple studies, it is clear that separate multipliers should be applied to different taxa, in order to avoid over- and under-estimates when extrapolating. The taxon which constitutes the highest proportion of prey caught will have the greatest influence on the resulting multiplication factor. For example, if rodents are the most frequently captured prey (as is the case here), the resulting multiplier will most closely reflect the cats' behaviour after rodent predation (i.e. whether prey are returned, eaten, or discarded). This may lead to only a moderate under-estimate of rodents (where rodents are most frequently predated), yet a rather larger over-estimate of birds and insectivores. Data from Seymour *et al.*

(2020) show that the insectivore multiplication factor should be x1 (i.e. no multiplication, based on n = 4 insectivores), which is far lower than that used for all taxa (x5.65) in the same study. However, since insectivores are less frequently predated, far more video data are required to make a reliable assessment.

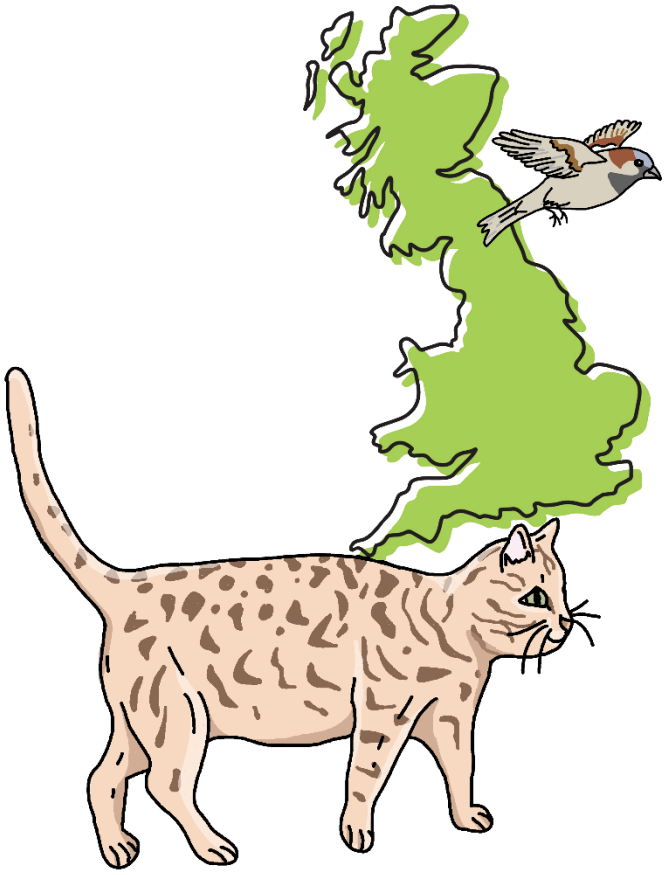
4.5 **Conclusions**

Accuracy is of key importance to producing reliable extrapolated estimates of cat predation. Even a seemingly small difference between multipliers can greatly affect the resulting figures. Here, applying the more reliable first method (calculating proportion returned home to estimate a multiplier) to the return data from Chapter 3, it is suggested that around 188.4million vertebrates are caught by cats in the UK each year. However, this is likely to be an over-estimate for some taxa, as data were not sufficient (birds, insectivores, herptiles) to apply a taxon-specific multiplication factor, and this multiplier (x1.22 - 1.57) is therefore likely more reflective of rodents. It is important to recognise that different taxa may vary in the way that they are handled by cats. Therefore, research should be focussed to develop taxon-specific multiplication factors in future, in order to avoid over-estimation of taxa that are more frequently returned and detected (for example, those which are highly detectable or not likely to be eaten due to unpalatability), or under-estimation of animals that are difficult to detect, or are often eaten or discarded away from home.

The multiplication factor put forward by Kays and DeWan (2004) has been routinely cited in the past and used for subsequent extrapolations and calculations (for example, Baker *et al.*, 2005; Baker *et al.*, 2008; Thomas *et al.*, 2012). This figure (3.3x multiplication of return results), derived from the less reliable method (method 2), leads to a far greater extrapolated figure than the multiplier generated here (a preliminary single multiplier of x1.22 - 1.57, using method 1). However, despite producing this higher multiplier, Kays and DeWan (2004) suggest that the predation pressure from pet cats was not enough to affect prey populations. The impact of predation by cats in the UK will be further assessed in Chapter 5.

Chapter 5

Impact



Hannah Lockwood

5.1 **Introduction**

5.1.1 Predation by cats

Domestic cats are a non-native species in the UK and many are given freedom to roam outdoors, unrestricted (between around 74% and 97% roam unsupervised outdoors, Sims *et al.*, 2008; Finka *et al.*, 2019). Although they are predators and obligate carnivores, the majority of owned cats do not appear to regularly hunt (58% of cats returned ≤6 prey annually, see Chapter 3) since they receive ample food at home. This regular food provision by their owners, along with effective medical care and regular vaccinations, means that owned domestic cats can exist in unnaturally high densities (Liberg *et al.*, 2000; Sims *et al.*, 2008). Cat populations are closely associated with human populations and household density, with greater numbers concentrated in more urban areas (Aegerter *et al.*, 2017).

Cat owners in the UK do not appear as concerned about the potential impacts of outdoor cats as those in Australasia, the USA, Japan, or China (Hall *et al.*, 2016). When asked, owners in the UK largely disagreed that there was a need for cat legislation (74.5% disagreed with legislation) or that cats should be confined to the owners' property (93.1% disagreed, Hall *et al.*, 2016). However, all were in agreement that wildlife is important in cities, towns, and rural areas (Hall *et al.*, 2016). It is therefore of great public concern that the impacts of predation by cats are fully understood, in order to minimise future species declines.

5.1.2 Prey population trends

Although five of the 70 bird species (7.14%) currently listed on the UK Red List (Stanbury *et al.*, 2021) were present in prey return records (in Chapter 3), only one (house sparrow) was one of the ten most frequently returned avian species (Table 5. 1). While the house sparrow is red-listed due to long term population declines in the UK (declines of more than 50% since 1969), this trend

has slowed and largely stabilised since the mid-1990s (Figure 5.1, Newson *et al.*, 2009; Massimino *et al.*, 2022). However, in urban areas, the decline is more apparent (Table 5.1, Newson *et al.*, 2009; Martay and Noble, 2022), with a particularly large fall in abundance in London (attributed to avian malaria, Dadam *et al.*, 2019). Overall, seven of the ten most returned bird species experienced an urban population increase of more than 10% between 1995 and 2011 (Table 5.1, Baillie *et al.*, 2014; Martay and Noble, 2022). However, UK-wide trends varied slightly and covered an extended period, with a large decline in chaffinch abundance from around 2010 onwards (linked with an outbreak of disease, Hanmer *et al.*, 2022, Table 5.1).

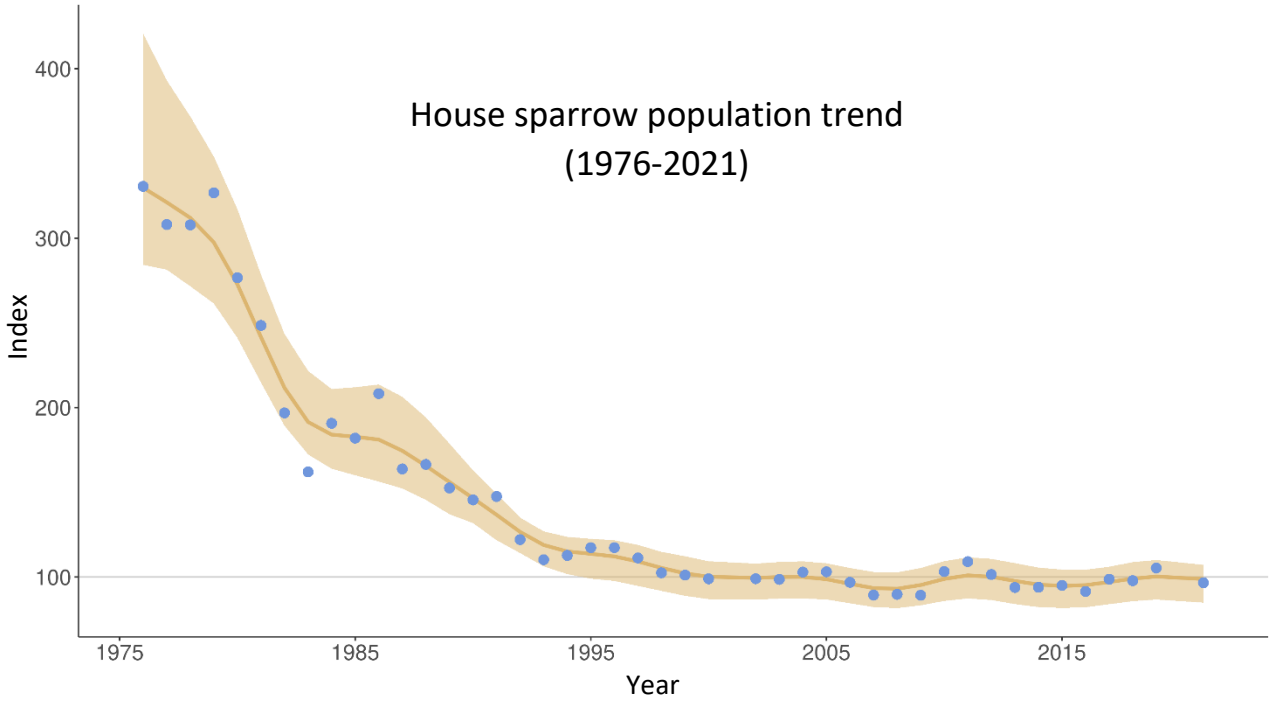


Figure 5. 1. Population trend for the house sparrow in England from 1976 to 2021, showing stabilisation in the mid-1990s. Plot adapted from Massimino *et al.* (2022). Smoothed trend line and shaded uncertainty around the trend line (based on 85% confidence limits). The index at 100 (horizontal line) indicates that for every 100 birds currently present, point data show how many were present in an earlier year. For example, there were roughly twice as many house sparrows in the early 1980s (index=200) than there currently are. Points represent values for individual years. Note that this is throughout England only, in both urban and rural sites.

Table 5. 1. The Red List status of the ten most frequently returned bird species by cats in the UK (as found in Chapter 3), along with the associated percentage of total prey returns. The population trends in urban and suburban areas in the UK for each species were taken from Baillie *et al.* (2014) and describe the change in abundance from 1995 to 2011. The UK-wide trends are also given, as taken from Harris *et al.* (2022), describing trends from 1995 to 2020. The percentage change is also given for each trend. Where populations change by ≤10%, the trend is described as stable. Latin species names are given in Appendix 5. 1.

Species	Red List status	% of total prey	Urban trend (1995-2011)	% change (Urban, 1995-2011)	UK-wide trend (1995-2020)	% change (UK, 1995-2020)
House sparrow	Red	2.96	Decline ↘	-30	Stable —	0
Blackbird	Green	1.46	Increase ↗	12	Increase ↗	20
Robin	Green	1.43	Increase ↗	43	Increase ↗	22
Blue tit	Green	1.07	Stable —	2	Stable —	1
Dunnock	Amber	1.04	Increase ↗	38	Increase ↗	14
Wren	Amber	0.94	Stable —	9	Increase ↗	22
Woodpigeon	Amber	0.83	Increase ↗	210	Increase ↗	33
Goldfinch	Green	0.50	Increase ↗	206	Increase ↗	156
Great tit	Green	0.41	Increase ↗	41	Increase ↗	32
Chaffinch	Green	0.36	Increase ↗	24	Decline ↘	-26

Surveying for mammals is not a regular, standardised practice (unlike methods used for birds) and therefore, the reliability of data available can vary (Mathews and Harrower, 2020). Assessing the trends of the ten most returned mammals (as identified in Chapter 3), data were only sufficient for three species (wood mouse, house mouse, and European rabbit, Table 5.2, Mathews and Harrower, 2020). Wood mice were the most returned mammal (in Chapter 3), constituting over 20% of all prey returned. Although predated in large numbers by cats across the UK, the population of wood mice appears stable (Table 5. 2). Indeed, 44.4% of all prey recorded in Chapter 3 are commonly thought of as pests (Baker *et al.*, 2020), while only 0.21% (n = 15) were European Protected Species (EPSs). Of these, nine were bats (of at least three species, see Chapter 3), and six were hazel dormice (*Muscardinus avellanarius*, although only one was confirmed with a photograph).

EPSs include all bat species in the UK (18 species), with legislation in place to protect populations across Europe (The Habitats Directive, 1992 in the European Union; The Conservation of Habitats and Species Regulations, 2010 in the UK). Of these, three are considered urban indicator species: common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), and noctule (*Nyctalus noctula*) (Office for National Statistics, 2022b). Despite predation by cats being cited as a key source of mortality (Ancillotto *et al.*, 2013), these urban bat species are not thought to be declining across Great Britain. In fact, the common pipistrelle population in Britain increased by 77% between 1999 and 2021, while that of the soprano pipistrelle and noctule have increased by 20% and 31%, respectively, over the same period (Bat Conservation Trust, 2022). Overall, bats made up 0.12% of all returned vertebrate prey in Chapter 3. While species were not specified, three *Pipistrellus* individuals were returned over the 3.5-year questionnaire study, and a further four individuals returned were simply stated as 'bat species'. No individual in the return survey was identified as a noctule bat.

Table 5. 2. The British Red List status (as described by Mathews and Harrower, 2020) of the ten most frequently returned mammal species by cats in the UK (as found in Chapter 3), along with the associated percentage of total prey returns. The population trends UK-wide for each species were taken from Mathews *et al.* (2018) and describe the trends from 1995 to 2016. Where data were deficient, the estimated future trend is given in parentheses (assessed by Mathews *et al.*, 2018). Species which are non-native are identified with an *. Latin species names are given in Appendix 5. 2.

Species	Red List status	% of total prey	UK-wide trend (1995-2016)
Wood mouse	Least concern	20.62	Stable —
Field vole	Least concern	9.70	Data deficient (future stable)
Bank vole	Least concern	7.86	Data deficient (future stable)
House mouse	NA	3.91	Stable —
Brown rat*	NA	3.25	Data deficient (future stable/increase)
European rabbit*	NA	3.09	Decline ↘
Common shrew	Least concern	2.01	Data deficient (future stable/decline)
Pygmy shrew	Least concern	1.53	Data deficient (future stable/decline)
Yellow-necked mouse	Least concern	0.39	Data deficient (future increase)
Harvest mouse	Near threatened	0.23	Data deficient (future decline)

While generally, data have been deficient to apply to population trend estimations in small mammals (Table 5. 2), an alternative metric has recently been used to monitor British species. Occupancy monitoring (recording the proportion of sites occupied) has shown that overall, small mammal occupancy is decreasing (from 1970 to 2016, Coomber *et al.*, 2021). It is important to note, however, that occupancy is not equal to abundance or population size.

5.1.3 Urbanisation and prey responses

Over the last three decades, the human population in the UK has risen from 57.4 million (in 1991) to 67 million (in 2021), an increase of 16.7% (Office for National Statistics, 2022a). With this rise, human population density has increased from 236 to 276 people per km^2 over the same period (Office for National Statistics, 2022a). While 10.5% of land in England is classed as 'built-up' (Department for Levelling Up Housing and Communities, 2022), a large majority (around 83%) of the human population live in these urbanised areas (Government Office for Science, 2021).

Between 1990 and 2019, almost 500,000 hectares of land in the UK was developed from green-field sites into urban settlement (Office for National Statistics, 2022b). The UK government aims for 300,000 new dwellings to be built per year, a target which has consistently not been reached, peaking recently at 243,000 in 2019/20 (Office for National Statistics, 2023). Over the ten year period from 2011 to 2021, around 1.7million new houses were built in the UK (Office for National Statistics, 2023), along with almost 3,000 miles (4,828km) of new roads in Britain, the majority of which (75.8%) were minor roads (likely residential, Department for Transport, 2022). Over 12% of this built-up land was previously woodland (in 1990), and 80% was farmland habitat (Office for National Statistics, 2022b). While some may consider this a great loss of natural habitat, biodiversity on agricultural land has been greatly reduced recently due to intensive farming methods, such as hedgerow loss and degradation, pesticide use, and field margin reductions (Donald *et al.*, 2001; Firbank *et al.*, 2007; McKinney, 2008). Indeed, intensive farming has been found to be the leading cause of bird declines across Europe (Rigal *et al.*, 2023).

Both biodiversity and the abundance of bird populations have been found to be closely associated with human density (McKinney, 2008; Gillings, 2019). While some species do avoid built-up areas, others are able to adapt effectively, with overall benefits to bird abundance being observed in areas of 50-200 people per km^2 (Gillings, 2019). This suggests that built-up areas and garden habitats can be beneficial to some species, although not beyond the threshold of about 200 people per km^2 (Gillings, 2019). For context, London has a population density of around 5,600 people per km^2, while Wales houses 150 people per km^2 (Office for National Statistics, 2021). Similarly, bird species composition in gardens in the UK has been linked to supplementary feeding by humans, with species which utilise bird feeders experiencing population increases (Plummer *et al.*, 2019). In addition, the bird populations which benefit from this food provision may be kept at artificially high levels in built-up areas. For example, Fuller *et al.* (2012) found that of the six UK species best adapted to the urban garden environment (as identified by Cannon, 2005), three showed a significant positive correlation with feeder density (blackbird, house sparrow, and starling). As urban greenspace is limited, gardens provide a valuable resource for many species. However, for mammals, it is mainly small-bodied food and habitat generalist species (such as grey squirrels, *Sciurus carolinensis*, and mice) which are best able to adapt and utilise urban gardens (Baker and Harris, 2007).

While many private gardens in the UK can provide excellent cover, nesting opportunities, and food resources for common prey populations, habitat degradation and loss is increasing, with artificial plastic grass, flowers, shrubs, and hedges becoming more popular (Cameron, 2023). Although not easily quantified, artificial lawns appear to be increasing in popularity, along with the removal of vegetation from front gardens (often to increase car parking availability, Aviva, 2022). Indeed, searches for 'artificial grass' using Google Shopping doubled between summer 2017 and summer 2021 in the UK (Google Trends, 2023). Perhaps unsurprisingly, areas where artificial lawns are in place have been found to have reduced bird species richness and abundance (Sánchez-Sotomayor *et al.*, 2023).

More than half of households in Britain provide supplementary food to garden birds (Davies *et al.*, 2012), but this can have an adverse effect on populations, due to increased disease transmission (Robinson *et al.*, 2010; Lawson *et al.*, 2018). Avian trichomonosis is a protozoal

disease which has recently been found in finch species, but also birds of prey and columbiforms in the UK, reducing adult survival (Forrester and Foster, 2008; Lawson *et al.*, 2018; Hanmer *et al.*, 2022). It is thought to be the leading cause of the substantial national declines of the greenfinch (67% decline between 2008 and 2018) and chaffinch (29% decline between 2008 and 2018), since it was first detected in 2005 (Hanmer *et al.*, 2022). As avian trichomonosis can cause individuals to regurgitate whilst feeding, transmission via saliva is likely common at garden bird feeding stations (Lawson *et al.*, 2018).

Gregarious urban species, such as the house sparrow, can also be affected by salmonellosis (primarily found in passerine species) and avian pox, the prevalence of which increase near supplemental feeding areas and gardens (Lawson *et al.*, 2018). Ultimately, transmission rates can be expected to rise with increasing contact between individuals (Bradley and Altizer, 2007). Increased transmission of mammalian diseases can also be expected to increase in more populated areas, although as previously mentioned, small mammals are less conspicuous and not as rigorously monitored.

5.1.4 The cat population

Although cat numbers are greater in more urban environments (where housing density is highest), overall predation by cats is not necessarily higher per unit area, since urban cats have been observed to kill fewer prey per cat, than those in rural areas (Thomas *et al.*, 2012; Blancher, 2013). There is, however, a difference in the predated taxa between urban and rural environments. Urban cats have been found to kill three times as many birds per cat as rural individuals in Poland, suggesting increased bird densities and availability in urban areas (Krauze-Gryz *et al.*, 2017), with a similar pattern being observed in Australia (Barratt, 1997) and Finland (Kauhala *et al.*, 2015). In contrast, over twelve times as many shrews were returned by rural cats (3.8 per cat) than those in urban environments (0.3 per cat) in the same Polish study (over a mean of 12 months per cat, Krauze-Gryz *et al.*, 2017).

As well as killing prey directly, cats can also influence prey species assemblages indirectly, through sublethal fear effects (Beckerman *et al.*, 2007; Bonnington *et al.*, 2013). The presence of predation risks can lead to reduced fecundity and overall population declines in some prey species, commonly termed the 'fear effect' (Loss and Marra, 2017). The threat of predation has been found to alter foraging and spatial behaviour of prey species (Preisser *et al.*, 2005). Indeed, using a taxidermy cat model, Bonnington *et al.* (2013) demonstrated that cat presence can lead to a reduction in parental behaviours (feeding chicks) by adult blackbirds in the UK, although food load size (the amount of food returned overall) did not alter in the presence of the cat model. The antipredator behaviour of birds has been shown to differ between urban and rural habitats, with escape behaviours (biting and wriggling) being related to susceptibility to cat predation (Møller and Ibanez-Alamo, 2012). It should also be noted that direct disturbance and close proximity to humans have been found to reduce breeding success in blue tits (Glądalski *et al.*, 2016) and great tits (Seress *et al.*, 2021), similar to that seen with predator presence.

A negative correlation has been found between cat density and the density of four bird species in the UK (blackcap *Sylvia atricapilla*, pied wagtail *Motacilla alba*, robin, and song thrush *Turdus Philomelos,* Sims *et al.*, 2008). However, the same study showed no relationship with a further 12 species (Sims *et al.*, 2008), seven of which were identified as one of the top ten avian prey in Chapter 3 (blackbird, blue tit, chaffinch, dunnock, great tit, woodpigeon, and wren, Table 5. 1). Indeed, although Baker *et al.* (2003) found that wood mouse abundance was negatively associated with that of pet cats in British gardens, it is not clear whether this may be a causal relationship. While in the UK, cat abundance increases with housing density (Aegerter *et al.*, 2017), there are a number of other factors which are also linked to an increasing human population. For example, habitat fragmentation (Liu *et al.*, 2016), chemical pollution (Strokal *et al.*, 2021), and disease prevalence (Bradley and Altizer, 2007) are also linked with increased housing density and urbanisation, and are also likely to impose limiting pressures on these prey populations, resulting in very complex interactions (**Error! Not a valid bookmark self-reference.**).

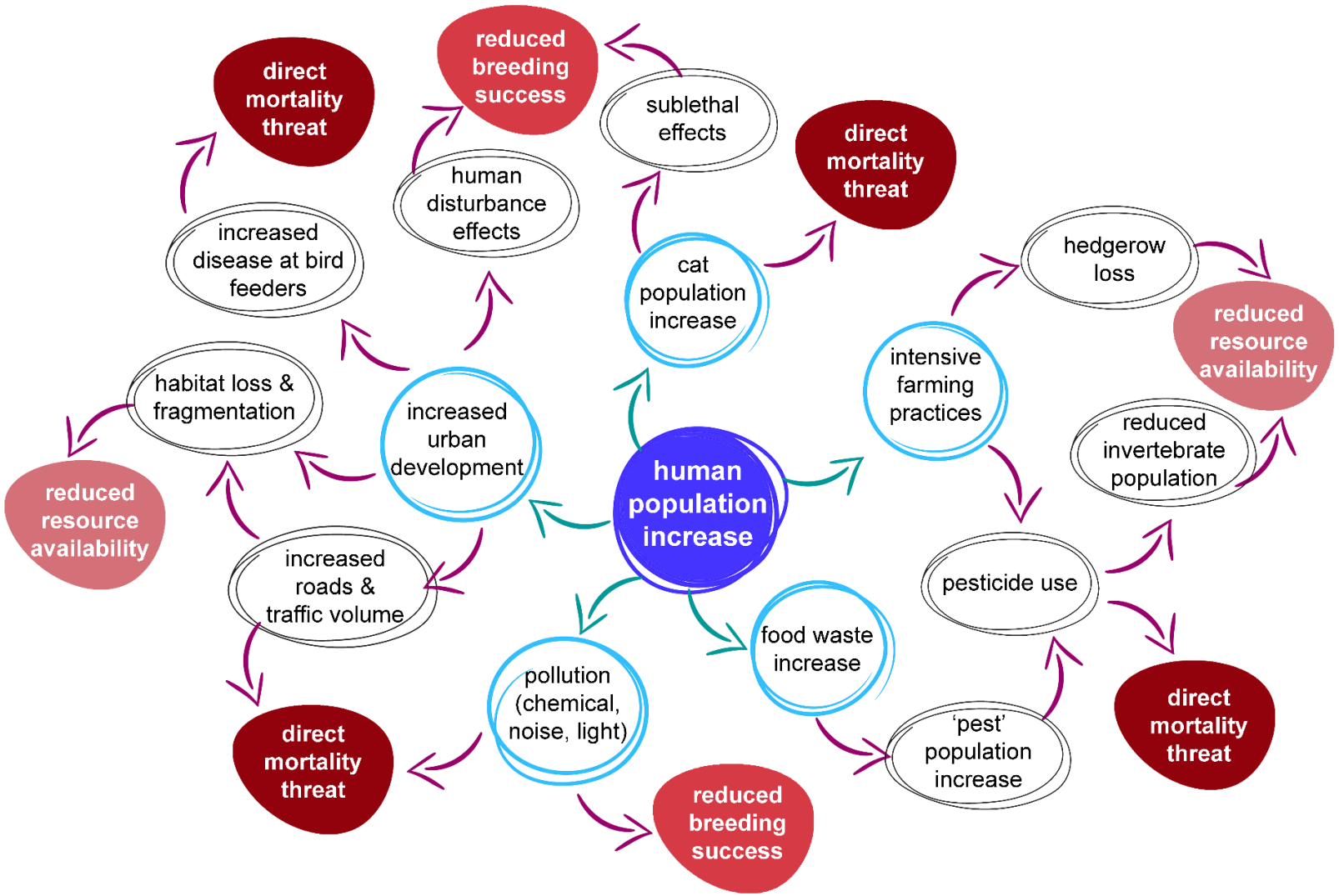


Figure 5. 2. The interconnectedness of key threats to wildlife in the UK. Arrows lead out from cause to effect. The shapes in different shades of red indicate factors which can directly lead to population declines. Potentially beneficial effects of predation by cats are not shown, for example mesopredator suppression.

5.1.5 Natural predators

After reviewing mortality records of ringed birds in the UK, Mead (1982) suggested that cats did not present as big a predation threat to small birds as natural predators would (had they not been displaced by urban development). However, this assessment of cat impacts is now over 40 years old and both bird and cat populations have altered since then, along with other anthropogenic threats to some extent. While urban and rural areas are home to rather different predator species assemblages, these differences would likely exist regardless of pet cat presence. For example, in the UK, natural mammalian predators have largely been displaced in urban garden environments (particularly larger-bodied species) due to inaccessibility (hard boundaries) and habitat changes (Baker and Harris, 2007; Fischer *et al.*, 2012). It does not appear to be a result of competition for food (with pet cats), but rather a lack of suitable habitat and increased human disturbance (Lovell *et al.*, 2022). If cat activity outdoors was reduced or eliminated, the inaccessibility of gardens to larger predators would likely lead to prey populations thriving. However, since many of the common mammalian prey species are commonly considered to be pests in the UK (such as mice and voles, Baker *et al.*, 2020), population booms may increase the use of pest control measures, including poisons. Rodenticides and other poisons have been found to negatively affect non-target carnivores (Shore *et al.*, 2003; Koivisto *et al.*, 2018), herbivores (Twigg *et al.*, 1999), and insectivores (Dowding *et al.*, 2010) of different taxa.

Like larger-bodied mammals, birds of prey have been found to be more commonly associated with rural areas than urban gardens, whereas the opposite is true of cats (Møller and Ibanez-Alamo, 2012). Many raptors which typically hunt small mammals catch their prey in open habitat such as agricultural fields (for example, barn owls *Tyto alba* and buzzards *Buteo buteo*), and are less likely to take prey in enclosed gardens, although others have adapted to more closed urban spaces (such as the sparrowhawk, Cooper *et al.*, 2022). In these urban settings, fences, walls, and buildings can offer effective vantage points for species which hunt using perches and artificial lighting can help to locate prey (Mak *et al.*, 2021). Recolonisation by the sparrowhawk (from 1970) has also been linked to long-term declines in house sparrows, suggesting that the

temporary reduction in predation pressure led to changes in escape behaviour, making them particularly vulnerable when these raptors recolonised built-up areas (Bell *et al.*, 2010). Sparrowhawks are potentially also impacting populations of starlings and blue tits in the UK (Swallow *et al.*, 2019), although complex interactions with anthropogenic and environmental factors such as climate change are not fully understood for many species.

5.1.6 Influence of climate change

Since 1880, global temperatures have risen by around 1.1°C and around two-thirds of this warming has occurred since the mid-1970s (NASA, 2023). The 2021 Intergovernmental Panel on Climate Change (IPCC) report stated that "it is unequivocal that human influence has warmed the atmosphere, ocean and land since pre-industrial times" (Eyring *et al.*, 2021). Indeed, despite a small dip during the COVID-19 pandemic, carbon dioxide emissions were the highest on record in 2022 (Friedlingstein *et al.*, 2022). As well as a general warming effect, there has also been an increase in the frequency of extreme weather events, such as prolonged droughts, storms and flooding (IPCC, 2022; Met Office, 2023).

Such changes in climatic variables over time can affect some bird populations, through decreases in invertebrate food sources and altered vegetation phenology (Both *et al.*, 2006; Menzel *et al.*, 2006; Stephens *et al.*, 2016). The Woodland Trust's citizen science database, 'Nature's Calendar', records phenology data throughout the year on trees and shrubs, flowers, migratory and resident birds, and insects (Sparks *et al.*, 2021). This research has recently found that the signs of spring are now being observed over a week earlier (8.4 days on average) than in the first half of the 20th century, leading to a mismatch between some species and their food sources (Reid *et al.*, 2021). For example, warmer or earlier spring seasons can cause oak trees to leaf earlier and caterpillar abundance to peak before blue tits and great tits have hatched (Reed *et al.*, 2013; Burgess *et al.*, 2018). Despite this, research also shows that blue tits are adapting their breeding activity, mating earlier when temperatures are favourably warm (Marrot *et al.*, 2018; Shutt *et al.*, 2019). However, for migrants such as warblers, untimely temperature changes can lead to asynchrony

between food resource peaks and their arrival in the UK (Pearce-Higgins *et al.*, 2015; Mallord *et al.*, 2017). These climatic changes and (increasingly frequent) extreme weather events can affect nestling growth and successful fledging, likely due to food availability (Marrot *et al.*, 2017), as well as the length of reproductive seasons and overall fitness of birds (Halupka *et al.*, 2021).

A further effect of climate change is the continuing reduction in invertebrate availability, which appears to be contributing to the decline of insectivorous bird species (Pearce-Higgins *et al.*, 2015; Tallamy and Shriver, 2021; Martay *et al.*, 2023), although detailed, long-term invertebrate data are lacking in some areas (Pearce-Higgins and Morris, 2022). Importantly, terrestrial birds in North America which rely on invertebrate prey have declined dramatically over a 50 year period, while overall, those which are not reliant on invertebrates have increased (Tallamy and Shriver, 2021). This may also be affecting insectivorous mammals, such as shrews and bats (Newman and Macdonald, 2015).

Despite their abundance, rodents are known to be vulnerable to environmental changes and some species experience natural periods of boom (high population density) and bust (reduced population density), which are well documented (for example, Cornulier *et al.*, 2013). These fluctuations may become more pronounced with an increase in unseasonable and extreme weather conditions (Bierman *et al.*, 2006; Newman and Macdonald, 2015). In addition, unseasonably high temperatures in winter can affect hibernation cycles of bat species and hazel dormice, leading to inefficiency of the process of metabolic suppression (Pretzlaff and Dausmann, 2012; Sherwin *et al.*, 2013). This can, in turn, reduce body condition and negatively affect breeding success, thus impacting populations (Pretzlaff and Dausmann, 2012; Findlay-Robinson *et al.*, 2023).

5.1.7 Measuring impact

Since there are many environmental variables which could affect prey assemblages (such as latitude, climatic factors, and specific habitat conditions), the most effective way to measure

impact would be to experimentally alter the cat population, monitoring prey populations in the same area with varying densities of cats. However, this would not show causality between cat presence and prey population health, unless all other factors were controlled for. Additionally, the introduction of cats to a wild landscape would not be ethically feasible and the eradication of existing populations would be extremely challenging. There may also be mesopredator release effects once cats are removed from the environment, with a population boom of some prey species (such as rats) increasing predation of, for example, ground-nesting, vulnerable species (Courchamp *et al.*, 2003). The effects of domestic cat curfews in some parts of Australia have not yet been evaluated, but may be negligible as feral cats are still roaming free in urban and semi-urban areas (Legge *et al.*, 2020).

The condition of prey returns has been used to determine whether predation by cats is largely compensatory or additive (Møller and Erritzøe, 2000; Baker *et al.*, 2008; Péron, 2013). Measures of fitness in birds include overall mass, fat, and muscle mass (Baker *et al.*, 2008). Spleen size has also been used as an indicator of condition, since a smaller spleen is related to a weakened immune system (Møller and Erritzøe, 2000). These measures have been used to compare cat-killed individuals with those which died as a result of accidental causes (e.g. collisions with windows or cars), showing that generally, those predated upon by cats were in poorer condition (Møller and Erritzøe, 2000; Baker *et al.*, 2008).

A further consideration when assessing impact of predation is the productivity of different prey species. For example, mammalian prey (e.g. mice and voles) generally produce more offspring than bird species, having multiple large litters throughout the year (Couzens *et al.*, 2017). Therefore, small mammal populations may be more resilient to losses due to predation. One clear exception to this is bat species in the UK, which breed once per year and typically bear just one pup per season (although twins are occasionally observed, Dietz and Kiefer, 2018).

Comparing cat predation data for British bird species with productivity rates, Baker *et al.* (2005) found that cats may be having a negative effect on three species (house sparrow, dunnock, and robin). However, the same study found the effects of cats on other common garden birds in the UK to be less impactful (blue tit, great tit, blackbird, starling, and wren, Baker *et al.*, 2005).

Particularly concerning analyses suggest that predation rates may not be sustainable in some locations for five out of six bird species monitored (blackbird, house sparrow, robin, dunnock, great tit, Thomas *et al.*, 2012).

However, if cats do indeed have a negative impact on prey populations, it could be expected that prey species would exist in greater densities where cats are less commonly found. Therefore, impact may be measured by comparing prey species density or abundance in areas of high and low cat density (e.g. Kays and DeWan, 2004; Sims *et al.*, 2008). However, given the difficulties with directly measuring impact, this is a proxy approach. So far, this has not been conducted on a large spatial scale in the UK, although Sims *et al.* (2008) surveyed 30km^2 in England and Wales (urban areas only). Therefore, the reliability of such data could be improved by increasing the sample area.

5.1.8 Aims and hypotheses

The primary aim here is to assess whether domestic cats are likely to influence the abundance of avian prey species. While overall, (1) cats are not expected to have an impact on bird populations (due to mortality being largely compensatory, Møller and Erritzøe, 2000; Baker *et al.*, 2008), (2) their impact is likely to vary between species (as found by Baker *et al.*, 2005; Thomas *et al.*, 2012).

The collation and analyses of third-party survey data are expected to show that other factors are also likely to have an effect on prey populations. It is thought that (3) climatic variables (minimum, maximum, and mean air temperature), as well as (4) land cover (habitat) will have an effect on bird populations, since climate can impact breeding success (Marrot *et al.*, 2017; Halupka *et al.*, 2021) and changes to habitat alter resource availability, and thus, carrying capacity (Rigal *et al.*, 2023).

5.2 **Methods**

5.2.1 Data acquisition

Data concerning temperature, land cover, bird species abundance, and cat density per km^2 (British National Grid) were retrieved from third-party sources (Table 5. 3). Due to data unavailability for recent years (at the $1km^2$ scale) and issues concerning comparability between datasets, the years 2000 and 2015 were selected for analyses. Cat density data were only available for 2015 at the $1km^2$ scale. However, despite likely temporal changes in cat density (associated with an increase in housing density), overall distribution patterns are unlikely to alter much over time (e.g. cat distribution will not be affected by environmental changes over time, such as climate or fluctuations in resource availability).

Table 5. 3. Details of data retrieved for analysis, describing the organisations which provided data, and acknowledging the source of each. All data were at the 1km^2 scale (British National Grid squares).

Data	Years	Detail	Organisation	Source(s)
Cat density	2015	Density per km^2 (based on location and capacity of veterinary services)	Animal and Plant Health Agency (APHA)	Animal and Plant Health Agency (2016b)
Temperature (mean annual)	2000, 2015	Mean of daily mean air temperature. Data interpolated from an average of 540 temperature stations (UK-wide)	UK Met Office	Met Office *et al.* (2018)
Temperature (min annual)	2000, 2015	Mean of daily minimum air temperature. Data interpolated from an average of 540 temperature stations (UK-wide)	UK Met Office	Met Office *et al.* (2018)
Temperature (max annual)	2000, 2015	Mean of daily maximum air temperature. Data interpolated from an average of 540 temperature stations (UK-wide)	UK Met Office	Met Office *et al.* (2018)
Dominant land cover	2000, 2015	Describes which habitat (out of ten classifications) is dominant per 1km grid square	Centre for Ecology and Hydrology (CEH)	Fuller *et al.* (2002), Rowland *et al.* (2017)
Bird counts	2000, 2015	Breeding Bird Survey (BBS) count data collected by volunteers at 1km squares across the UK. Data retrieved for house sparrow, dunnock, blue tit, robin, and blackbird	British Trust for Ornithology (BTO)	BTO (2023c)

Cat density data were derived from the locations and individual capacity of veterinary practices across Britain (Aegerter *et al.*, 2017). This took an estimate of the total British owned cat population (10,114,764 cats, from Murray *et al.*, 2015), along with an estimate of the percentage registered for veterinary care (86.4%, Murray and Gruffydd-Jones, 2012), and generated a complete dataset at the 1km^2 scale. This approach used the road network surrounding each practice (including the road type and speed limit) to identify the areas where pet cats live, assuming that owners were registered with their most accessible practice, and is therefore robust to impermeable boundaries in the landscape.

Temperature data were retrieved from the UK's Met Office for both 2000 and 2015 (Table 5. 3). Minimum, maximum, and mean air temperatures were available for each grid square, as interpolated from 540 weather stations across the country, and represent the mean of daily temperatures across the year. For example, the minimum air temperature is not the absolute minimum recorded that year, but the mean of daily minimum values. Interpolation, conducted by the Met Office, used Inverse-Distance Weighted (IDW) averaging across the UK grid after regression analyses to account for differences in variables such as altitude and terrain (as described by Hollis *et al.*, 2019).

The dominant land cover type (or habitat) data for each 1km grid square were gathered by the Centre for Ecology and Hydrology (CEH), describing one of ten classifications (Appendix 5. 3) from satellite data (CEH, 2017). Although data are reported at a fine scale using polygons, these were converted to represent the dominant class (i.e. that which made up the highest percentage) for each square in raster form, in order to make data comparable with other sets. Due to inconsistent habitat classification codes in the 2000 and 2015 land cover datasets, the 2000 data were adapted and aligned with the 2015 classifications (as given in Appendix 5. 3). There were other methodological changes between these two sets of data, although none that would affect the output used here (CEH, 2017). Due to insufficient sample sizes, changes in land cover between 2000 and 2015 were not suitable for analyses. However, there were adequate data for four key habitats for garden birds (broadleaf woodland, arable, built-up, and improved grassland), where these land cover types remained the same between the two study years. It is important to note that where the dominant land classification (habitat) remained the same between 2000 and

2015, this does not mean that the habitat in the entire 1km square has stayed the same, but merely that the dominant type has not altered. For example, a square may be 60% woodland and 40% arable land in the first year of study, but this may change to 40% woodland, 30% arable, and 30% built-up (Figure 5. 3). In both cases the dominant land class is woodland, despite there being an overall loss in this habitat type and a gain of built-up land. Similarly, when there is a change in dominance from x to y, either there has been a reduction in the area of x or a gain in y (or both may apply, see Figure 5. 3 for a further example).

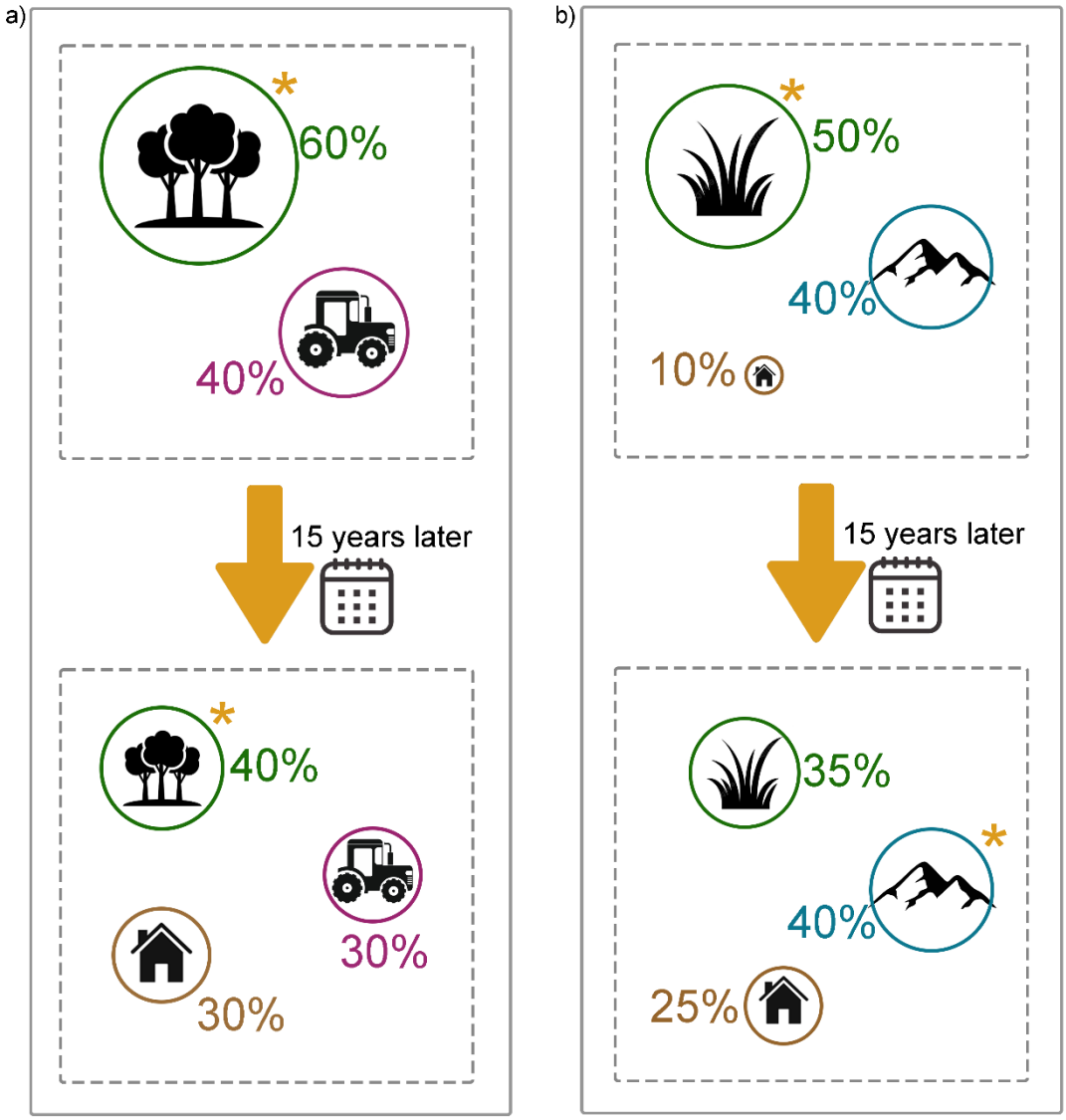


Figure 5. 3. Two examples of how using dominant land class can a) fail to show changes between years when dominance remains unchanged, and b) infer changes (gains of habitat) that have not occurred. In a), the dominant land class remains as broadleaf woodland over the 15 years, yet there have been overall losses of natural habitat and creation of built-up areas. In b), improved grassland has been developed into built-up land, but the mountainous habitat becomes the dominant class, despite size remaining unchanged. In both examples, there has been a gain of built-up land, but when looking solely at dominant types, this would not be apparent. Dashed line boxes represent the same km square over time and the dominant land cover type is marked with an orange *.

The bird species for which data were retrieved have been identified as the five most frequently returned avian species (Chapter 3). Although constituting just under 8% of overall prey returns, these five species made up around half (49.47%) of all birds returned by cats (Chapter 3). The data were collected by voluntary recorders as part of the annual Breeding Bird Survey (BBS), a standardised, long-running transect survey (Table 5.3, BTO, 2020). Data were in the form of counts, and absence in a grid square was assumed where the target species was not recorded, but others were. This survey requires two visits to each square per year, an early visit (April to mid-May) coinciding with the start of the breeding season, and a late visit (mid-May to late June) at least four weeks later (BTO, 2020). Here, the highest count of the two was selected for analyses. Counts represent all adult birds (both male and female) observed along the set line transects within the survey square and can be used as a measure of relative abundance.

5.2.2 Data analyses

As data were not always available for Northern Ireland or the Isle of Man, these areas were excluded from analyses.

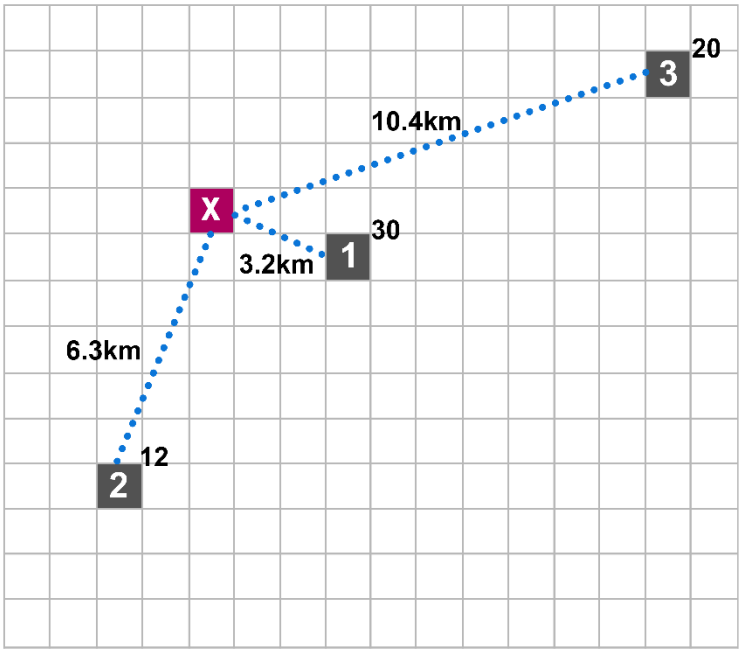
For all squares where bird counts did not take place in both 2000 and 2015, Inverse-Distance Weighted (IDW) interpolation was used to generate predicted values, using a distance coefficient (P) of two. IDW interpolation assumes that objects close to each other are more alike than those further away, and therefore, have a greater influence on predicted values (Longley *et al.*, 2011, see Figure 5.4 for a worked example). The value of P = 2 was deemed most suitable for these data, as when P is increased, the influence of more distant points decrease (ESRI, 2023). A distance coefficient greater than two was found to give a much less smooth map surface.

The distance coefficient or power function, P, is used in the IDW calculation:

$$x = \frac{\sum_{i=1}^{n}(\frac{z_i}{d_i^P})}{\sum_{i=1}^{n}(\frac{1}{d_i^P})}$$

Where:

d=	distance between points
P=	Distance coefficient or power function
n=	Number of known squares
z=	Known square value



Count value at each known point:
1= 30 birds
2= 12 birds
3= 20 birds

Distance from square x:
1= 3.2km
2= 6.3km
3= 10.4km

$$x = \frac{\left(\frac{30}{3.2^2}\right) + \left(\frac{12}{6.3^2}\right) + \left(\frac{20}{10.4^2}\right)}{\left(\frac{1}{3.2^2}\right) + \left(\frac{1}{6.3^2}\right) + \left(\frac{1}{10.4^2}\right)}$$

$$x = 24\ birds$$

Figure 5. 4. An example of the process of Inverse-Distance Weighted (IDW) interpolation, where x represents the data square to be interpolated (of no known value) and squares 1-3 are measured bird counts. Squares 1-3 are numbered by influence, with the nearest of the squares (1) having the greatest influence on x. The equation is given for estimating the value of square x, which given the known values in this example, equals 24 birds. This example uses a distance coefficient of two, as distances are squared in the calculation.

IDW was, however, only used for visualisation purposes, in the creation of maps. The interpolated data (n = 230,164 total grid squares) were not used in formal analyses, as IDW assumes a homogenous landscape (unless barrier polygons are set) and points are only weighted by distance (not accounting for differences in resource availability, for example, ESRI, 2023). Only squares where a true value was obtained (i.e. where bird counts took place in both years), and where land cover remained as one of the four key classifications were used for analyses (a total of 988 grid squares, Table 5. 4).

Data were formally analysed with Generalised Linear Models (GLMs), using stepwise model selection based on the Akaike Information Criterion (AIC) to determine the best fitting model for

each bird species. In the full model, the dependent variable was the difference in bird counts per km^2 between 2000 and 2015 (2015 count minus 2000 count). The independent variables were: cat density per km^2, difference in minimum temperature, difference in maximum temperature, difference in average (mean) temperature, x coordinate, y coordinate, and land cover (where built-up, arable, improved grassland, and broadleaf woodland remained dominant between years). Additionally, the two-way interactions between cat density per km^2 and the following were included: difference in minimum temperature, difference in maximum temperature, difference in average (mean) temperature, x coordinate, and y coordinate.

After the initial testing process found several significant, but weak relationships, the sample size was reduced and re-analysed using the same process. As data points were largely clustered between zero and approximately 500 cats per km^2 (i.e. the majority of km squares where bird counts took place were of relatively low cat density) and no strong pattern was evident, a subset was created to include only those squares for which cat density was estimated at less than 500 (see Figure 5. 5 for spatial distribution). A total of 59 data squares (5.9% of the total dataset) had cat densities of 500 or over, and these were removed from the dataset. Since less than 6% of data squares represented the top 75% of cat density values (ranging from 500 to 2000 cats per km^2), these few squares would likely have an unduly high influence on the model outcomes. Removing these increases the reliability of test outputs. Further GLM tests were applied to the remaining data (a total of 929 grid squares, Table 5. 4).

Table 5. 4. Sample sizes used in analyses, for each dataset or subset.

Dataset	Description	Number of grid squares (n)
All bird data	Squares where: • bird counts took place in both 2000 and 2015	1445
Full GLM dataset	Squares where: • bird counts took place in both 2000 and 2015 • land cover stayed the same, as one of the four key classifications (arable, broadleaf woodland, built-up, improved grassland)	988
GLM subset	Squares where: • bird counts took place in both 2000 and 2015 • land cover stayed the same, as one of the four key classifications (arable, broadleaf woodland, built-up, improved grassland) • cat density was lower than 500 cats per km^2	929

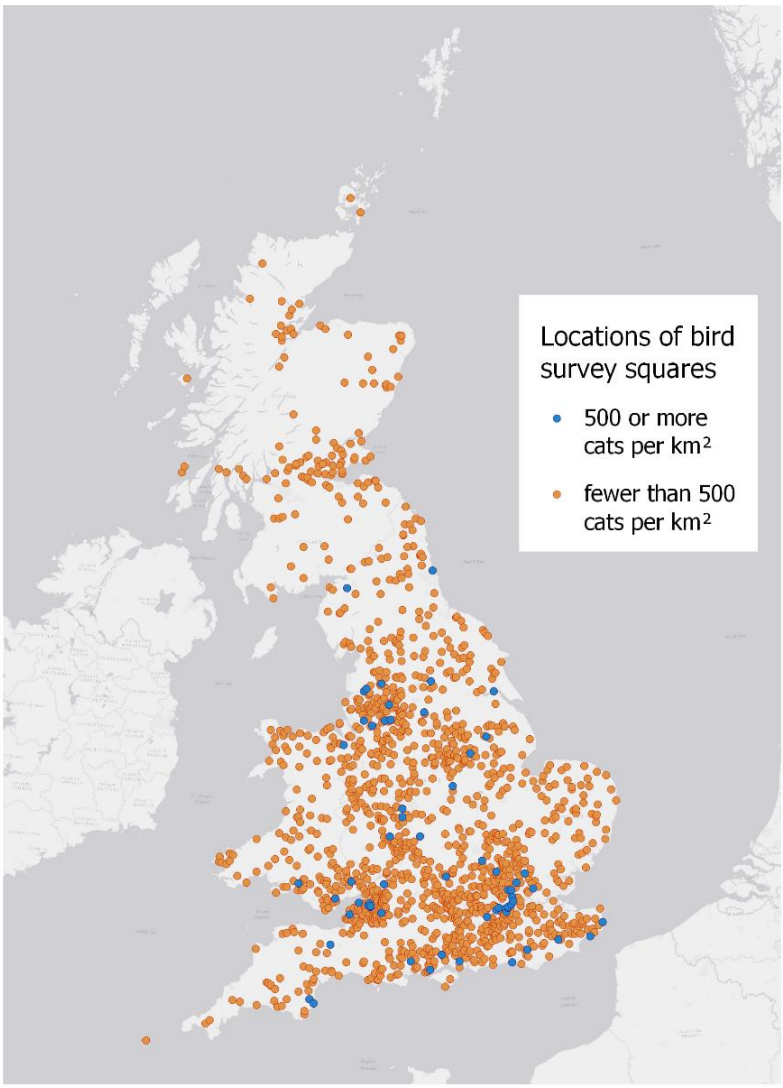


Figure 5. 5. Locations of all bird survey km squares across Britain, which were surveyed in both 2000 and 2015. Orange points represent the subset containing squares with cat density lower than 500 (n = 988 data points), whereas blue points are those squares which were removed from analyses (n = 59 points).

Post-test residual checks were conducted, along with k-fold cross validation techniques, to determine the most appropriate approach (Smith and Warren, 2019; James *et al.*, 2022). Ten-fold cross validation techniques were used, using a subset representing 90% of the data to make predictions and test against the remaining 10%. This process was run ten times using a different randomly selected portion of the data. This allowed for comparison of model strength between

those using the entire set of data, and those using the subset containing only squares with fewer than 500 cats per km^2.

All maps were produced using QGIS 3.22 software (QGIS Development Team, 2023), utilising the 'TomBio tools' plugin (Burkmar, 2023). All formal analyses were conducted using R version 4.2.1 (R Core Team, 2022) and R Studio (R Studio Team, 2020), using the following packages: boot (Canty and Ripley, 2022), dismo (Hijmans *et al.*, 2023). Graphical plots were created using the R package ggplot2 (Wickham, 2016).

5.3 **Results**

5.3.1 Overview

There were 1,445 km squares for which bird count data were recorded in both 2000 and 2015, allowing differences (positive or negative) to be calculated between years (230,164 total 1km grid squares across Britain). Overall, the count of birds increased (between the two study years) in between 33% and 52% of grid squares monitored but decreased in between 37% and 44%, depending on the species (Table 5. 5). While counts of most species monitored were observed to moderately increase, house sparrow counts decreased slightly, overall (Table 5. 5, Figure 5. 6**Error! Reference source not found.**).

Table 5. 5. Percentage of squares (out of 1,445) where each bird species was observed to increase and decrease in count between 2000 and 2015, followed by the maximum change (positive or negative) observed for each species. The mean difference between 2000 and 2015 counts is also given (either positive or negative) for each species.

Species	% of squares		Maximum change in count		Mean change in count
	Increased count	Decreased count	Increased count	Decreased count	
Blackbird	49.83	42.35	+50	-42	+0.41
Blue tit	46.02	43.67	+74	-41	+0.26
Dunnock	43.11	37.65	+16	-26	+0.29
House sparrow	33.01	36.82	+115	-94	-0.50
Robin	52.25	36.82	+30	-38	+0.89

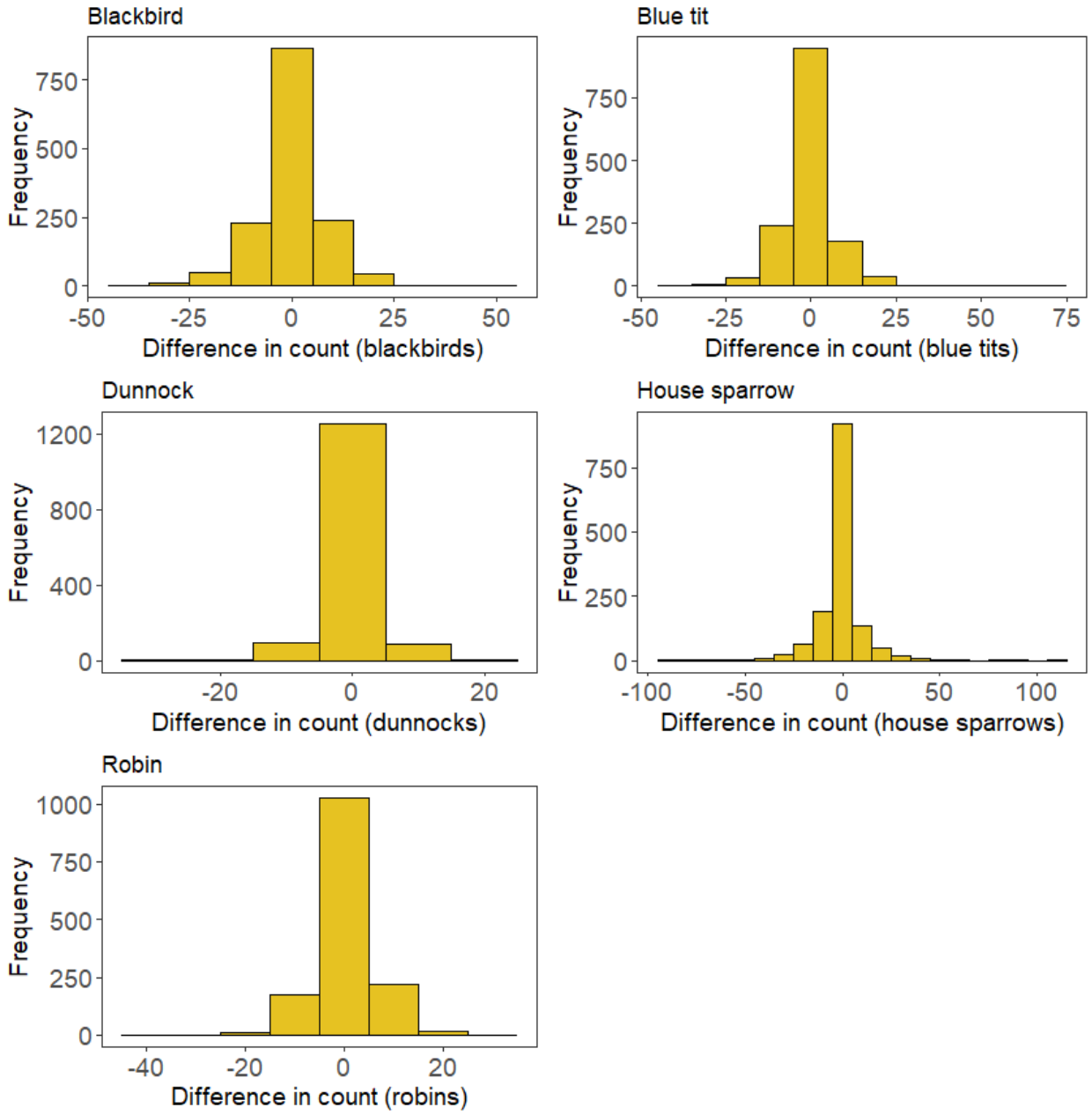


Figure 5. 6. Histograms of the change in bird counts between 2000 and 2015 for the five most returned species (in Chapter 3), with a bin width of 10.

Although data were not available to measure change over time, cat density in Great Britain was found to be significantly positively related to human population density (Spearman's Rank test: $r_s = 0.51$, n = 2269, $p < 0.001$, Figures 5.7 and 5.8), with cats living most densely in cities and towns.

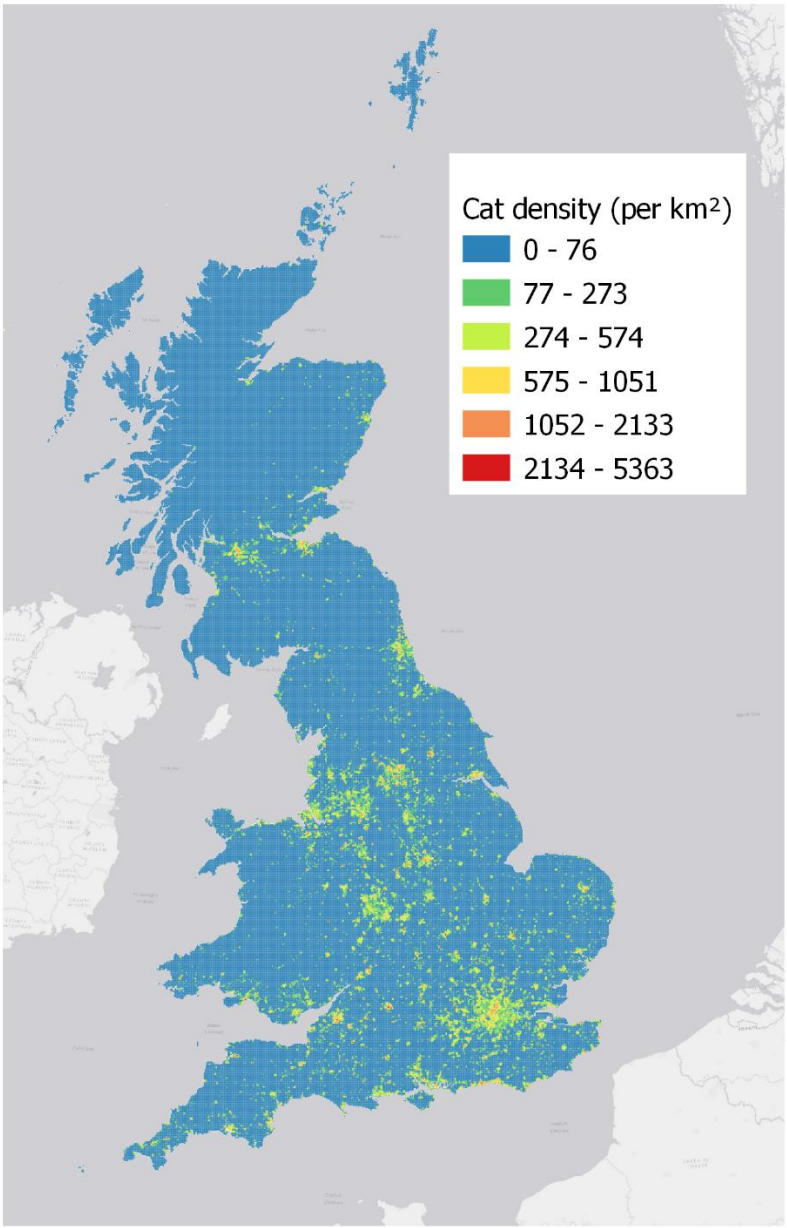


Figure 5. 7. The density of cats across Britain, by km^2. Data were provided by the Animal and Plant Health Agency (2016b), as estimated by Aegerter *et al.* (2017) using locations and capacity of veterinary practices.

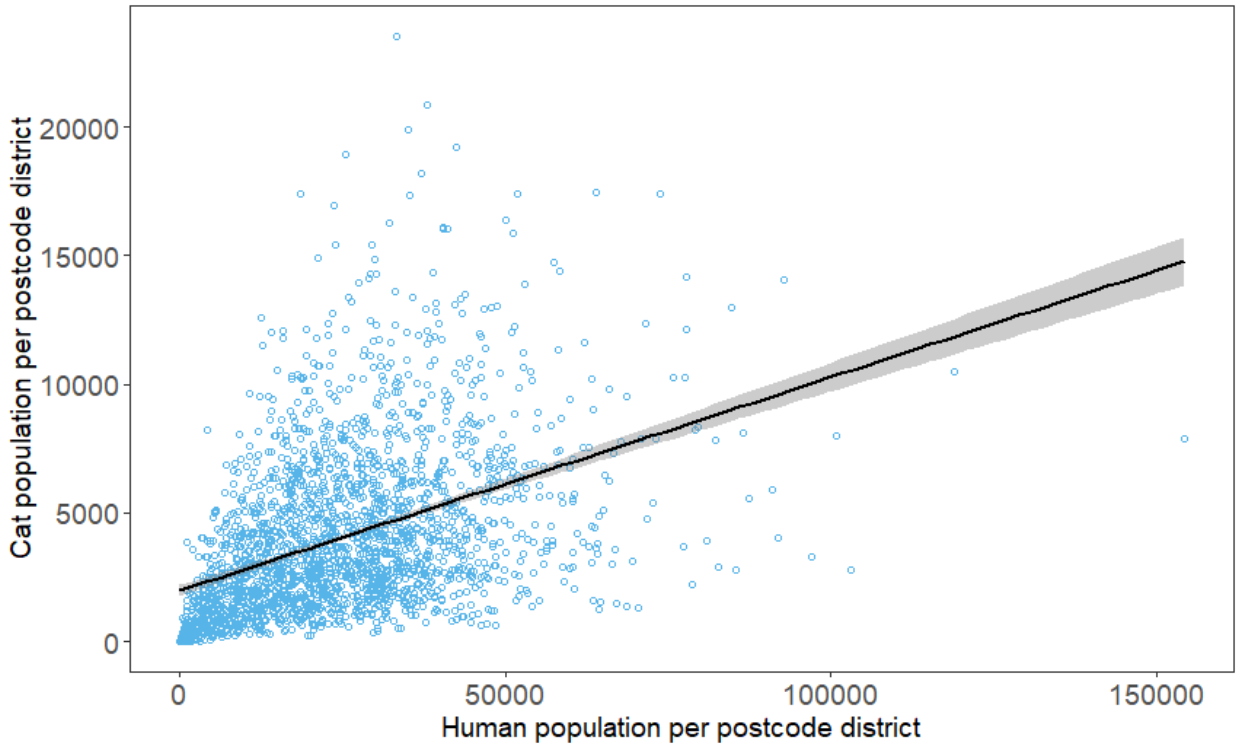


Figure 5. 8. Relationship between human population density and cat density (by postcode district). Data were adapted from Animal and Plant Health Agency (2016a) and Office for National Statistics (2016). The regression line (computed using parametric methods, not ranked data) is in black, and error is shaded grey.

5.3.2 Influencers of bird population changes

When visualising the data, it was apparent that the vast majority of 1km grid squares contained relatively few cats, with most points clustered below 500 cats per km^2 (Figure 5. 9). Testing the whole dataset, one species (house sparrow) showed a positive correlation with cat density (Linear Model: t = 1.99, n = 988, p = 0.046, Appendix 5. 4), but it was weak with an estimate

suggesting that where cat density increases by one, house sparrow count would increase by 0.02 individuals (Appendix 5. 4).

Upon testing the two datasets (all 988 squares and only those containing fewer than 500 cats) and their most appropriate-fitting models against each other using k-fold cross validation, it was apparent that the subset (fewer than 500 cats per km^2) returned the lowest prediction error (Appendix 5. 5). It was therefore decided that this subset was more reliable when examining the relationships tested here (having removed outlying, influential data points).

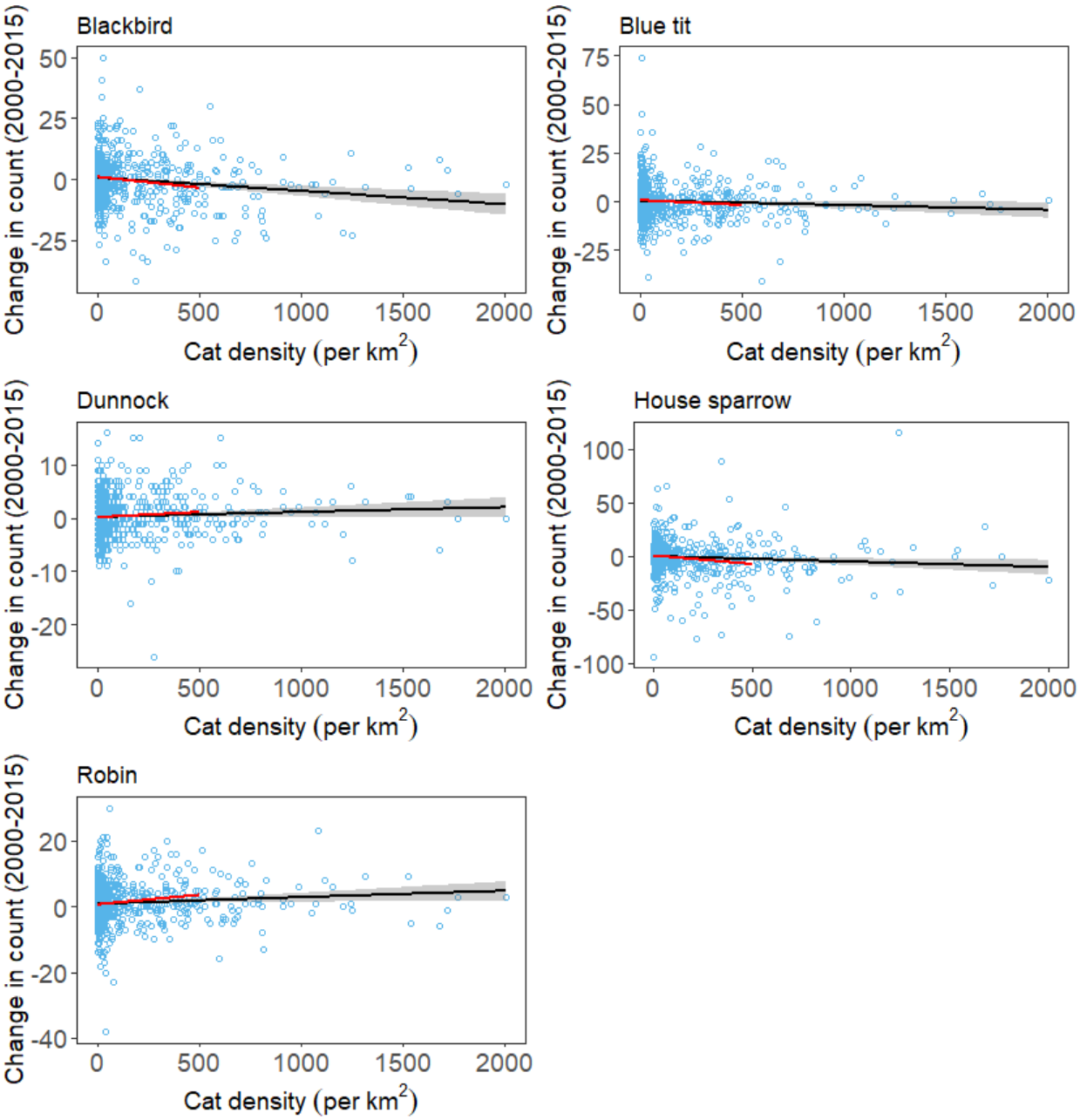


Figure 5. 9. Relationships between cat density (per km^2) and the difference in count between 2000 and 2015, for each of the five bird species (all 988 data squares represented). A change of <0 indicates a reduction in the number of birds recorded, whereas values of >0 represent an increase in count within the same survey square. For each plot, the regression line is in black, and error is shaded grey. The regression line for the squares with fewer than 500 cats is in red (929 data squares). Bird species is given above each plot. Note the varying scales of y.

The subset showed that for blue tits, only x coordinate, maximum and average temperature were included in the best model, and none had a significant relationship with change in count. Similarly for dunnocks, only cat density and average temperature were included in the model, yet neither were related to change in count, Table 5. 6).

5.3.2.1 Land cover effects

There was a significant relationship between land cover type and change in count of blackbirds, with built-up areas experiencing greater decreases in counts over the 15 year study period than arable (Linear Model: t = -3.47, n = 929, $p < 0.001$), improved grassland (Linear Model: t = 4.05, n = 929, $p < 0.001$), and broadleaf woodland habitats (Linear Model: t = 2.91, n = 929, $p = 0.004$, Table 5. 6, Figures 5.10 and 5.11). A similar pattern was found between house sparrows and land cover, with counts in built-up areas decreasing significantly more over time when compared to counts in arable-dominated squares (Linear Model: t = -2.46, n = 929, $p = 0.014$, Table 5. 6, Figures 5.10 and 5.11).

5.3.2.2 Latitude and longitude

In addition to land class, house sparrows also experienced a relationship with longitude (x coordinate), with decreases in counts across the east of the UK, compared to the west (Linear Model: t = -4.51, n = 929, $p < 0.001$, Table 5. 6, Appendix 5. 9). Potentially related to climatic variables, there was a significant interaction for house sparrow data, between latitude (y coordinate) and cat density (Linear Model: t = 4.78, n = 929, $p < 0.001$, Table 5. 6), such that in the south, cat density has a greater effect than in the north, with lower counts further south when cat density increased (Figure 5. 12).

Table 5. 6. GLM test output showing the results of the models which best fit the data for squares where cat density was below 500 per km^2 (n = 988km squares). Under 'Variable', * denotes an interaction between two variables. Significant effects are highlighted in bold. Land classifications are: A = remained arable, BU = remained built-up, G = remained improved grassland, W = remained broadleaved woodland. When interpreting the 'estimate' values, it should be noted that the x and y coordinates are in meters.

Species	Variable	Estimate	t value	*p* value
Blackbird	Temperature (max)	-2.92	-1.57	0.117
	Land: A > BU	**-3.09**	**-3.47**	**<0.001**
	A = G	0.60	0.92	0.360
	A = W	0.84	0.72	0.475
	BU < G	**3.69**	**4.05**	**<0.001**
	BU < W	**3.93**	**2.91**	**0.004**
	G = W	0.24	0.20	0.845
Blue tit	x coordinate (W-E)	$-2*10^{-6}$	-0.60	0.546
	Temperature (mean)	-2.53	-0.74	0.459
	Temperature (max)	2.81	0.09	0.931
Dunnock	Cat density	$2*10^{-3}$	1.80	0.072
	Temperature (mean)	-0.44	-0.46	0.645
House sparrow	**Cat density**	**-0.10**	**-4.47**	**<0.001**
	x coordinate (W-E)	**$-3*10^{-5}$**	**-4.51**	**<0.001**
	y coordinate (S-N)	$-6*10^{-6}$	-1.37	0.171
	Temperature (min)	-3.90	-1.03	0.306
	Temperature (max)	0.46	0.11	0.913
	Land: A > BU	**-4.72**	**-2.46**	**0.014**
	A = G	-1.89	-1.78	0.076
	A = W	-0.44	-0.25	0.800
	BU = G	2.83	1.48	0.139
	BU = W	4.28	1.76	0.079
	G = W	1.44	0.80	0.426
	Cat density * y coordinate	**$2*10^{-7}$**	**4.78**	**<0.001**
	Cat density * Temperature (min)	**0.09**	**2.49**	**0.013**
	Cat density * Temperature (max)	**0.09**	**3.02**	**0.003**
Robin	Cat density	$8*10^{-4}$	-0.21	0.834
	Temperature (mean)	-1.71	-1.04	0.300
	Cat density * Temperature (mean)	**0.03**	**2.04**	**0.042**

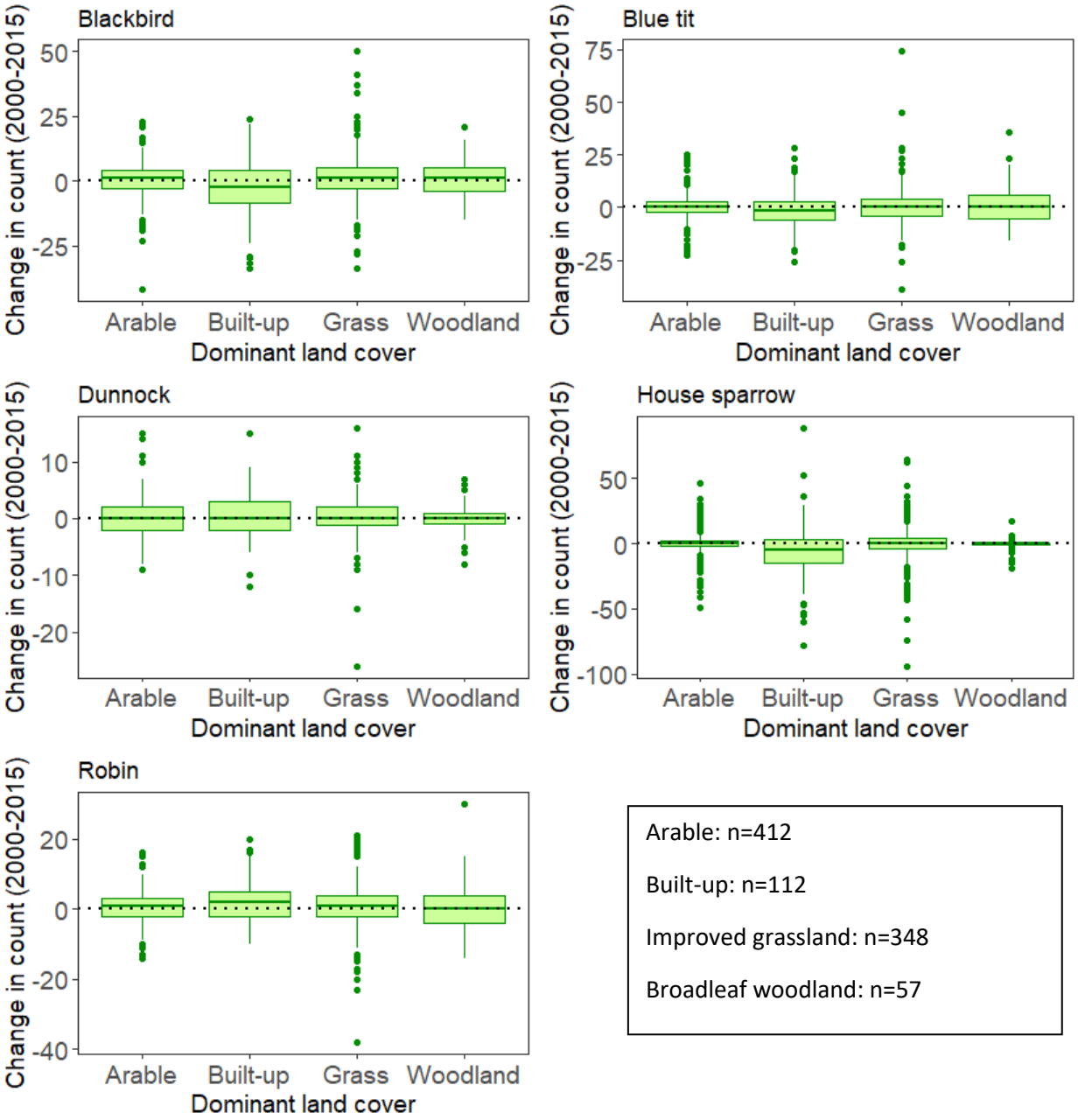


Figure 5. 10. The difference between the change in bird count (increase or decrease, 2000 to 2015) for four key habitats of interest (arable, built-up, improved grassland, and broadleaf woodland), where dominant land cover remained the same over time (for squares containing <500 cats, only). The dotted horizontal line represents a change of zero. Data plotted above this line indicate an increase in bird count between years, whereas data below the line represent a decrease. Bird species is given above each plot. Note the varying scales of y. Sample sizes (number of km squares) for each land cover class are given in the lower right box.

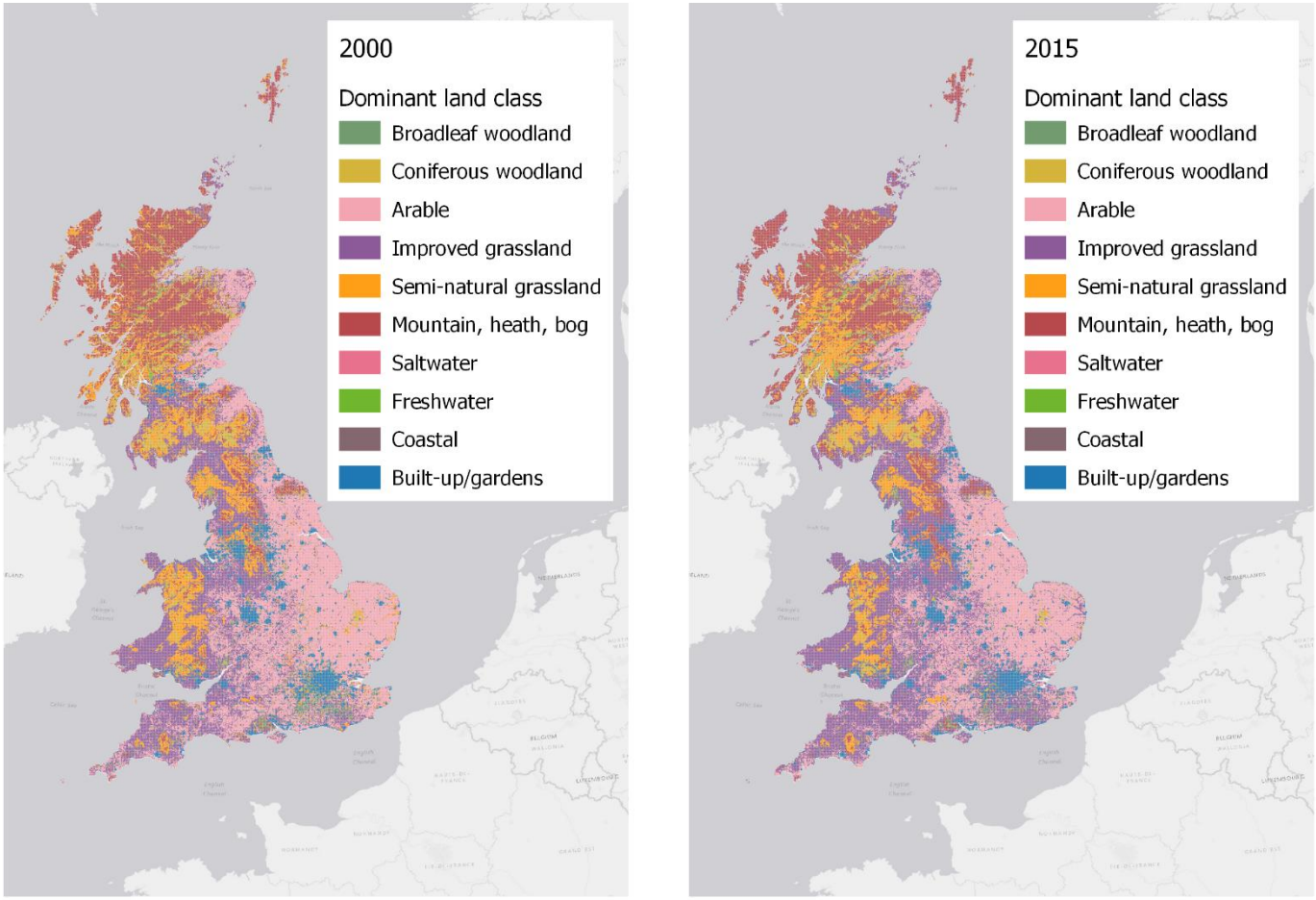


Figure 5. 11. The dominant land cover class for each km square across Great Britain for 2000 and 2015, including ten classes (data exclude the Isle of Man and the Channel Islands). Data were adapted from Fuller *et al.* (2002) and Rowland *et al.* (2017). Category descriptions can be found in Appendix 5. 3.

5.3.2.3 Temperature interaction effects

There was a clear difference, particularly in maximum and mean temperatures, between 2000 and 2015, with the east and south becoming warmer (Figure 5. 13). Upon testing, it became apparent that although none of the bird species counts were related directly to one of the three temperature variables, there were interactions with cat density for both house sparrows and robins (Table 5. 6). For house sparrows, the linear model showed that increasing maximum temperature increased the effect of cat density by 0.09 (Table 5. 6). However, conditional plots showed that where maximum temperature increased by around 0.5-0.6°C, increasing cat density was related to a reduction in count, whereas for decreases in temperature or stronger or weaker increases, the effect of cat density was minimal (Linear Model: t = 3.02, n = 929, p = 0.003, Table 5. 6, Figure 5. 14). Similarly, where the minimum temperature reduced the most between the two study years, there was little effect of cat density, but as this increased, cat density had a negative relationship with count of house sparrows (Linear Model: t = 2.49, n = 929, p = 0.013, Table 5. 6, Figure 5. 15). Again, this showed that as temperature increased, the effect of cat density increased by 0.09 (Table 5. 6**Error! Reference source not found.**).

For robins, there was an interaction between cat density and mean temperature change, such that where temperatures increased the most over the 15-year period, cat density had a positive relationship with count difference (Linear Model: t = 2.04, n = 929, p = 0.042, Table 5. 6, Figure 5. 16). The linear model showed that when mean temperature and cat density both increased, the effect on robin count was larger than the sum of each. Indeed, increases in the mean temperature increased the effect of growing cat density by 0.03 (Table 5. 6). In this instance, the positive relationship was more pronounced at temperature increases of 0.2°C and above. The interpolated maps are available in Appendices 5.6 - 5.10 for all five bird species.

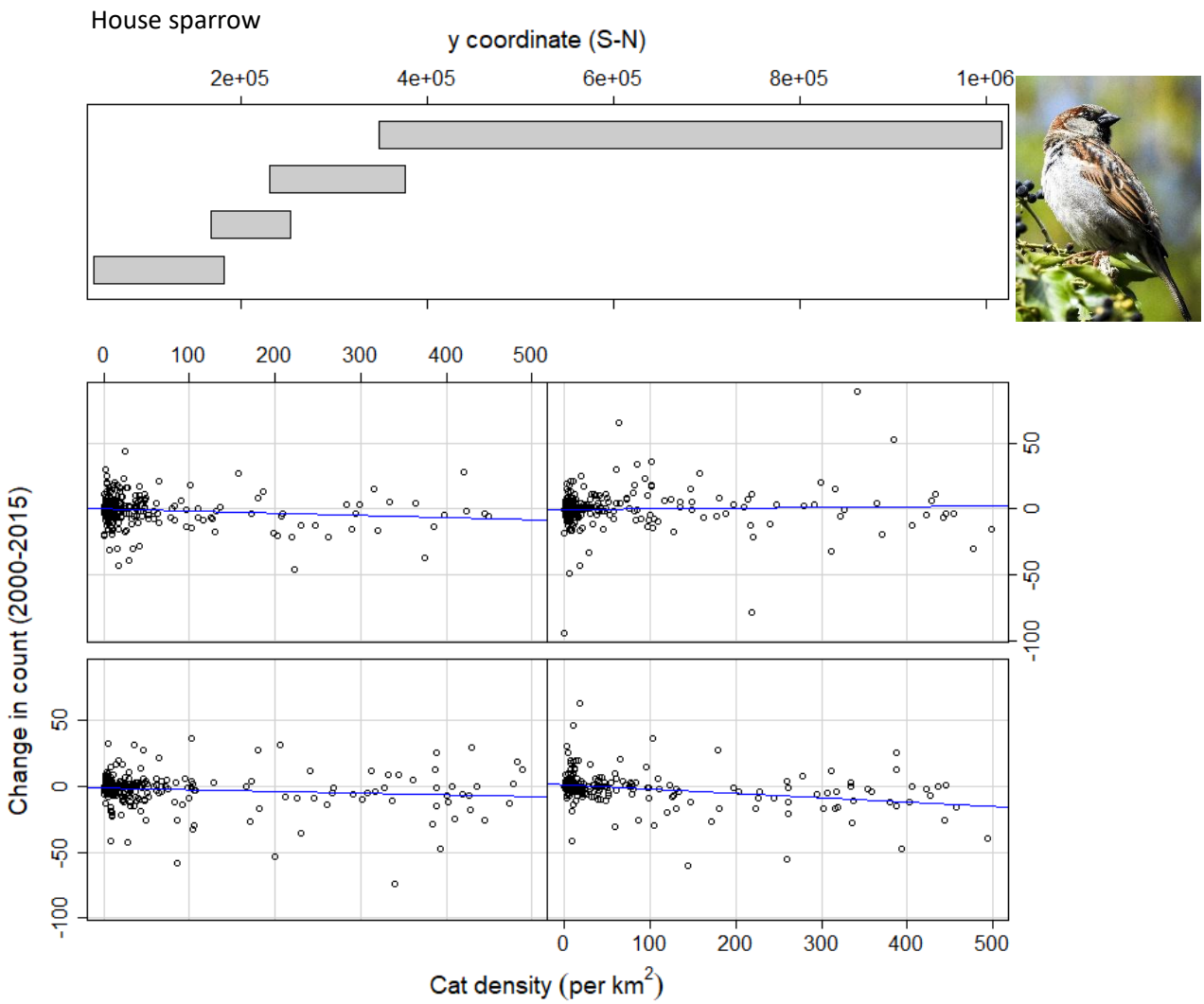


Figure 5. 12. The relationship between cat density (per km^2) and the change in house sparrow count (between 2000 and 2015), split depending on the y coordinate (south to north). The bottom left plot represents the squares furthest south, followed by the bottom right, top left, and furthest north in the top right. For each plot, a regression line is shown in blue.

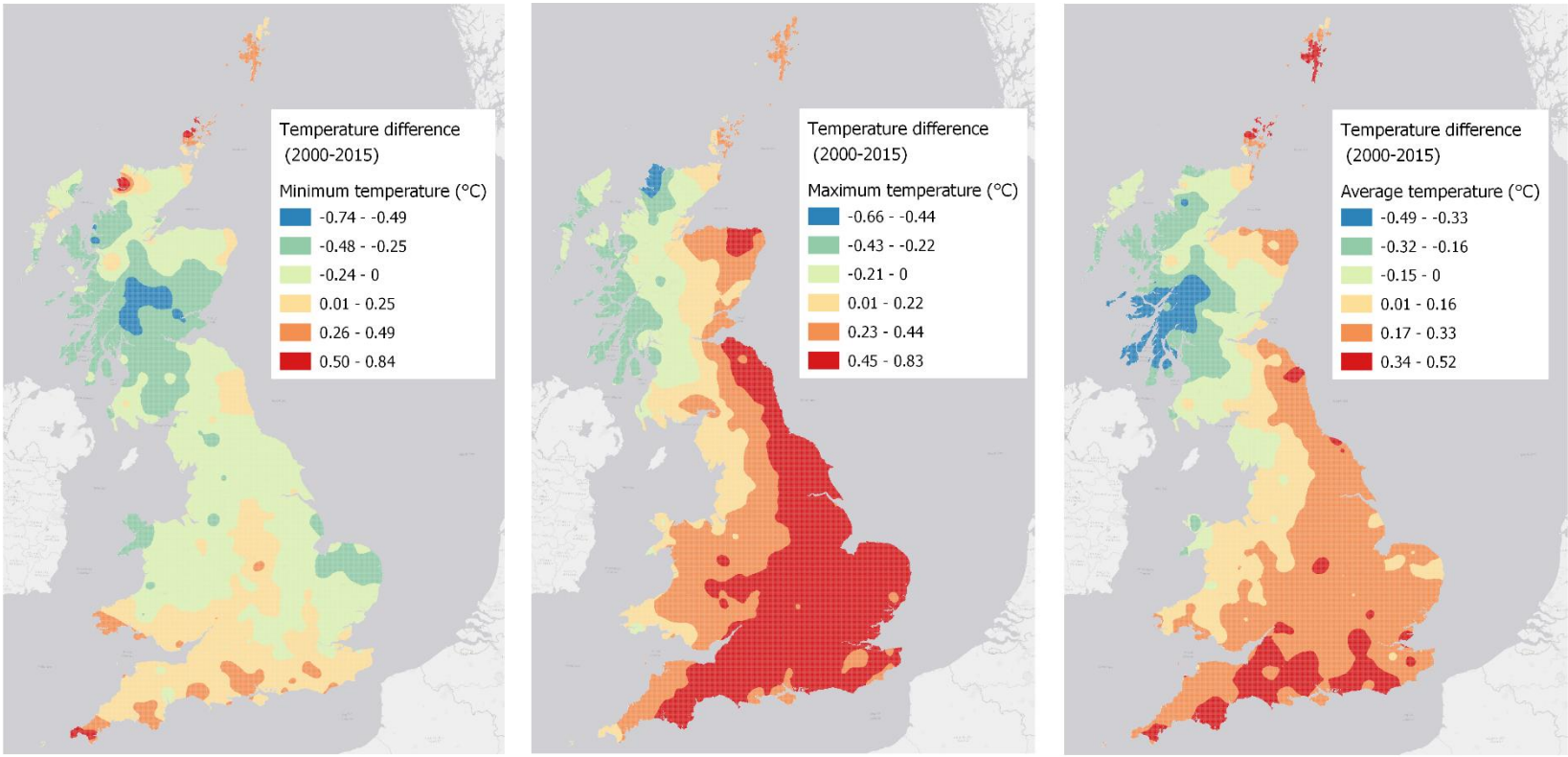


Figure 5. 13. The difference in temperature (°C) between 2000 and 2015 across Great Britain (data exclude the Isle of Man and the Channel Islands). The maps show (left to right) the difference in minimum, maximum, and mean temperature between the two years, where the green and blue colours denote a decrease in temperature (or zero change in some cases) and the yellow to red colours show temperature increases. Data are derived from weather stations across the country, and interpolated using Inverse Distance Weighted (IDW) methods (Met Office *et al.*, 2018).

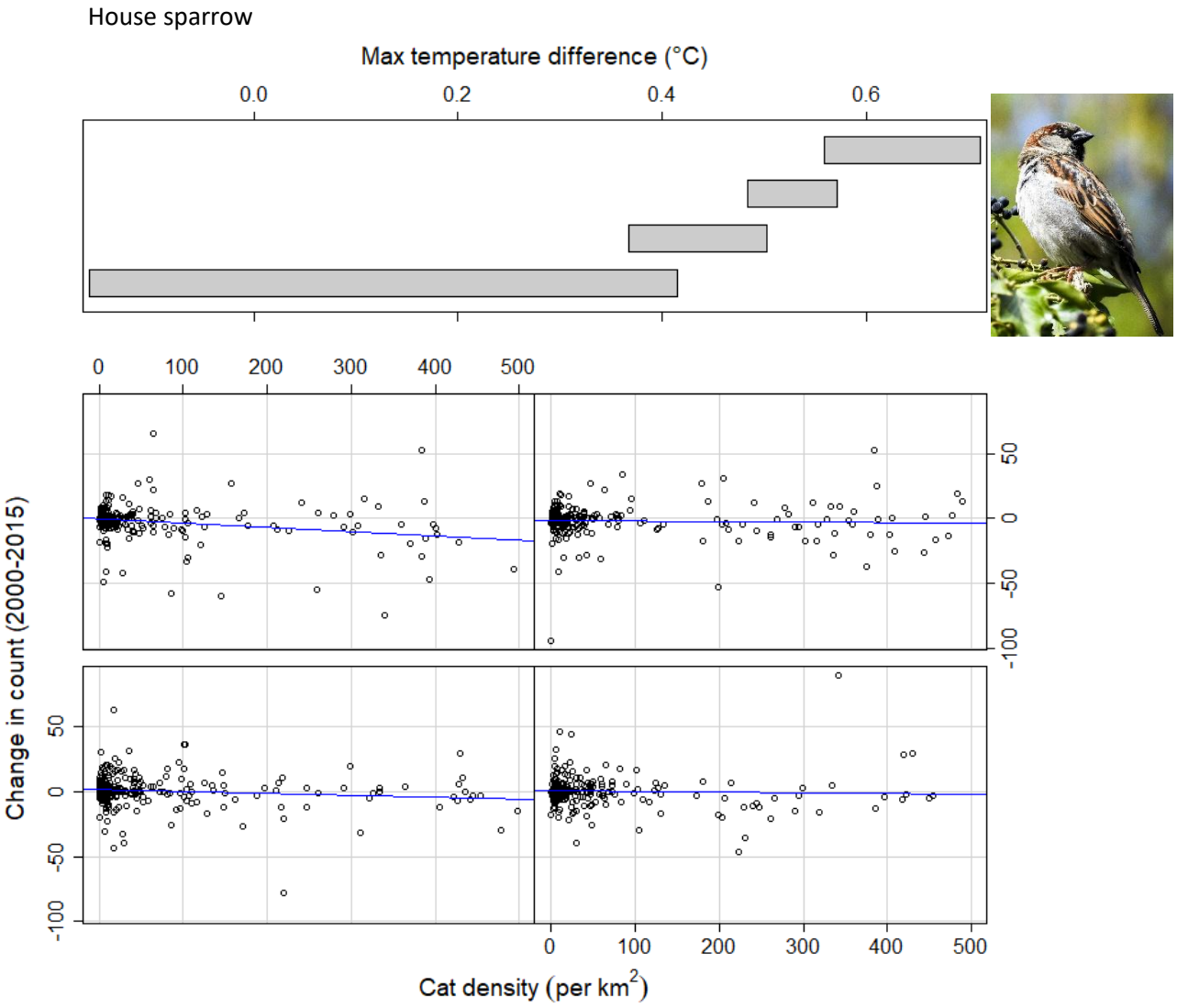


Figure 5. 14. The relationship between cat density (per km^2) and the change in house sparrow count (between 2000 and 2015), split depending on the difference in maximum temperature (°C) between the two study years. The bottom left plot represents the lowest temperature range, followed by the bottom right, top left, and top right. For each plot, a regression line is shown in blue.

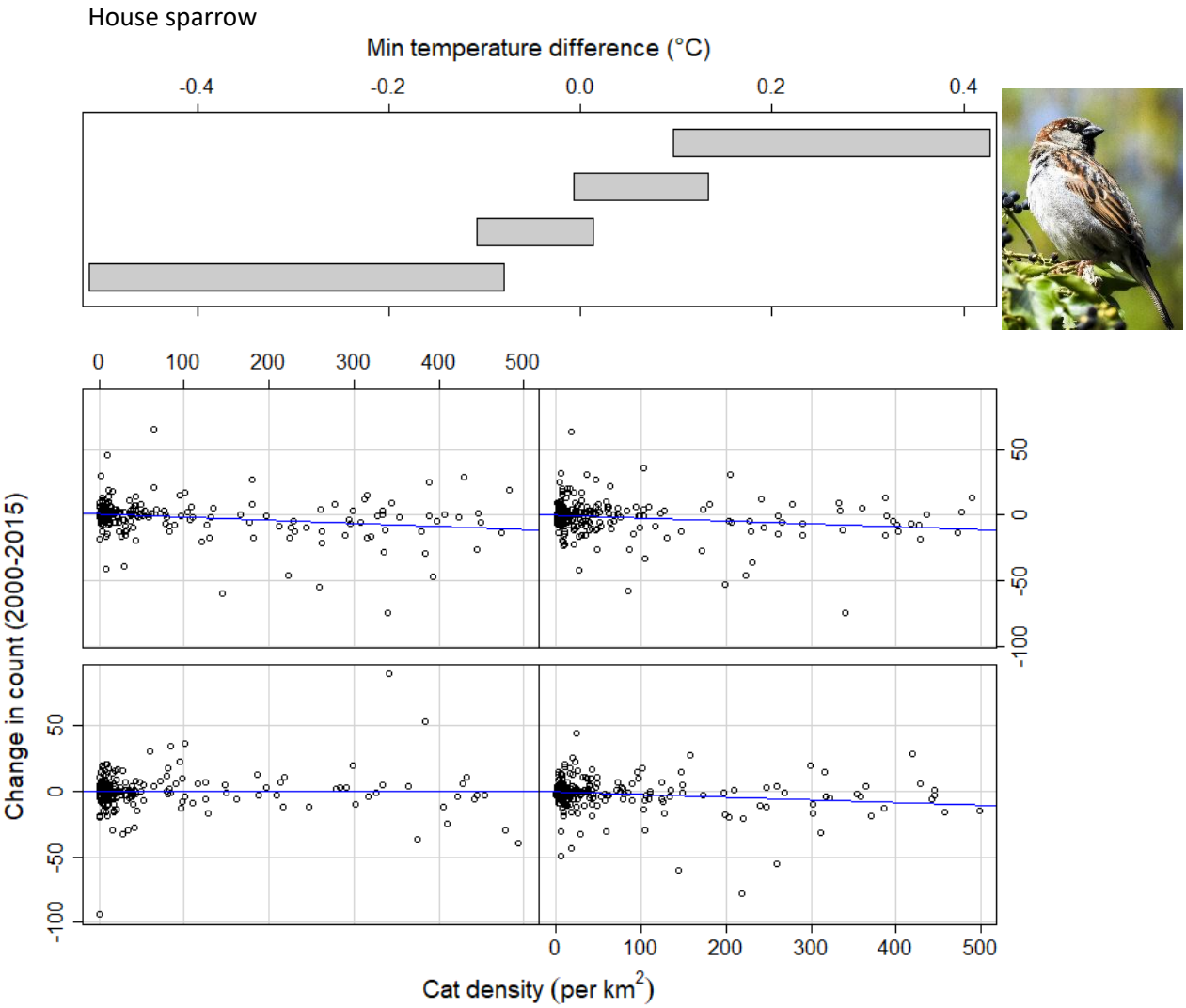


Figure 5. 15. The relationship between cat density (per km^2) and the change in house sparrow count (between 2000 and 2015), split depending on the difference in minimum temperature (°C) between the two study years. The bottom left plot represents the lowest temperature range, followed by the bottom right, top left, and top right. For each plot, a regression line is shown in blue.

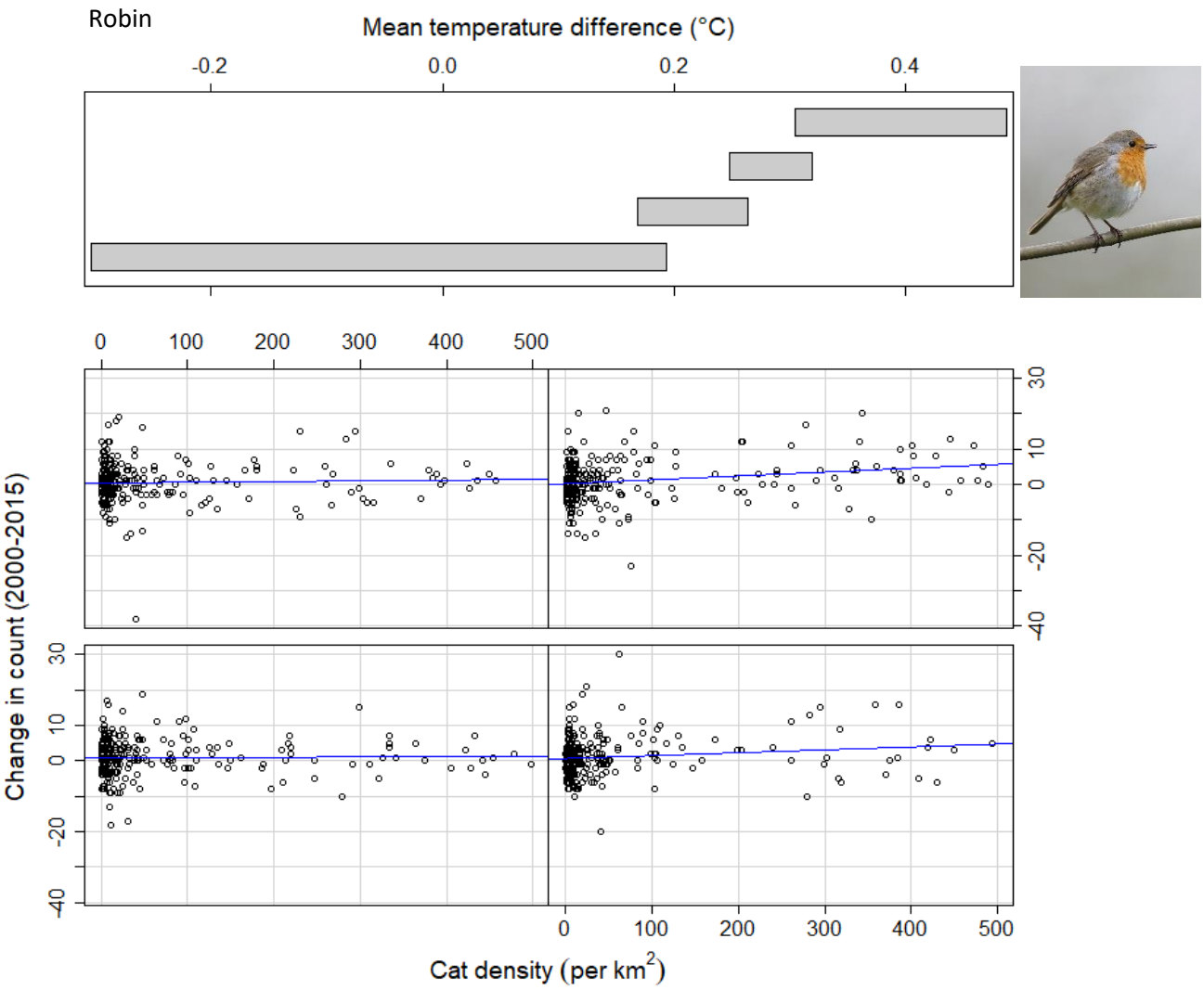


Figure 5. 16. The relationship between cat density (per km^2) and the change in robin count (between 2000 and 2015), split depending on the difference in mean temperature (°C) between the two study years. The bottom left plot represents the lowest temperature range, followed by the bottom right, top left, and top right. For each plot, a regression line is shown in blue.

5.4 **Discussion**

5.4.1 Influence of cat density

While some studies suggest that cats (directly or indirectly) can negatively impact prey species populations (Doherty *et al.*, 2016), others have found no evidence of this (Mead, 1982; Kays and DeWan, 2004). Here, there was no significant relationship between cat density and dunnock count or that of blue tits or blackbirds. There were, however, a number of significant interactions between cat density and temperature variables, as well as the y coordinate (latitude). This lack of relationship between cats and blackbirds, and cats and blue tits has also been shown previously (using similar BBS bird data, Sims *et al.*, 2008).

For house sparrows, there was a negative effect on count when cat density increased, but only at certain temperatures and latitudes. While this effect may be partly linked with predation by cats, the house sparrow population is stable, overall (Massimino *et al.*, 2022). Therefore, these reduced counts in areas of high cat density are offset by likely increases elsewhere, due to some factor or factors not measured here. Despite a 30% decline in house sparrows in urban areas between 1995 and 2011 (Baillie *et al.*, 2014), populations have not fluctuated substantially since the mid-1990s (Harris *et al.*, 2022; Massimino *et al.*, 2022). In urban areas (namely London, but potentially elsewhere), there have been recent outbreaks of avian malaria within house sparrow communities, leading to substantial declines (London abundance has declined by over 70% since the mid 1990s, Dadam *et al.*, 2019). Outbreaks of avian diseases are linked with high population densities and congregation of large groups, particularly at bird feeding stations. As a gregarious species, house sparrows may be more susceptible to disease transmission than other species, which may partly account for the urban declines observed by Baillie *et al.* (2014).

As well as direct mortality, indirect (sublethal) effects could lead to population declines in some species (Beckerman *et al.*, 2007; Bonnington *et al.*, 2013). For example, the presence of predators can impact fecundity in birds, as the threat of predation reduces nest provisioning and offspring care (Tilgar *et al.*, 2011; Bonnington *et al.*, 2013), which can reduce nestling health and growth (Dunn *et al.*, 2010). By briefly introducing a perceived predation threat (a

taxidermy cat model), Bonnington *et al.* (2013) found that blackbirds reduced nest provisioning visits by more than one-third after exposure to the cat model when compared with a control. Therefore, where cats are present, the threat of predation may be substantial enough to cause a reduction in bird fecundity.

However, breeding success (per breeding pair) may not be the most appropriate measure of impact, as when populations increase, intraspecific competition can lead to reduced breeding success per pair. For example, the productivity of blue tits in the UK fell by more than 50% in a 25-year period, yet populations steadily increased (Baillie *et al.*, 2014). Therefore, reduced breeding success can be in response to a population boom. In contrast, for blackbirds, dunnocks, and house sparrows, the number of fledgelings per breeding attempt has recently increased in some areas despite all three species having experienced declines in such areas (Baillie *et al.*, 2014). Again, this may be the result of ongoing fluctuation cycles in population size.

5.4.2 Human disturbance

Since cat density is strongly correlated with that of the human population in the UK, the relationships between bird counts and cats observed here, may in fact be more indicative of a number of (or cumulative effect of) different anthropogenic impacts.

Proximity to human activity and direct disturbance can affect assemblage structure, breeding success, nestling care, and foraging behaviour (Remacha *et al.*, 2016). A study into human disturbance in Spain monitored blue tit chick growth and condition in times of high and low human presence (Remacha *et al.*, 2016). This found that when disturbance was highest, the growth rate of chicks reduced and individuals fledged with a lower body weight (Remacha *et al.*, 2016). This may make the fledged juveniles more likely to become prey, as low condition has been linked to predation risk (Møller and Erritzøe, 2000).

For mammals, the impacts of disturbance are less well understood, as individuals can be more elusive than birds and are not monitored in the same, standardised way. However, recent culling of badgers (*Meles meles*) may suggest that disturbance can lead to communities

shifting their range and adopting new, more favourable territories (Tuyttens *et al.*, 2000). However, due to fragmentation of habitat (through barriers such as large roads and impermeable central reservations), this is not without mortality risk.

Recently, the COVID-19 global pandemic has provided a unique opportunity for species monitoring in an altered environment. Birds largely reduced their activity in parks and other recreational areas, as human disturbance increased in these areas (Warrington *et al.*, 2022). In the USA, it was found that the increase in hikers (and other visitors) to protected areas led to increased habitat fragmentation and a reduction in useable habitat by around a third, due to the formation of new walking trails (Primack and Terry, 2021). However, in urban centres, human activity decreased as shops, restaurants, and offices closed. This led to decreased activity of feral pigeons (*Columba livia*) in cities, as anthropogenic food availability dropped significantly (Soh *et al.*, 2021). This shows that while some species (specialists) experience fear effects of increased human disturbance, others (food and habitat generalists) thrive in close proximity to humans.

5.4.3 Climatic changes

For house sparrows, there was an interaction effect between cat density and the minimum and maximum temperature change, showing that this relationship was strongest under certain climatic conditions. This interaction suggested that the effect of cats was only apparent where minimum temperature had altered by between -0.1°C and +0.4°C (no apparent effect where temperature dropped by more than 0.1°C), and maximum temperature by around +0.5°C to +0.6°C (no apparent effect until temperature increase reached 0.5°C). It appears that warmer winters can cause house sparrows to decline more severely in areas where cats are most densely populated. The same appears true of warmer summers and temperature increases, generally. This shows that increasing temperatures (more than decreasing temperatures) have an influence on house sparrow population size and perhaps distribution. Looking at monthly temperatures, rather than annual, Pearce-Higgins *et al.* (2015) identified a negative relationship between British bird populations and hot, dry summer periods, with a one-year lag before the effects became apparent. In addition,

a long-term decrease in blue tit, great tit, and coal tit (*Periparus ater*) body mass correlates with an increase in mean winter temperature (Furness and Robinson, 2018). Despite this apparent loss of body condition, none of these three species have experienced recent long-term population declines in either urban areas (Baillie *et al.*, 2014) or across the UK as a whole (Harris *et al.*, 2022).

For robins, neither minimum nor maximum temperature had an effect, but the mean temperature between years (together with cat density) did show a relationship. Temperature decrease and moderate increase (by up to around 0.2°C) had little to no effect, but as the average temperature increased beyond 0.2°C between years, cat density began to negatively affect robin counts. Previous research has also found a negative effect of cat density on robin populations, although temperature changes were not measured (Sims *et al.*, 2008).

Effects of latitude and longitude were observed for house sparrows monitored here, where count was negatively affected towards the east of the UK (which may in part be, again, related to climatic conditions and changing weather fronts). The y coordinate alone had no significant effect, but it was found that further south, house sparrow count reduced more where cat density was highest. Many southern species (in Europe) are gradually moving their range further northwards, which is thought to be an effect of a warming climate (Virkkala and Lehikoinen, 2017).

There were no observed effects of climate (or latitude and longitude) on blackbirds, blue tits, or dunnocks, which may suggest that they are more able to adapt to temperature changes. Monitoring blue tit responses to extreme weather events, Marrot *et al.* (2017) found both positive and negative effects of extreme heat on fledgelings and nestlings, respectively. This therefore suggests that high temperatures can be beneficial, as long as they do not occur too early in the year. Of course, other species (reliant on different diets and other resources) can respond negatively to such conditions.

5.4.4 Land cover

Since residential gardens in the UK comprise one quarter of all urban, built-up land cover (Loram *et al.*, 2007), these areas can provide important resources for urban and suburban wildlife (Plummer *et al.*, 2019). However, here it was found that blackbirds showed a larger decline in count in built-up areas than in arable, improved grassland, or broadleaf woodland-dominated squares. Despite this, blackbirds are recognised as the fifth most frequent avian visitor to gardens in the UK (RSPB, 2023). For blackbirds, dominant land cover was the only variable significantly related to change in count, although it is important to note that interaction effects between land cover and other variables were not measured here.

House sparrows showed a similar pattern to blackbirds, where the decline in count was greater in built-up areas than other land classifications. However, this was only significant between built-up and arable habitats (although almost significant between built-up and broadleaf woodland, also). This is perhaps unsurprising, as house sparrows have been found to suffer large-scale declines in intensively farmed areas (Hole *et al.*, 2002), yet they are currently the most frequently recorded garden bird (RSPB, 2023). However, there do appear to be ongoing significant declines in England, while Scotland and Wales are seeing increased populations, with the most pronounced declines in central west and south east England, and the largest increases in Welsh urban and suburban areas (Robinson *et al.*, 2005). This effect is shown in the latitudinal and longitudinal effects on house sparrows found here.

In the present study, monitoring the effect of change in dominant land cover was not possible, due to low sample size of bird survey squares for most combinations (e.g. arable to built-up, woodland to arable etc.). The type of land cover may be rather biased when examining only squares used for BBS bird monitoring, as counts often take place along transects in publicly accessible spaces. In addition, there are potential issues with detectability of birds, particularly in closed habitat, such as woodland or built-up areas. For instance, when walking an urban, public transect, the detection of singing birds may be limited by traffic noise, and that of non-singing individuals (perhaps feeding) will likely be limited by garden fences or other structures. Therefore, gregarious bird species in larger groups may be easier to detect

and identify, leaving more solitary (and perhaps, smaller-bodied) species undetected (if not vocalising).

A further citizen science-based survey of birds in private gardens (Big Garden Birdwatch from RSPB) takes place every winter and is gaining more participants each year, with contributions from over 500,000 gardens across the UK in 2023 (RSPB, 2023). In future, these data may be combined with those of the BBS for similar analyses. Interestingly, Chamberlain *et al.* (2004) analysed early weekly BTO Garden Birdwatch data for winters 1994/95 and 2001/02 (note that this differs from the RSPB's 'Big Garden Birdwatch' which occurs over one weekend per year) and found that overall, seven out of 40 species were most likely to occur in more urban gardens, including house sparrows, whereas 15 out of 40 showed a significant association with rural and suburban areas, including blackbirds, blue tits, and robins. For all five of the species monitored in the present study, Chamberlain *et al.* (2004) found that probability of occurrence was higher in gardens which provided food, although the vast majority of participating gardens offered food at least occasionally (95%). It appears that participants of such surveys are more likely to have an existing interest in wildlife and may therefore provide a more bird-friendly garden, meaning that these data have inherent biases.

5.4.5 An artificial system

Although domestic cats are not native to the UK, it could be argued that the areas most commonly occupied by cats are becoming increasingly artificial, unnatural systems. Such areas are perhaps more likely to be heterogenous mosaics of different habitats, such as gardens and amenity spaces, as well as urbanised towns and cities. While predation by cats is undoubtedly the cause of mortality for millions of prey animals per year in the UK (see Chapter 4 for extrapolations), the most commonly caught species (mice and voles, see Chapter 3) are not thought to be experiencing declines (see section 5.1.2) and may indeed be considered pests (Baker *et al.*, 2020). Even the top-most commonly caught bird species are mostly stable, although the house sparrow is declining in certain areas. Previous research has suggested that declines in house sparrow populations may be due to a number of factors, including disease (Dadam *et al.*, 2019), and lack of suitable nesting and food resources (Peach

et al., 2015), or a combination of such factors. Here, urbanised land cover, temperature increases, cat density, and latitude and longitude were all found to affect house sparrow count, illustrating the complexities of this issue.

While domestic cats are more densely located in urban areas, so too are anthropogenic food sources for both birds and mammals. Areas with consistent provision of food through all seasons, along with increased opportunities for shelter and nesting are likely favoured, particularly by generalist species and those more able to adapt (Palacio, 2020). In urban areas, individuals are perhaps less vulnerable to extreme weather events than those occupying a more natural setting. Conversely, populations may be limited due to habitat fragmentation and degradation (Baker *et al.*, 2003), along with increased chemical (Peach *et al.*, 2008), noise (Kareklas *et al.*, 2019), and light pollution (Raap *et al.*, 2015), direct human disturbance (Remacha *et al.*, 2016), and predation pressure from cats and other synanthropic species such as corvids (Capstick *et al.*, 2019) and rodents (Hanmer *et al.*, 2017). For birds, clutch size has been found to be lower in urban areas for some species (including blackbirds and blue tits, Chamberlain *et al.*, 2009; Capilla-Lasheras *et al.*, 2022). While this may be partially linked to sublethal effects of cat and human disturbance, Peach *et al.* (2008) found that for house sparrows, fledgeling body mass was related to concentrations of nitrogen dioxide (NO_2), as well as impacts of temperature, rainfall, and quality of chick diet. In built-up areas, house sparrows have been found to exhibit higher breeding success when supplemental food provision is of high quality (Peach *et al.*, 2014), suggesting that this has a significant influence on reproductive factors.

The reduction or removal of predation by cats may lead to a number of undesirable and unintentional effects. Since the vast majority of prey caught and returned by cats are commonly thought of as pests (for example, mice and rats, Baker *et al.*, 2020), removal of cats from the environment could lead to increased quantities of chemical pesticides being used in residential gardens as a means of control. Non-target species are vulnerable to such poisons, and this could therefore have a further impact on the conservation efforts of species such as hedgehogs and birds. Pet dogs may also directly ingest pesticides and other carnivores may be affected if consuming contaminated prey. Furthermore, increasing survival and booming prey populations can also lead to outbreaks of disease, particularly where individuals

congregate (such as near food resources), which could then have implications for human health.

5.5 **Conclusion**

Although linked with the count trends of two species here (negatively for house sparrows and robins, although partly influenced by other factors), cat density is strongly correlated with that of humans and urban areas which are further associated with pollution, habitat loss and fragmentation, and direct disturbance. From the results presented here, it does not appear that cats are a primary threat to the bird species analysed, although predation surely adds to other existing stressors. Indeed, it has been estimated that predation by cats equates to just 10.6% of anthropogenic mortality sources of birds in the USA (Erickson *et al.*, 2005). In addition, Mead (1982) found that cats were not the leading cause of small bird mortality in the UK, when assessing ringed bird deaths. For example, around 20% of house sparrow deaths were due to cats, along with 31% for both dunnocks and robins, 22% of blue tit deaths, and 19% for blackbirds (Mead, 1982). Even these are likely to be over-estimates due to ring recovery reporting biases, with reports potentially being highest for returned prey (compared with window or car collisions, for example). It is also likely that many of these predated individuals were of poorer body condition, suggesting that this is largely a compensatory source of mortality (Møller and Erritzøe, 2000; Baker *et al.*, 2008).

One statistic that is regularly cited, is that house sparrow populations in the UK have halved since the 1970s, leading to their inclusion on the UK's Red List (Stanbury *et al.*, 2021). While this is true, little change has been observed for around 25-30 years (Harris *et al.*, 2022; Massimino *et al.*, 2022). The breeding population of house sparrows in the UK appears stable, and the BTO have predicted a minimal impact of climate change on this species (Pearce-Higgins, 2021). Of the top five returned bird species (Chapter 3), the remaining four are not showing any significant urban declines (Baillie *et al.*, 2014). Since cat density is likely to have increased during the last 25 years throughout the UK, the stability of these most commonly returned avian prey species over this period (as described by Harris *et al.*, 2022) may suggest

negligible population-level impacts of predation by cats. However, these data are of course not directly comparable.

Prey populations in the UK have evolved under sublethal pressures, as well as predation pressure from terrestrial mammals (unlike prey of New Zealand, for example). Evolving alongside predators of adults and nestlings (such as European wildcats, rats, mustelids, and corvids), garden bird species are perhaps able to sustain losses without suffering population declines. This can either be a result of high productivity to cope with losses, or evolved escape behaviour and crypsis to avoid predation (Gibbons *et al.*, 2007). Interestingly, differences in escape behaviour of birds have been found between urban (where cats are densely populated) and rural areas (where raptors are particularly common, Møller and Ibanez-Alamo, 2012), suggesting adaptation to urbanisation and to changing threats.

Of course, there will be a limit to the amount of predation sustained before populations do indeed decline and struggle to maintain stability. While cats exist in densities far higher than a natural predator (with cats reaching up to 4000 per $1km^2$ in the most densely populated parts of the UK, Aegerter *et al.*, 2017), overall predation has been found not to necessarily increase with cat density, such that rural cats predate more per individual than those in more densely populated areas (Thomas *et al.*, 2012). However, bird predation has been found to be proportionally higher (although not numerically higher) in urban areas, compared with other taxa (Barratt, 1997; Kauhala *et al.*, 2015; Krauze-Gryz *et al.*, 2017). At current densities, cats do not appear to have a population-level effect on avian prey populations, although this may be a delicate balance in an unnatural system.

Chapter 6

Synthesis

Hannah Lockwood

The main aim of this thesis was to assess the impact of predation by domestic pet cats on British wildlife populations. In order to achieve this, a long-term prey return study was conducted, relying on data from members of the general public, and appropriate multipliers were developed through the use of cat cameras. This allowed total annual predation to be estimated, albeit cautiously, due to insufficient data for taxon-specific estimates. The impacts of cats on the five most frequently returned bird species were then assessed, although it was apparent that the relationships here are complex.

6.1 **Reliability of data**

6.1.1 Citizen science: engagement and quality of data

In order to effectively assess population-level impacts of predation, all data used must be as reliable and representative as possible. This assessment process requires many sources of information and relies on each to be of good quality. For example, estimates of predation rate depend on accurate return data from volunteers and a method of extrapolation which limits under- and over-estimation (Chapters 3 and 4). Similarly, bird counts used in Chapter 5 were also carried out solely by volunteers. While citizen science is a very valuable tool, allowing researchers to collect data which would otherwise remain unrecorded, these methods come with their own challenges.

Here, over 1,000 cats were initially registered to complete and submit a monthly 'cat diary' of predation events, yet data were retrieved from only just over half of these individuals (n = 553). The reasons behind this reduced engagement rate are unknown, but it may be that emails were being filtered as 'junk' and going unseen, or a number of factors related to the participants' circumstances. It is important that engagement is maximised to increase sample size, improving the reliability and power of analyses.

Cat owners tended to over-estimate their cats' return rates in both the warm and cold season, with some predicting that their cat would return ten or more prey per month more than the actual rate (Chapter 3). This suggests that the results of studies reliant on owner estimates and recall may be inherently flawed (such as Robertson, 1998; Silva-Rodriguez and Sieving,

2011). There may also have been a participation bias, with owners of frequent hunters more likely to register with the project. A study in New Zealand conducted a random telephone survey alongside a cat predation diary study and found that a greater proportion of participants in the predation diary study had active hunting cats than in the telephone survey (van Heezik *et al.*, 2010). Despite efforts in the study design here (emphasising that not only frequent predators were required), some participants who withdrew from the project early commented that they felt that they were not contributing anything of value, as their cat or cats did not return any prey. This suggests that lack of predation may have partly led to reduced engagement with the study, and therefore return data presented here may be overestimated.

Just under half of the prey items returned home by cats were recorded alongside a photograph, enabling identification confirmation. A relatively low proportion of those prey were found to be misidentified (around 7%). The taxon most frequently misidentified was rodents, with vole species being recorded as mice a total of 89 times. As efforts were made in the study design to reduce misidentification and improve data reliability (such as providing online and printable identification guides), it is unclear what proportion would have been misidentified had these efforts not been made.

Owner participants in the cat camera study used the camera over an average of 6 months, although this ranged from one month to 38 months. While the devices were not expected to be used frequently on the longer-term study cats, for those using the equipment for just one month (n = 11), a recording schedule of every 3 - 4 days was suggested. This would have collected footage of around 10 individual outdoor excursions, giving time in between to recharge the device and download footage recorded. However, five of the 20 cats retrieved less than one hour of outdoor footage each. This may be due to a lack of understanding of the project aims and may be resolved in future research by providing participants with greater insight into the purpose of the study.

It is advised that citizen science data collection should be designed to be flexible, maximising engagement levels of participants (Goad *et al.*, 2020). Although this was the aim here, engagement and excitement for the project certainly seemed to wane for some people. The process itself of recharging devices and downloading footage was designed to be as simple as possible, so it is unlikely that this was the source of difficulty. It is perhaps more likely that

due to other commitments, data collection was not prioritised, or simply that people forgot or temporarily misplaced the camera. In Chapter 4, it was found that often, cameras were used shortly after prey had been returned home, suggesting that evidence of predation acted as a prompt for participants to utilise the cameras.

Chapter 4 also explored the different approaches to estimating multiplication factors for extrapolation, finding that the use of owner estimates of outdoor time greatly inflated the resulting figures. As owners significantly over-estimated prey return rates, it is perhaps also likely that the average time spent outdoors was also far beyond the actual figure.

6.1.2 Producing multipliers for extrapolation

As with many other studies (such as Mitchell and Beck, 1992; Kays and DeWan, 2004; Baker *et al.*, 2008; Thomas *et al.*, 2012; Woinarski *et al.*, 2017), the prey return data collected here were used to extrapolate to actual capture rates of vertebrates. The multiplication factors used to extrapolate can vary greatly depending on the methods used to generate them. In Chapter 4, a multiplier produced using owner estimates of outdoor time along with hourly predation rates on video was nearly 13 times greater than that produced using the proportion of prey returned home and detected. It was clear that this multiplier was inflated and unrealistic, and therefore unsuitable to be applied to the return data collected here. It was also apparent that due to differences in the detectability of prey remains and palatability of the prey themselves, a single 'all taxa' multiplier is not appropriate. Reliable taxon-specific multiplication factors should be produced, accounting for differences in how the prey are treated by cats, in order to accurately extrapolate from return data to total predation rates.

6.1.3 Assessing impact

Simply calculating predation rates without setting them into the context of population-level impact is rather meaningless (for example, Loss *et al.*, 2013) and it is therefore important to assess prey population trends with increasing or decreasing predation pressure from cats.

This can be very challenging, as not all prey species populations are regularly monitored, and there are many other variables which may impact prey assemblages, which may not be consistent between study sites. Indeed, a population monitoring study was attempted here in 2018, but capture-mark-recapture data were insufficient for meaningful analysis. Initially, two villages of similar habitat structure, size, and latitude were selected for comparison and small mammals were caught in live traps in gardens, marked (by fur trimming), and released. However, over 10,000 trap hours and 2,580 trap checks yielded just 21 captures of six individuals across the two sites. Due to a break in study and the COVID-19 pandemic, it was not possible to repeat these methods. Therefore, a desk study using national datasets (Chapter 5) was deemed most appropriate here.

While the mapping methods used in Chapter 5 were a useful way of analysing data on a large scale, the use of third-party data was challenging to analyse effectively. There were a number of factors which were not accounted for in the analyses, such as human density (although this was strongly positively correlated with cat density), pollution levels, habitat fragmentation, and fine scale habitat changes.

The change in land cover over time was not analysed due to low and very unbalanced sample sizes for land classification changes. It would be interesting and valuable to assess the effects of these changes on prey at a smaller scale, as $1km^2$ data are perhaps not the most appropriate for species with small ranges (such as small mammals and many passerines, particularly during the breeding season, Morganti *et al.*, 2017). Ideally, analyses would take place at a finer spatial scale, comparing the bird and small mammal population health of structurally similar villages and towns.

While the methods used may have failed to recognise changes on a smaller spatial scale, the results show that the relationship between cats and their prey is a complex one, dependant on other factors such as temperature change.

6.2 **Impact of predation by domestic cats**

6.2.1 Historical impact

Domestic cats have been implicated in the extinctions of 63 species worldwide (Doherty *et al.*, 2016). Of course, 'implicated' is a vague term and the vast majority of these assessments (n = 62) were based on anecdotal evidence. Only one, the Choiseul pigeon (*Microgoura meeki*), was based on measurable data, although this was correlative and therefore does not necessarily indicate causation (see Supplimentary Dataset S1 in Doherty *et al.*, 2016). With robust evidence of past extinctions lacking, it is important that any current declines in prey species are monitored and the causes fully assessed. It should also be noted that Doherty *et al.* (2016) reported a particular pattern of extinctions and declines on small islands, compared with mainland areas.

Unlike species inhabiting small oceanic islands and other isolated land masses such as New Zealand, British prey species have developed adaptations to cope with terrestrial predation pressures, having evolved alongside mammalian predators, including the European wildcat. Since domestic cats are present in unnaturally high densities in the UK, there has been some concern about the ability of prey populations to successfully manage losses to predation. However, as the ranges and predatory habits of cats differ between urban and rural areas (with urban cats returning fewer prey per individual), areas of high cat density (urban) do not necessarily suffer higher prey losses than areas of low density (rural areas, Thomas *et al.*, 2012).

6.2.2 Owned, feral, and wildcats

Feral domestic cats in Europe appear to consume slightly lower numbers of vertebrate prey than European wildcats (Table 6. 1), perhaps as the diet of feral individuals may also contain food from anthropogenic sources (Cove *et al.*, 2018). However, it is estimated that pet cats take around 0.13 prey per day (Table 6. 1), which is 4.4% of that of a wildcat. According to

these estimates, European wildcats predate at a rate around 23 times higher than owned domestic cats.

Table 6. 1. Estimates of daily vertebrate predation by European wildcats (*Felis silvestris*), feral domestic cats, and owned domestic cats. For the purpose of these estimates, it is assumed that the contents of an individual's stomach represents one day of prey consumption (following Woinarski *et al.*, 2017).

Cat type	Reference	Location	Results	Vertebrate prey per day	Combined estimate per cat, per day
Wildcat	Tryjanowski *et al.* (2002)	Slovakia	192 prey in 38 stomachs	5.05[1]	2.98 prey
	Biró *et al.* (2005)	Hungary	52 prey in 22 stomachs	2.36	
	Germain *et al.* (2009)	France	40 prey in 26 stomachs	1.54	
Feral domestic	Biró *et al.* (2005)	Hungary	492 prey in 264 stomachs	1.86	1.79 prey
	Krauze-Gryz *et al.* (2012)	Poland	62 prey in 46 stomachs	1.35	
Owned domestic	This study	UK	0.05 prey returned per day multiplied by 1.57	0.08	0.13 prey
	This study	UK	0.05 prey returned per day multiplied by 1.22	0.06	
	Piontek *et al.* (2021)	Poland	25 prey in 81 stomachs	0.31	
	Loyd *et al.* (2013)	USA	Equivalent of 4.43 prey from 55 cats	0.08	

[1] Winter estimate only

Interestingly, there is a difference between the types of prey and size of prey taken by domestic cats and wildcats (Biró *et al.*, 2005). In Hungary, Biró *et al.* (2005) found that European wildcats and their hybrids tended to consume larger prey than feral domestic cats. Therefore, while wildcats consume around three prey per day, the average prey item is larger (taking more prey over 300g) than those taken by domestic cats (typically 15 - 50g). Biomass is therefore an important factor when comparing the impact of wildcats against that of domestic individuals. The same study also showed that arboreal prey species occur in the diet

of wildcats more frequently than in that of domestic individuals (Biró *et al.*, 2005). This suggests that wildcats are more adept at catching passerine birds, for example, than feral or owned domestic cats. These complications make it difficult to directly compare the potential impact of owned cats with that of feral or wildcats. It is clear that per individual, owned cats catch far fewer prey than feral or wildcats.

However, domestic cats are known to exist in higher densities than other predators, far exceeding natural carrying capacity. While owned domestic cat density in British suburban and urban studies ranges from 132 to 1580 per km^2 (mean of 331 per km^2, Baker *et al.*, 2005; Baker *et al.*, 2008; Sims *et al.*, 2008), wildcats (and hybrids) in Scotland exist at far lower densities of around 0.7 individuals per km^2 (Kilshaw *et al.*, 2015). This means that domestic cat densities are around 473 times that of Scottish wildcats. However, the habitats occupied by these two species and the prey densities found there are rather different. In order to assess impact, Chapter 5 investigated population-level effects of local cat density.

6.2.3 Prey population assessment

Chapter 5 found that while the cat population has grown, most prey populations have increased or remained stable over time. For example, the most frequently returned mammal (in Chapter 3) was the wood mouse, yet the population of this species across the UK is thought to be stable and the species is listed as 'least concern' (Mathews *et al.*, 2018; Mathews and Harrower, 2020). Such is the case for most other prey species, with many avian prey populations experiencing increases in national abundance. Although cats were occasionally found to return protected species or those of conservation concern, these made up a very low percentage of overall returns (for example, 0.12% of prey returns were bats).

Here, there was no significant relationship between cat density and the increases or decreases in survey counts of three out of five bird species (Chapter 5). Where there were relationships (i.e. for house sparrows and robins), these were complex and only observed under particular climatic conditions or at certain latitudes. Even under such conditions, it is not clear whether this association is causal, or merely a result of many other contributing

factors which were not measured here (such as human disturbance, habitat loss and fragmentation, and pollution).

6.3 Contributions to the field and recommendations

This study contributes to the understanding of predator-prey relationships concerning cats in the UK. Annual return rates and total predation rates have been established here, and the factors potentially influencing predation have been explored with a view to reducing impacts on wildlife populations.

The concepts of palatability of captured prey and detectability of returned remains have not been considered previously, but were fully discussed and explored here. It became apparent that applying a single multiplier to all taxa when extrapolating can lead to over- and under-estimation of different prey groups and should therefore be considered in future research.

When comparing extrapolation techniques, it was clear that the use of cat cameras was the most appropriate and accurate method of establishing multiplication factors. As slight differences in the calculations can produce vastly different extrapolated estimates of predation, it is very important that these multipliers are as accurate as possible. It is therefore recommended that further research is undertaken to establish robust estimates of the proportions of different taxa returned home and detected on the owners' property. This will then help to produce reliable multipliers that can be applied to individual prey groups.

It was also found that the mean prey returned per month was driven higher by the inclusion of 'super predator' data. Therefore, further work should also concentrate on these individuals, aiming to discover ways to reduce predatory behaviour in the most prolific hunters.

Overall, although cats are estimated to catch millions of prey in the UK, annually, there was no evidence that cats are solely responsible for any fluctuations in prey populations. Therefore, it is likely that prey species are adequately adapted to the presence of such terrestrial predators, despite the unnaturally high densities of cats in the UK. Where affected by cats, it is clear that this is one factor in a series of very complex interactions, and climatic

variables, as well as a relationship between cat density and other anthropogenic factors should also be considered.

References

ADAMEC, R. E. 1976. The interaction of hunger and preying in the domestic cat (*Felis catus*): An adaptive hierarchy? *Behavioral Biology,* 18(2)**,** 263-272.

AEGERTER, J., FOURACRE, D. & SMITH, G. C. 2017. A first estimate of the structure and density of the populations of pet cats and dogs across Great Britain. *PLOS ONE,* 12(4)**,** e0174709.

ALEXANDER, G. & MARAIS, J. 2007. *A Guide to the Reptiles of Southern Africa,* South Africa, Struik Nature.

ANCILLOTTO, L., SERANGELI, M. T. & RUSSO, D. 2013. Curiosity killed the bat: Domestic cats as bat predators. *Mammalian Biology,* 78(5)**,** 369-373.

ANDERSSON, M. & ERLINGE, S. 1977. Influence of predation on rodent populations. *Oikos,* 29(3)**,** 591-597.

ANDREASSEN, H. P., SUNDELL, J., ECKE, F., HALLE, S., HAAPAKOSKI, M., HENTTONEN, H., . . . YLÖNEN, H. 2021. Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia,* 195(3)**,** 601-622.

ANIMAL AND PLANT HEALTH AGENCY. 2016a. *Cat Population Per Postcode District* [Online]. Available: https://www.data.gov.uk/dataset/febd29ff-7e7d-4f82-9908-031f7f0e0860/cat-population-per-postcode-district [Accessed 23.09.2023].

ANIMAL AND PLANT HEALTH AGENCY. 2016b. *Cats Per Square Kilometre* [Online]. Available: https://www.data.gov.uk/dataset/9d475e06-3885-4a90-b8c0-77fea13f92e6/cats-per-square-kilometre [Accessed 23.09.2023].

ARTEAGA-TORRES, J. D., WIJMENGA, J. J. & MATHOT, K. J. 2020. Visual cues of predation risk outweigh acoustic cues: a field experiment in black-capped chickadees. *Proceedings of the Royal Society B-Biological Sciences,* 287(1936)**,** e20202002.

AVIVA. 2022. *Gardens Being Uprooted in Favour of Driveways and Artificial Grass, New Research Reveals* [Online]. Available: https://www.aviva.com/newsroom/news-releases/2022/07/gardens-being-uprooted-in-favour-of-driveways-and-artificial-grass-new-research-reveals/ [Accessed 01.05.2023].

BAILLIE, S. R., MARCHANT, J. H., LEECH, D. I., MASSIMINO, D., SULLIVAN, M. J. P., EGLINGTON, S. M., . . . ROBINSON, R. A. 2014. BirdTrends 2014: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds. Thetford: BTO.

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(1)**,** 95-100.

BAKER, P. J., BENTLEY, A. J., ANSELL, R. J. & HARRIS, S. 2005. Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review,* 35(3-4)**,** 302-312.

BAKER, P. J. & HARRIS, S. 2007. Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mammal Review,* 37(4)**,** 297-315.

BAKER, P. J., MOLONY, S. E., STONE, E., CUTHILL, I. C. & HARRIS, S. 2008. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? *Ibis,* 15086-99.

BAKER, S. E., MAW, S. A., JOHNSON, P. J. & MACDONALD, D. W. 2020. Not in my backyard: public perceptions of wildlife and 'pest control' in and around UK homes, and local authority 'pest control'. *Animals,* 10(2)**,** e222.

BARRATT, D. G. 1997. Predation by house cats, *Felis catus* (L), in Canberra, Australia .1. Prey composition and preference. *Wildlife Research,* 24(3)**,** 263-277.

BARRATT, D. G. 1998. Predation by house cats, *Felis catus* (L.), in Canberra, Australia. II. Factors affecting the amount of prey caught and estimates of the impact on wildlife. *Wildlife Research,* 25(5)**,** 475-487.

BAT CONSERVATION TRUST 2022. The National Bat Monitoring Programme Annual Report 2021. London: Bat Conservation Trust.

BEAUMONT, M., BARRATT, E. M., GOTTELLI, D., KITCHENER, A. C., DANIELS, M. J., PRITCHARD, J. K. & BRUFORD, M. W. 2001. Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology,* 10(2)**,** 319-336.

BECKERMAN, A. P., BOOTS, M. & GASTON, K. J. 2007. Urban bird declines and the fear of cats. *Animal Conservation,* 10(3)**,** 320-325.

BEGON, M., TOWNSEND, C. R. & HARPER, J. L. 2006. *Ecology: From Individuals to Ecosystems,* Oxford, Blackwell Publishing.

BELL, C. P., BAKER, S. W., PARKES, N. G., BROOKE, M. D. L. & CHAMBERLAIN, D. E. 2010. The role of the Eurasian sparrowhawk (*Accipiter nisus*) in the decline of the house sparrow (*Passer domesticus*) in Britain. *The Auk,* 127(2)**,** 411-420.

BELLOWS, J., CENTER, S., DARISTOTLE, L., ESTRADA, A. H., FLICKINGER, E. A., HORWITZ, D. F., . . . SHOVELLER, A. K. 2016. Evaluating aging in cats: How to determine what is healthy and what is disease. *Journal of Feline Medicine and Surgery,* 18(7)**,** 551-70.

BENDER, L. C. & ROSAS-ROSAS, O. C. 2016. Compensatory puma predation on adult female mule deer in New Mexico. *Journal of Mammalogy,* 97(5)**,** 1399-1405.

BERGSTROM, D. M., LUCIEER, A., KIEFER, K., WASLEY, J., BELBIN, L., PEDERSEN, T. K. & CHOWN, S. L. 2009. Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology,* 46(1)**,** 73-81.

BIBEN, M. 1979. Predation and predatory play behaviour of domestic cats. *Animal Behaviour,* 2781-94.

BIERMAN, STIJN M., FAIRBAIRN, JONATHAN P., PETTY, STEVE J., ELSTON, DAVID A., TIDHAR, D. & LAMBIN, X. 2006. Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). *The American Naturalist,* 167(4)**,** 583-590.

BIRDSBESAFE. 2019. *Birdsbesafe® Products: Highly Effective in UK Science Study* [Online]. Available: https://www.birdsbesafe.com/blogs/news/birdsbesafe-products-shown-to-be-highly-effective-in-science-study-in-scotland [Accessed 05.06.2020].

BIRÓ, Z., LANSZKI, J., SZEMETHY, L., HELTAI, M. & RANDI, E. 2005. Feeding habits of feral domestic cats (*Felis catus*), wild cats (*Felis silvestris*) and their hybrids: trophic niche overlap among cat groups in Hungary. *Journal of Zoology,* 266(2)**,** 187-196.

BLANCHER, P. 2013. Estimated number of birds killed by house cats (*Felis catus*) in Canada. *Avian Conservation and Ecology,* 8(2)**,** e3.

BLUE CROSS. 2022. *Cat Weight* [Online]. Available: https://www.bluecross.org.uk/advice/cat/food-and-weight/cat-weight#:~:text=An%20average%2C%20healthy%20moggy%20cat,from%203.6%20to%204.5%20kilograms. [Accessed 03.04.2023].

BONNAUD, E., BOURGEOIS, K., VIDAL, E., KAYSER, Y., TRANCHANT, Y. & LEGRAND, J. 2007. Feeding ecology of a feral cat population on a small Mediterranean island. *Journal of Mammalogy,* 88(4)**,** 1074-1081.

BONNAUD, E., MEDINA, F. M., VIDAL, E., NOGALES, M., TERSHY, B., ZAVALETA, E., . . . HORWATH, S. V. 2011. The diet of feral cats on islands: a review and a call for more studies. *Biological Invasions,* 13(3)**,** 581-603.

BONNINGTON, C., GASTON, K. J. & EVANS, K. L. 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *Journal of Applied Ecology,* 50(1)**,** 15-24.

BOTH, C., BOUWHUIS, S., LESSELLS, C. M. & VISSER, M. E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature,* 441(7089)**,** 81-83.

BRADLEY, C. A. & ALTIZER, S. 2007. Urbanization and the ecology of wildlife diseases. *Trends in Ecology & Evolution,* 22(2)**,** 95-102.

BRADSHAW, J. W. S., CASEY, R. A. & BROWN, S. L. 2012. *The Behaviour of the Domestic Cat,* Oxfordshire, UK, CABI.

BRICKNER-BRAUN, I., GEFFEN, E. & YOM-TOV, Y. 2007. The domestic cat as a predator of Israeli wildlife. *Israel Journal of Ecology & Evolution,* 53(2)**,** 129-142.

BRUCE, S. J., ZITO, S., GATES, M. C., AGUILAR, G., WALKER, J. K., GOLDWATER, N. & DALE, A. 2019. Predation and risk behaviors of free-roaming owned cats in Auckland, New Zealand via the use of animal-borne cameras. *Frontiers in Veterinary Science,* 6(205)**,** 1-12.

BRÜHL, C. A., BAKANOV, N., KÖTHE, S., EICHLER, L., SORG, M., HÖRREN, T., . . . LEHMANN, G. U. C. 2021. Direct pesticide exposure of insects in nature conservation areas in Germany. *Scientific Reports,* 11(1)**,** e24144.

BTO. 2011. *Maps of Population Density and Trends* [Online]. Available: https://www.bto.org/our-science/projects/bbs/latest-results/maps-population-density-and-trends [Accessed 23.09.2023].

BTO. 2020. *BirdTrends: Breeding Bird Survey* [Online]. Available: https://www.bto.org/our-science/publications/birdtrends/2019/methods/breeding-bird-survey [Accessed 30.07.2023].

BTO. 2023a. *BirdFacts: Blackbird Biometrics* [Online]. Available: https://www.bto.org/understanding-birds/birdfacts/blackbird [Accessed 13.06.2023].

BTO. 2023b. *BirdFacts: Species Pages* [Online]. Available: https://www.bto.org/understanding-birds/welcome-birdfacts [Accessed 01.07.2023].

BTO 2023c. Breeding Bird Survey Count Data for Years 2000 and 2015 (Data Provided by BTO). *BTO.* Thetford.

BURGESS, M. D., SMITH, K. W., EVANS, K. L., LEECH, D., PEARCE-HIGGINS, J. W., BRANSTON, C. J., . . . PHILLIMORE, A. B. 2018. Tritrophic phenological match–mismatch in space and time. *Nature Ecology & Evolution,* 2(6)**,** 970-975.

BURKMAR, R. 2023. *TomBio Tools Plugin for QGIS 3.22* [Online]. Field Studies Council. Available: https://plugins.qgis.org/plugins/TomBio/ [Accessed 23.09.2023].

CALVER, M., THOMAS, S., BRADLEY, S. & MCCUTCHEON, H. 2007. Reducing the rate of predation on wildlife by pet cats: The efficacy and practicability of collar-mounted pounce protectors. *Biological Conservation,* 137(3)**,** 341-348.

CAMERON, R. 2023. "Do we need to see gardens in a new light?" Recommendations for policy and practice to improve the ecosystem services derived from domestic gardens. *Urban Forestry & Urban Greening,* 80e127820.

CANNON, A. R. 2005. *Wild Birds in Urban Gardens: Opportunity or Constraint?* PhD, University of Sheffield.

CANTY, A. & RIPLEY, B. D. 2022. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-28.1.

CAPILLA-LASHERAS, P., THOMPSON, M. J., SÁNCHEZ-TÓJAR, A., HADDOU, Y., BRANSTON, C. J., RÉALE, D., . . . DOMINONI, D. M. 2022. A global meta-analysis reveals higher variation in breeding phenology in urban birds than in their non-urban neighbours. *Ecology Letters,* 25(11)**,** 2552-2570.

CAPSTICK, L. A., SAGE, R. B. & MADDEN, J. R. 2019. Predation of artificial nests in UK farmland by magpies (*Pica pica*): interacting environmental, temporal, and social factors influence a nest's risk. *European Journal of Wildlife Research,* 65(3)**,** e50.

CARRION, P. L. & VALLE, C. A. 2018. The diet of introduced cats on San Cristobal Island, Galapagos: cat feces as a proxy for cat predation. *Mammalian Biology,* 9074-77.

CARSS, D. N. 1995. Prey brought home by two cats (*Felis catus*) in northern Scotland. *Journal of Zoology,* 237(4)**,** 678-686.

CASPER, R. M. 2009. Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour,* 78(6)**,** 1477-1483.

CASTAÑEDA, I., DOHERTY, T. S., FLEMING, P. A., STOBO-WILSON, A. M., WOINARSKI, J. C. Z. & NEWSOME, T. M. 2022. Variation in red fox *Vulpes vulpes* diet in five continents. *Mammal Review,* 52(3)**,** 328-342.

CECCHETTI, M., CROWLEY, S. L., GOODWIN, C. E. D. & MCDONALD, R. A. 2021. Provision of high meat content food and object play reduce predation of wild animals by domestic cats *Felis catus*. *Current Biology,* 31(5)**,** e5.

CEH. 2017. *Land Cover Map 2015: Dataset Documentation* [Online]. Available: https://www.ceh.ac.uk/sites/default/files/LCM2015_Dataset_Documentation.pdf [Accessed 30.07.2023].

CHAMBERLAIN, D. E., CANNON, A. R. & TOMS, M. P. 2004. Associations of garden birds with gradients in garden habitat and local habitat. *Ecography,* 27(5)**,** 589-600.

CHAMBERLAIN, D. E., CANNON, A. R., TOMS, M. P., LEECH, D. I., HATCHWELL, B. J. & GASTON, K. J. 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis,* 151(1)**,** 1-18.

CHARRAD, M., GHAZZALI, N., BOITEAU, V. & NIKNAFS, A. 2014. NbClust: an R package for determining the relevant number of clusters in a data set. *Journal of Statistical Software,* 61(6)**,** 1-36.

CHURCHER, P. & LAWTON, J. 1987. Predation by domestic cats in an English village. *Journal of Zoology,* 212439-455.

CLEGG, C. 2017. *The Scottish Wildcat,* Shropshire, UK, Merlin Unwin Books.

COCKBURN, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences,* 273(1592)**,** 1375-1383.

COGGER, H. 2018. *Reptiles and Amphibians of Australia,* Victoria, CSIRO Publishing.

COOMBER, F. G., SMITH, B. R., AUGUST, T. A., HARROWER, C. A., POWNEY, G. D. & MATHEWS, F. 2021. Using biological records to infer long-term occupancy trends of mammals in the UK. *Biological Conservation,* 264e109362.

COOPER, D. S., SHULTZ, A. J., ŞEKERCIOĞLU, Ç. H., OSBORN, F. M. & BLUMSTEIN, D. T. 2022. Community science data suggest the most common raptors (Accipitridae) in urban centres are smaller, habitat-generalist species. *Ibis,* 164(3)**,** 771-784.

CORBETT, L. K. 1979. *Feeding Ecology and Social Organization of Wildcats (Felis silvestris) and Domestic Cats (Felis catus) in Scotland.* PhD, University of Aberdeen.

CORNULIER, T., YOCCOZ, N. G., BRETAGNOLLE, V., BROMMER, J. E., BUTET, A., ECKE, F., . . . LAMBIN, X. 2013. Europe-wide dampening of population cycles in keystone herbivores. *Science,* 340(6128)**,** 63-66.

COUGHLIN, C. E. & VAN HEEZIK, Y. 2015. Weighed down by science: do collar-mounted devices affect domestic cat behaviour and movement? *Wildlife Research,* 41(7)**,** 606-614.

COURCHAMP, F., CHAPUIS, J.-L. & PASCAL, M. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews,* 78(3)**,** 347-383.

COUZENS, D., SWASH, A., STILL, R. & DUNN, J. 2017. *Britain's Mammals,* Oxford, Princeton University Press.

COVE, M. V., GARDNER, B., SIMONS, T. R., KAYS, R. & O'CONNELL, A. F. 2018. Free-ranging domestic cats (*Felis catus*) on public lands: estimating density, activity, and diet in the Florida Keys. *Biological Invasions,* 20(2)**,** 333-344.

CRAWFORD, H., CALVER, M. & FLEMING, P. 2020. Subsidised by junk foods: factors influencing body condition in stray cats (*Felis catus*). *Journal of Urban Ecology,* 6(1)**,** e4.

DADAM, D., ROBINSON, R. A., CLEMENTS, A., PEACH, W. J., BENNETT, M., ROWCLIFFE, J. M. & CUNNINGHAM, A. A. 2019. Avian malaria-mediated population decline of a widespread iconic bird species. *Royal Society Open Science,* 6(7)**,** e182197.

DAVIES, Z. G., FULLER, R. A., DALLIMER, M., LORAM, A. & GASTON, K. J. 2012. Household factors influencing participation in bird feeding activity: a national scale analysis. *PLOS ONE,* 7(6)**,** e39692.

DEPARTMENT FOR LEVELLING UP HOUSING AND COMMUNITIES. 2022. *Land Use Statistics: England 2022* [Online]. Available: https://www.gov.uk/government/statistics/land-use-in-england-2022/land-use-statistics-england-2022 [Accessed 13.04.2023].

DEPARTMENT FOR TRANSPORT. 2022. *Road Length Statistics (RDL): Road length (Miles) by Road Type in Great Britain* [Online]. Available: https://www.gov.uk/government/statistical-data-sets/road-length-statistics-rdl [Accessed 09.05.2023].

DICKINSON, E. R., STEPHENS, P. A., MARKS, N. J., WILSON, R. P. & SCANTLEBURY, D. M. 2020. Best practice for collar deployment of tri-axial accelerometers on a terrestrial quadruped to provide accurate measurement of body acceleration. *Animal Biotelemetry,* 8(1)**,** e9.

DICKMAN, C. R. & NEWSOME, T. M. 2015. Individual hunting behaviour and prey specialisation in the house cat Felis catus: Implications for conservation and management. *Applied Animal Behaviour Science,* 17376-87.

DIETZ, C. & KIEFER, A. 2018. *Bats of Britain and Europe,* London, Bloomsbury Publishing.

DOHERTY, T. S., GLEN, A. S., NIMMO, D. G., RITCHIE, E. G. & DICKMAN, C. R. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America,* 113(40)**,** 11261-11265.

DONALD, P. F., GREEN, R. E. & HEATH, M. F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 268(1462)**,** 25-29.

DOWDING, C. V., SHORE, R. F., WORGAN, A., BAKER, P. J. & HARRIS, S. 2010. Accumulation of anticoagulant rodenticides in a non-target insectivore, the European hedgehog (*Erinaceus europaeus*). *Environmental Pollution,* 158(1)**,** 161-166.

DRISCOLL, C. A., MENOTTI-RAYMOND, M., ROCA, A. L., HUPE, K., JOHNSON, W. E., GEFFEN, E., . . . MACDONALD, D. W. 2007. The Near Eastern origin of cat domestication. *Science,* 317(5837)**,** 519-23.

DUNN, E. H. & TESSAGLIA, D. L. 1994. Predation of birds at feeders in winter. *Journal of Field Ornithology,* 65(1)**,** 8-16.

DUNN, J. C., HAMER, K. C. & BENTON, T. G. 2010. Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. *Journal of Applied Ecology,* 47(5)**,** 994-1002.

ELIZONDO, E. C. & LOSS, S. R. 2016. Using trail cameras to estimate free-ranging domestic cat abundance in urban areas. *Wildlife Biology,* 22(5)**,** 246-252.

ERICKSON, W. P., JOHNSON, G. D. & YOUNG, D. P. J. 2005. A Summary and Comparison of Bird Mortality from Anthropogenic Causes with an Emphasis on Collisions. *In:* RALPH, C. J. & RICH, T. D. (eds.) *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. 2002 March 20-24; Asilomar, California, Volume 1.* U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

ESRI. 2023. *How Inverse Distance Weighted Interpolation Works* [Online]. Available: https://pro.arcgis.com/en/pro-app/latest/help/analysis/geostatistical-analyst/how-inverse-distance-weighted-interpolation-works.htm [Accessed 02.09.2023].

EYENIMAL. 2022. *Num'axes Eyenimal* [Online]. Available: https://www.numaxes.com/en/ [Accessed 19.04.2022].

EYRING, V., GILLETT, N. P., ACHUTA RAO, K. M., BARIMALALA, R., BARREIRO PARILLO, M., BELLOUIN, N., . . . SUN, Y. 2021. Human Influence on the Climate System. *In:* MASSON-DELMOTTE, V., ZHAI, P., PIRANI, A., CONNORS, S. L., PÉAN, C., BERGER, S., CAUD, N., CHEN, Y., GOLDFARB, L., GOMIS, M. I., HUANG, M., LEITZELL, K., LONNOY, E., MATTHEWS, J. B. R., MAYCOCK, T. K., WATERFIELD, T., YELEKÇI, O., YU, R. & ZHOU, B. (eds.) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge: Cambridge University Press.

FELIWAY. 2022. *Feliway* [Online]. Available: https://www.feliway.com/uk [Accessed 18.04.2022].

FINDLAY-ROBINSON, R., DEECKE, V. B., WEATHERALL, A. & HILL, D. L. 2023. Effects of climate change on life-history traits in hibernating mammals. *Mammal Review,* 53(2)**,** 84-98.

FINKA, L. R., WARD, J., FARNWORTH, M. J. & MILLS, D. S. 2019. Owner personality and the wellbeing of their cats share parallels with the parent-child relationship. *PLoS One,* 14(2)**,** e0211862.

FIRBANK, L. G., PETIT, S., SMART, S., BLAIN, A. & FULLER, R. J. 2007. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363(1492)**,** 777-787.

FISCHER, J. D., CLEETON, S. H., LYONS, T. P. & MILLER, J. R. 2012. Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *BioScience,* 62(9)**,** 809-818.

FITZGERALD, B. M., KARL, B. J. & VEITCH, C. R. 1991. The diet of feral cats (*Felis catus*) on Raoul Island, Kermadec Group. *New Zealand Journal of Ecology,* 15(2)**,** 123-129.

FLUX, J. E. C. 2007. Seventeen years of predation by one suburban cat in New Zealand. *New Zealand Journal of Zoology,* 34(4)**,** 289-296.

FOREMAN-WORSLEY, R., FINKA, L. R., WARD, S. J. & FARNWORTH, M. J. 2021. Indoors or outdoors? An international exploration of owner demographics and decision making associated with lifestyle of pet cats. *Animals (Basel),* 11(2)**,** e253.

FORRESTER, D. J. & FOSTER, G. W. 2008. Trichomonosis. *In:* ATKINSON, C. T., THOMAS, N. J. & HUNTER, D. B. (eds.) *Parasitic Diseases of Wild Birds.* USA: Wiley-Blackwell.

FOSTER, J., DRIVER, D., WARD, R. & WILKINSON, J. 2021. IUCN Red List Assessment of Amphibians and Reptiles at Great Britain and Country Scale. *Report to Natural England.* Bournemouth: ARC.

FRANK, A. S. K., JOHNSON, C. N., POTTS, J. M., FISHER, A., LAWES, M. J., WOINARSKI, J. C. Z., . . . LEGGE, S. 2014. Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. *Journal of Applied Ecology,* 51(6)**,** 1486-1493.

FRIEDLINGSTEIN, P., O'SULLIVAN, M., JONES, M. W., ANDREW, R. M., GREGOR, L., HAUCK, J., . . . ZHENG, B. 2022. Global Carbon Budget 2022. *Earth Syst. Sci. Data,* 14(11)**,** 4811-4900.

FULLER, R. A., IRVINE, K. N., DAVIES, Z. G., ARMSWORTH, P. R. & GASTON, K. J. 2012. Interactions between People and Birds in Urban Landscapes. *In:* LEPCZYK, C. A. & WARREN, P. S. (eds.) *Urban Bird Ecology and Conservation.* Oakland, CA: University of California Press.

FULLER, R. M., SMITH, G. M., SANDERSON, J. M., HILL, R. A., THOMSON, A. G., COX, R., . . . GERARD, F. F. 2002. *Land Cover Map 2000 (1km Dominant Aggregate Class, GB).* [Online]. Available: https://doi.org/10.5285/b8b8a266-9162-40d8-98a6-f44178d31543 [Accessed 16.07.2023].

FURNESS, E. N. & ROBINSON, R. A. 2018. Long-term declines in winter body mass of tits throughout Britain and Ireland correlate with climate change. *Ecology and Evolution,* 91202 - 1210.

GEORGE, W. G. 1974. Domestic cats as predators and factors in winter shortages of raptor prey. *The Wilson Bulletin,* 86(4)**,** 384-396.

GERMAIN, E., RUETTE, S. & POULLE, M.-L. 2009. Likeness between the food habits of European wildcats, domestic cats and their hybrids in France. *Mammalian Biology,* 74(5)**,** 412-417.

GIBBONS, D. W., AMAR, A., ANDERSON, G. Q. A., BOLTON, M., BRADBURY, R. B., EATON, M., . . . WILSON, J. D. 2007. Predation of Wild Birds in the UK: A Review of its Conservation Impact and Management. *RSPB Research Report no.23.* Sandy: RSPB.

GILLIES, C. & CLOUT, M. 2003. The prey of domestic cats (*Felis catus*) in two suburbs of Auckland City, New Zealand. *Journal of Zoology,* 259309-315.

GILLINGS, S. 2019. Bird responses to housing development in intensively managed agricultural landscapes. *Urban Ecosystems,* 22(6)**,** 1007-1017.

GLĄDALSKI, M., BAŃBURA, M., KALIŃSKI, A., MARKOWSKI, M., SKWARSKA, J., WAWRZYNIAK, J., . . . BAŃBURA, J. 2016. Effects of human-related disturbance on breeding success of urban and non-urban blue tits (*Cyanistes caeruleus*). *Urban Ecosystems,* 19(3)**,** 1325-1334.

GOAD, R., MASI, S. & VITT, P. 2020. Retaining citizen scientists. *In:* LEPCZYK, C. A., BOYLE, O. D. & VARGO, T. L. V. (eds.) *Handbook of citizen science in ecology and conservation.* California: University of California Press.

GOOGLE TRENDS. 2023. *'Artificial Grass': Interest Over Time* [Online]. Available: https://trends.google.com/trends/explore?date=2015-01-04%202023-05-01&geo=GB&gprop=froogle&q=artificial%20grass&hl=en-GB [Accessed 01.05.2023].

GORDON, J. K., MATTHAEI, C. & VAN HEEZIK, Y. 2010. Belled collars reduce catch of domestic cats in New Zealand by half. *Wildlife Research,* 37(5)**,** 372-378.

GORMAN, M. L. & TROWBRIDGE, B. J. 1989. The Role of Odor in the Social Lives of Carnivores. *In:* GITTLEMAN, J. L. (ed.) *Carnivore Behavior, Ecology, and Evolution.* Boston, MA: Springer US.

GOVERNMENT OFFICE FOR SCIENCE. 2021. *Trend Deck 2021: Urbanisation* [Online]. Available: https://www.gov.uk/government/publications/trend-deck-2021-urbanisation/trend-deck-2021-urbanisation [Accessed 13.04.2023].

GURNELL, J. & FLOWERDEW, J. 2019. *Live Trapping Small Mammals. A Practical Guide,* England, The Mammal Society.

HALL, C. M., ADAMS, N. A., BRADLEY, J. S., BRYANT, K. A., DAVIS, A. A., DICKMAN, C. R., . . . CALVER, M. C. 2016. Community attitudes and practices of urban residents regarding predation by pet cats on wildlife: an international comparison. *Plos One,* 11(4)**,** e0151962.

HALUPKA, L., BOROWIEC, M., NEUBAUER, G. & HALUPKA, K. 2021. Fitness consequences of longer breeding seasons of a migratory passerine under changing climatic conditions. *Journal of Animal Ecology,* 90(7)**,** 1655-1665.

HANMER, H. J., CUNNINGHAM, A. A., JOHN, S. K., MAGREGOR, S. K., ROBINSON, R. A., SEILERN-MOY, K., . . . LAWSON, B. 2022. Habitat-use influences severe disease-mediated population declines in two of the most common garden bird species in Great Britain. *Scientific Reports,* 12(1)**,** e15055.

HANMER, H. J., THOMAS, R. L. & FELLOWES, M. D. E. 2017. Provision of supplementary food for wild birds may increase the risk of local nest predation. *Ibis,* 159(1)**,** 158-167.

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,* Peterborough, JNCC.

HARRIS, S. J., MASSIMINO, D., BALMER, D. E., KELLY, L., NOBLE, D. G., PEARCE-HIGGINS, J. W., . . . GILLINGS, S. 2022. *The Breeding Bird Survey 2021,* Thetford, British Trust for Ornithology.

HERNANDEZ, S. M., LOYD, K. A. T., NEWTON, A. N., CARSWELL, B. L. & ABERNATHY, K. J. 2018. The use of point-of-view cameras (Kittycams) to quantify predation by colony cats (*Felis catus*) on wildlife. *Wildlife Research,* 45(4)**,** 357-365.

HIJMANS, R. J., PHILLIPS, S., LEATHWICK, J. & ELITH, J. 2023. dismo package: Species Distribution Modelling. R package version 1.3-14.

HOLDEN, P. & CLEEVES, T. 2014. *RSPB Handbook of British Birds,* London, Bloomsbury Publishing.

HOLE, D. G., WHITTINGHAM, M. J., BRADBURY, R. B., ANDERSON, G. Q. A., LEE, P. L. M., WILSON, J. D. & KREBS, J. R. 2002. Widespread local house-sparrow extinctions. *Nature,* 418(6901)**,** 931-932.

HOLLIS, D., MCCARTHY, M., KENDON, M., LEGG, T. & SIMPSON, I. 2019. HadUK-Grid—A new UK dataset of gridded climate observations. *Geoscience Data Journal,* 6(2)**,** 151-159.

HOWES, C. A. 2002. Red in tooth and claw: 2 studies on the natural history of the domestic cat *Felis catus* Lin. in Yorkshire. *The Naturalist,* 127101-130.

HOY, S. R., PETTY, S. J., MILLON, A., WHITFIELD, D. P., MARQUISS, M., DAVISON, M. & LAMBIN, X. 2015. Age and sex-selective predation moderate the overall impact of predators. *Journal of Animal Ecology,* 84(3)**,** 692-701.

HUCK, M. 2022. *RE: Personal Communication. Behavioural assessment of cats wearing collar-mounted cameras.*

HUCK, M. & WATSON, S. 2019. The use of animal-borne cameras to video-track the behaviour of domestic cats. *Applied Animal Behaviour Science,* 21763-72.

HUME, R., STILL, R., SWASH, A., HARROP, H. & TIPLING, D. 2016. *Britain's Birds,* Oxford, Princeton University Press.

HUTCHINGS, S. 2003. The diet of feral house cats (*Felis catus*) at a regional rubbish tip, Victoria. *Wildlife Research,* 30(1)**,** 103-110.

INNS, H. 2009. *Britain's Reptiles and Amphibians,* Hampshire, UK, WildGuides.

IPCC. 2022. *Climate Change 2022: Impacts, Adaptation and Vulnerability* [Online]. Available: https://www.ipcc.ch/report/ar6/wg2/downloads/report/IPCC_AR6_WGII_FullReport.pdf [Accessed 07.07.2023].

IUCN. 2020. *Mammals of New Zealand* [Online]. Available: https://www.iucnredlist.org/search/list?landRegions=NZ&searchType=species [Accessed 01.09.2020].

JAMES, G., WITTEN, D., HASTIE, T. & TIBSHIRANI, R. 2022. *An Introduction to Statistical Learning: with Applications in R,* New York, Springer.

JANSSON, C., EKMAN, J. & VON BRÖMSSEN, A. 1981. Winter mortality and food supply in tits Parus spp. *Oikos,* 37(3)**,** 313-322.

JONES, H. P., TERSHY, B. R., ZAVALETA, E. S., CROLL, D. A., KEITT, B. S., FINKELSTEIN, M. E. & HOWALD, G. R. 2008. Severity of the effects of invasive rats on seabirds: a Global review. *Conservation Biology,* 22(1)**,** 16-26.

JONES, N. 2020. *How to Let Your Kitten Outside* [Online]. Available: https://www.petplan.co.uk/pet-information/kitten/advice/safety-precautions-for-taking-kittens-outside/ [Accessed 04.08.2022].

KAREKLAS, K., WILSON, J., KUNC, H. P. & ARNOTT, G. 2019. Signal complexity communicates aggressive intent during contests, but the process is disrupted by noise. *Biology Letters,* 15(4)**,** e20180841.

KAUHALA, K., TALVITIE, K. & VUORISALO, T. 2015. Free-ranging house cats in urban and rural areas in the north: useful rodent killers or harmful bird predators? *Folia Zoologica,* 64(1)**,** 45-55.

KAYS, R. W. & DEWAN, A. A. 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. *Animal Conservation,* 7273-283.

KILSHAW, K., JOHNSON, P. J., KITCHENER, A. C. & MACDONALD, D. W. 2015. Detecting the elusive Scottish wildcat *Felis silvestris silvestris* using camera trapping. *Oryx,* 49(2)**,** 207-215.

KITTS-MORGAN, S. E., CAIRES, K. C., BOHANNON, L. A., PARSONS, E. I. & HILBURN, K. A. 2015. Free-ranging farm cats: home range size and predation on a livestock unit In northwest Georgia. *Plos One,* 10(4)**,** e0120513.

KOIVISTO, E., SANTANGELI, A., KOIVISTO, P., KORKOLAINEN, T., VUORISALO, T., HANSKI, I. K., . . . KOIVISTO, S. 2018. The prevalence and correlates of anticoagulant rodenticide exposure in non-target predators and scavengers in Finland. *Science of The Total Environment,* 642(2018)**,** 701-707.

KRAUZE-GRYZ, D., GRYZ, J. & GOSZCZYNSKI, J. 2012. Predation by domestic cats in rural areas of central Poland: an assessment based on two methods. *Journal of Zoology,* 288(4)**,** 260-266.

KRAUZE-GRYZ, D., ZMIHORSKI, M. & GRYZ, J. 2017. Annual variation in prey composition of domestic cats in rural and urban environment. *Urban Ecosystems,* 20(4)**,** 945-952.

KUTT, A. S. 2011. The diet of the feral cat (*Felis catus*) in north-eastern Australia. *Acta Theriologica,* 56(2)**,** 157-169.

LAWSON, B., ROBINSON, R. A., TOMS, M. P., RISELY, K., MACDONALD, S. & CUNNINGHAM, A. A. 2018. Health hazards to wild birds and risk factors associated with anthropogenic food provisioning. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1745)**,** e20170091.

LEGGE, S., WOINARSKI, J. C. Z., DICKMAN, C. R., MURPHY, B. P., WOOLLEY, L.-A. & CALVER, M. C. 2020. We need to worry about Bella and Charlie: the impacts of pet cats on Australian wildlife. *Wildlife Research,* 47(8)**,** 523-539.

LEISCH, F. 2006. A Toolbox for K-Centroids Cluster Analysis. *Computational Statistics and Data Analysis,* 51(2)**,** 526-544.

LEPCZYK, C. A., MERTIG, A. G. & LIU, J. G. 2004. Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation,* 115(2)**,** 191-201.

LEYHAUSEN, P. 1979. *Cat Behaviour: The Predatory and Social Behaviour of Domestic and Wild Cats,* New York, Garland Publishing.

LIBERG, O., SANDELL, M., PONTIER, D. & NATOLI, E. 2000. Density, Spatial Organisation and Reproductive Tactics in the Domestic Cat and Other Felids. *In:* TURNER, D. & BATESON, P. (eds.) *The Domestic Cat: The Biology of its Behaviour.* Cambridge: Cambridge University Press.

LIU, F. & KONG, Y. 2019. zoib: Bayesian Inference for Beta Regression and Zero-or-One Inflated Beta Regression. R package version 1.6.

LIU, Z., HE, C. & WU, J. 2016. The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities. *PLOS ONE,* 11(4)**,** e0154613.

LIVERPOOL, L. 2020. Put That Down, Kitty. *New Scientist.* London: New Scientist.

LONGLEY, P. A., GOODCHILD, M. F., MAGUIRE, D. J. & RHIND, D. W. 2011. *Geographic Information Systems and Science,* USA, John Wiley & Sons.

LORAM, A., TRATALOS, J., WARREN, P. H. & GASTON, K. J. 2007. Urban domestic gardens (X): the extent & structure of the resource in five major cities. *Landscape Ecology,* 22(4)**,** 601-615.

LOSS, S. R. & MARRA, P. P. 2017. Population impacts of free-ranging domestic cats on mainland vertebrates. *Frontiers in Ecology and the Environment,* 15(9)**,** 502-509.

LOSS, S. R., WILL, T. & MARRA, P. P. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications,* 4e1396.

LOVELL, C., LI, S., TURNER, J. & CARBONE, C. 2022. The effect of habitat and human disturbance on the spatiotemporal activity of two urban carnivores: The results of an intensive camera trap study. *Ecology and Evolution,* 12(3)**,** e8746.

LOYD, K. A. T. 2023. *RE: Detailed data collected in Athens County, Georgia for PhD study.*

LOYD, K. A. T., HERNANDEZ, S. M., CARROLL, J. P., ABERNATHY, K. J. & MARSHALL, G. J. 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation,* 160183-189.

LU, D., ZHOU, C. & LIAO, W. B. 2014. Sexual size dimorphism lacking in small mammals. *North-Western Journal of Zoology,* 1053-59.

MAK, B., FRANCIS, R. A. & CHADWICK, M. A. 2021. Living in the concrete jungle: a review and socio-ecological perspective of urban raptor habitat quality in Europe. *Urban Ecosystems,* 24(6)**,** 1179-1199.

MALLORD, J. W., ORSMAN, C. J., CRISTINACCE, A., STOWE, T. J., CHARMAN, E. C. & GREGORY, R. D. 2017. Diet flexibility in a declining long-distance migrant may allow it to escape the consequences of phenological mismatch with its caterpillar food supply. *Ibis,* 159(1)**,** 76-90.

MARROT, P., CHARMANTIER, A., BLONDEL, J. & GARANT, D. 2018. Current spring warming as a driver of selection on reproductive timing in a wild passerine. *Journal of Animal Ecology,* 87(3)**,** 754-764.

MARROT, P., GARANT, D. & CHARMANTIER, A. 2017. Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 372(1723)**,** e20160372.

MARTAY, B., LEECH, D. I., SHORTALL, C. R., BELL, J. R., THACKERAY, S. J., HEMMING, D. L. & PEARCE-HIGGINS, J. W. 2023. Aerial insect biomass, but not phenological mismatch, is associated with chick survival of an insectivorous bird. *Ibis,* 165(3)**,** 790-807.

MARTAY, B. & NOBLE, D. 2022. Scoping the Feasibility of Developments to the Terrestrial Bird Indicator for Scotland – Urban, Farmland and Wetland Indicators. *NatureScot Research Report 1300.* Scotland.

MASSIMINO, D., WOODWARD, I. D., HAMMOND, M. J., BARBER, L., BARIMORE, C., HARRIS, S. J., . . . ROBINSON, R. A. 2022. BirdTrends 2021: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds. *BTO Research Report 732.* Thetford: BTO.

MATHEWS, F. & HARROWER, C. 2020. *IUCN–Compliant Red List for Britain's Terrestrial Mammals. Assessment by the Mammal Society Under Contract to Natural England, Natural Resources Wales and Scottish Natural Heritage,* Peterborough, Natural England.

MATHEWS, F., KUBASIEWICZ, L. M., GURNELL, J., HARROWER, C., MCDONALD, R. A. & SHORE, R. F. 2018. A review of the population and conservation status of British mammals: technical summary. A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Peterborough: Natural England.

MATIAS, R. & CATRY, P. 2008. The diet of feral cats at New Island, Falkland Islands, and impact on breeding seabirds. *Polar Biology,* 31(5)**,** 609-616.

MCCLEERY, R., MONADJEM, A., CONNER, L. M., SAUSTIN, J. D. & TAYLOR, P. J. 2021. *Methods for Ecological Research on Terrestrial Small Mammals,* Baltimore, Johns Hopkins University Press.

MCDONALD, J. L., MACLEAN, M., EVANS, M. R. & HODGSON, D. J. 2015. Reconciling actual and perceived rates of predation by domestic cats. *Ecology and Evolution,* 5(14)**,** 2745-2753.

MCGREGOR, H., LEGGE, S., JONES, M. E. & JOHNSON, C. N. 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *Plos One,* 10(8)**,** e0133915.

MCKINNEY, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems,* 11(2)**,** 161-176.

MEAD, C. J. 1982. Ringed birds killed by cats. *Mammal Review,* 12(4)**,** 183-186.

MEDINA, F. M., BONNAUD, E., VIDAL, E., TERSHY, B. R., ZAVALETA, E. S., DONLAN, C. J., . . . NOGALES, M. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology,* 17(11)**,** 3503-3510.

MEDINA, F. M., LOPEZ-DARIAS, M., NOGALES, M. & GARCIA, R. 2008. Food habits of feral cats (*Felis silvestris catus* L.) in insular semiarid environments (Fuerteventura, Canary Islands). *Wildlife Research,* 35(2)**,** 162-169.

MELLA-MÉNDEZ, I., FLORES-PEREDO, R., AMAYA-ESPINEL, J. D., BOLÍVAR-CIMÉ, B., MAC SWINEY G, M. C. & MARTÍNEZ, A. J. 2022. Predation of wildlife by domestic cats in a Neotropical city: a multi-factor issue. *Biological Invasions,* 24(5)**,** 1539-1551.

MENZEL, A., SPARKS, T. H., ESTRELLA, N., KOCH, E., AASA, A., AHAS, R., . . . ZUST, A. N. A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology,* 12(10)**,** 1969-1976.

MERRITT, J. F. 2010. *The Biology of Small Mammals,* USA, Johns Hopkins University Press.

MET OFFICE. 2023. *Effects of Climate Change* [Online]. Available: https://www.metoffice.gov.uk/weather/climate-change/effects-of-climate-change [Accessed 07.07.2023].

MET OFFICE, HOLLIS, D., MCCARTHY, M., KENDON, M., LEGG, T. & SIMPSON, I. 2018. *HadUK-Grid Gridded and Regional Average Climate Observations for the UK* [Online]. Centre for Environmental Data Analysis. Available: http://catalogue.ceda.ac.uk/uuid/4dc8450d889a491ebb20e724debe2dfb [Accessed 05.07.2023].

MILLÁN, J. 2010. Feeding habits of feral cats *Felis silvestris catus* in the countryside of Majorca Island, Spain. *Wildlife Biology in Practice,* 6(1)**,** 32-38.

MITCHELL, J. C. & BECK, R. A. 1992. Free-ranging domestic cat predation on native vertebrates in rural and urban Virginia. *Virginia Journal of Science,* 43197-208.

MØLLER, A. P., CZESZCZEWIK, D., FLENSTED-JENSEN, E., ERRITZØE, J., KRAMS, I., LAURSEN, K., . . . WALANKIEWICZ, W. 2021. Abundance of insects and aerial insectivorous birds in relation to pesticide and fertilizer use. *Avian Research,* 12(1)**,** e43.

MØLLER, A. P. & ERRITZØE, J. 2000. Predation against birds with low immunocompetence. *Oecologia,* 122(4)**,** 500-504.

MØLLER, A. P. & IBANEZ-ALAMO, J. D. 2012. Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour,* 84(2)**,** 341-348.

MOLSHER, R., NEWSOME, A. & DICKMAN, C. 1999. Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research,* 26(5)**,** 593-607.

MORELAND CITY COUNCIL. 2022. *Impacts of a Cat Curfew* [Online]. Available: https://conversations.moreland.vic.gov.au/cat-curfew/impacts-cat-curfew [Accessed 31.05.2022].

MORGAN, S. A., HANSEN, C. M., ROSS, J. G., HICKLING, G. J., OGILVIE, S. C. & PATERSON, A. M. 2009. Urban cat (*Felis catus*) movement and predation activity associated with a wetland reserve in New Zealand. *Wildlife Research,* 36(7)**,** 574-580.

MORGANTI, M., ASSANDRI, G., AGUIRRE, J. I., RAMIREZ, Á., CAFFI, M. & PULIDO, F. 2017. How residents behave: home range flexibility and dominance over migrants in a Mediterranean passerine. *Animal Behaviour,* 123(1)**,** 293-304.

MURRAY, J. K. & GRUFFYDD-JONES, T. J. 2012. Proportion of pet cats registered with a veterinary practice and factors influencing registration in the UK. *Veterinary Journal,* 192(3)**,** 461-466.

MURRAY, J. K., GRUFFYDD-JONES, T. J., ROBERTS, M. A. & BROWNE, W. J. 2015. Assessing changes in the UK pet cat and dog populations: numbers and household ownership. *Veterinary Record,* 177(10)**,** e259.

NAGY, K. A., GIRARD, I. A. & BROWN, T. K. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition,* 19(1)**,** 247-77.

NASA. 2023. *World of Change: Global Temperatures* [Online]. Available: https://earthobservatory.nasa.gov/world-of-change/global-temperatures [Accessed 06.07.2023].

NELSON, S. H., EVANS, A. D. & BRADBURY, R. B. 2005. The efficacy of collar-mounted devices in reducing the rate of predation of wildlife by domestic cats. *Applied Animal Behaviour Science,* 94(3-4)**,** 273-285.

NEWMAN, C. & MACDONALD, D. W. 2015. The Implications of Climate Change for Terrestrial UK Mammals. *Living With Environmental Change Partnership.* Oxford: NERC.

NEWSON, S. E., OCKENDON, N., JOYS, A., NOBLE, D. G. & BAILLIE, S. R. 2009. Comparison of habitat-specific trends in the abundance of breeding birds in the UK. *Bird Study,* 56(2)**,** 233-243.

NEWTON, I. 1999. Age ratios in a Bullfinch *Pyrrhula pyrrhula* population over six years. *Bird Study,* 46(3)**,** 330-335.

NOGALES, M., MARTIN, A., DELGADO, G. & EMMERSON, K. 1988. Food spectrum of the feral cat (*Felis catus* L., 1758) in the juniper woodland on El Hierro (Canary Islands). *Bonner Zoologische Beiträge,* 39(1)**,** 1-6.

NOGALES, M. & MEDINA, F. M. 1996. A review of the diet of feral domestic cats (*Felis silvestris f catus*) on the Canary Islands, with new data from the laurel forest of La Gomera. *Zeitschrift für Säugetierkunde,* 61(1)**,** 1-6.

NOGALES, M., VIDAL, E., MEDINA, F. M., BONNAUD, E., TERSHY, B. R., CAMPBELL, K. J. & ZAVALETA, E. S. 2013. Feral cats and biodiversity conservation: the urgent prioritization of island management. *Bioscience,* 63(10)**,** 804-810.

OFFICE FOR NATIONAL STATISTICS. 2016. *UK Population by Postcode* [Online]. Available: https://www.nomisweb.co.uk/census/2011/ks101ew [Accessed 17.08.2023].

OFFICE FOR NATIONAL STATISTICS. 2021. *Population Estimates for the UK, England, Wales, Scotland and Northern Ireland: Mid-2021* [Online]. Available:

https://www.ons.gov.uk/peoplepopulationandcommunity/populationandmigration/populationestimates/bulletins/annualmidyearpopulationestimates/mid2019 [Accessed 05.07.2023].
OFFICE FOR NATIONAL STATISTICS. 2022a. *Estimates of the Population for the UK, England, Wales, Scotland and Northern Ireland* [Online]. ONS. Available: https://www.ons.gov.uk/peoplepopulationandcommunity/populationandmigration/populationestimates/datasets/populationestimatesforukenglandandwalesscotlandandnorthernireland [Accessed 14.04.2023].
OFFICE FOR NATIONAL STATISTICS. 2022b. *Habitat Extent and Condition, Natural Capital, UK: 2022* [Online]. ONS. Available: https://www.ons.gov.uk/economy/environmentalaccounts/bulletins/habitatextentandconditionnaturalcapitaluk/2022#urban [Accessed 13.04.2023].
OFFICE FOR NATIONAL STATISTICS. 2023. *House Building, UK: Permanent Dwellings Started and Completed by Country* [Online]. Available: https://www.ons.gov.uk/peoplepopulationandcommunity/housing/datasets/ukhousebuildingpermanentdwellingsstartedandcompleted [Accessed 12.07.2023].
OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., . . . WAGNER, H. 2019. vegan: Community Ecology Package. R package version 2.5-6. ed.: R package version 2.5-2.
PALACIO, F. X. 2020. Urban exploiters have broader dietary niches than urban avoiders. *Ibis,* 162(1)**,** 42-49.
PALMAS, P., JOURDAN, H., RIGAULT, F., DEBAR, L., DE MERINGO, H., BOURGUET, E., . . . VIDAL, E. 2017. Feral cats threaten the outstanding endemic fauna of the New Caledonia biodiversity hotspot. *Biological Conservation,* 214(1)**,** 250-259.
PALTRIDGE, R., GIBSON, D. & EDWARDS, G. 1997. Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research,* 24(1)**,** 67-76.
PDSA. 2022. *PAW Report 2022* [Online]. Available: https://www.pdsa.org.uk/media/12965/pdsa-paw-report-2022.pdf [Accessed 16.07.2023].
PEACH, W. J., MALLORD, J. W., OCKENDON, N., ORSMAN, C. J. & HAINES, W. G. 2015. Invertebrate prey availability limits reproductive success but not breeding population size in suburban House Sparrows Passer domesticus. *Ibis,* 157(3)**,** 601-613.
PEACH, W. J., SHEEHAN, D. K. & KIRBY, W. B. 2014. Supplementary feeding of mealworms enhances reproductive success in garden nesting house sparrows *Passer domesticus*. *Bird Study,* 61(3)**,** 378-385.
PEACH, W. J., VINCENT, K. E., FOWLER, J. A. & GRICE, P. V. 2008. Reproductive success of house sparrows along an urban gradient. *Animal Conservation,* 11(6)**,** 493-503.
PEARCE-HIGGINS, J. W. 2021. Climate Change and the UK's Birds. *BTO Report.* Thetford, Norfolk.
PEARCE-HIGGINS, J. W., EGLINGTON, S. M., MARTAY, B. & CHAMBERLAIN, D. E. 2015. Drivers of climate change impacts on bird communities. *Journal of Animal Ecology,* 84(4)**,** 943-954.
PEARCE-HIGGINS, J. W. & MORRIS, R. K. A. 2022. Declines in invertebrates and birds – could they be linked by climate change? *Bird Study,* 69(3-4)**,** 59-71.
PEMBERTON, C. & RUXTON, G. D. 2020. Birdsbesafe® collar cover reduces bird predation by domestic cats (Felis catus). *Journal of Zoology,* 310(2)**,** 106-109.
PÉRON, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *Journal of Animal Ecology,* 82(2)**,** 408-417.
PFMA. 2020a. *Calorie Factsheet* [Online]. Available: https://www.pfma.org.uk/calorie-factsheet [Accessed 12.05.2020 2020].
PFMA. 2020b. *Market Data 2019* [Online]. Available: https://www.pfma.org.uk/market-data-2019 [Accessed 12.05.2020 2020].
PHILLIPS, R. 07.09.2021 2021. *RE: Email communication.*
PIONTEK, A. M., WOJTYLAK-JURKIEWICZ, E., SCHMIDT, K., GAJDA, A., LESIAK, M. & WIERZBOWSKA, I. A. 2021. Analysis of cat diet across an urbanisation gradient. *Urban Ecosystems,* 24(1)**,** 59-69.

PIRIE, T. J., THOMAS, R. L. & FELLOWES, M. D. E. 2022. Pet cats (*Felis catus*) from urban boundaries use different habitats, have larger home ranges and kill more prey than cats from the suburbs. *Landscape and Urban Planning,* 220e104338.

PLUMMER, K. E., RISELY, K., TOMS, M. P. & SIRIWARDENA, G. M. 2019. The composition of British bird communities is associated with long-term garden bird feeding. *Nature Communications,* 10(1)**,** e2088.

PONTIER, D., SAY, L., DEBIAS, F. O., BRIED, J., THIOULOUSE, J., MICOL, T. & NATOLI, E. 2002. The diet of feral cats (*Felis catus* L.) at five sites on the Grande Terre, Kerguelen archipelago. *Polar Biology,* 25(11)**,** 833-837.

PREISSER, E., BOLNICK, D. & BENARD, M. 2005. Scared to death? The effects of intimidation and consumption In predator-prey interactions. *Ecology,* 86(1)**,** 501-509.

PRETZLAFF, I. & DAUSMANN, K. H. 2012. Impact of Climatic Variation on the Hibernation Physiology of Muscardinus avellanarius. *In:* RUF, T., BIEBER, C., ARNOLD, W. & MILLESI, E. (eds.) *Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations.* Berlin, Heidelberg: Springer Berlin Heidelberg.

PRIMACK, R. B. & TERRY, C. 2021. New social trails made during the pandemic increase fragmentation of an urban protected area. *Biological Conservation,* 255e108993.

QGIS DEVELOPMENT TEAM 2023. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R CORE TEAM 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

R CORE TEAM 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

R STUDIO TEAM 2020. RStudio: Integrated Development for R. RStudio. Boston, MA: R Studio.

RAAP, T., PINXTEN, R. & EENS, M. 2015. Light pollution disrupts sleep in free-living animals. *Scientific Reports,* 5(1)**,** e13557.

RAYNER, M. J., HAUBER, M. E., IMBER, M. J., STAMP, R. K. & CLOUT, M. N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences,* 104(52)**,** 20862-20865.

READ, J. L., DAGG, E. & MOSEBY, K. E. 2018. Prey selectivity by feral cats at central Australian rock-wallaby colonies. *Australian Mammalogy,* 41(1)**,** 132-141.

REED, T. E., JENOUVRIER, S. & VISSER, M. E. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology,* 82(1)**,** 131-144.

REID, C., HORNIGOLD, K., MCHENRY, E., NICHOLS, C., TOWNSEND, M., LEWTHWAITE, K., . . . HUGI, M. 2021. State of the UK's Woods and Trees 2021. UK: Woodland Trust.

REMACHA, C., DELGADO, J. A., BULAIC, M. & PÉREZ-TRIS, J. 2016. Human disturbance during early life impairs nestling growth in birds inhabiting a nature recreation area. *PLOS ONE,* 11(11)**,** e0166748.

REYNOLDS, J. C. & AEBISCHER, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review,* 21(3)**,** 97-122.

RIGAL, S., DAKOS, V., ALONSO, H., AUNIŅŠ, A., BENKŐ, Z., BROTONS, L., . . . DEVICTOR, V. 2023. Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences,* 120(21)**,** e2216573120.

RITCHIE, E. G. & JOHNSON, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters,* 12(9)**,** 982-998.

ROBERTSON, I. D. 1998. Survey of predation by domestic cats. *Australian Veterinary Journal,* 76(8)**,** 551-554.

ROBINSON, R. A., LAWSON, B., TOMS, M. P., PECK, K. M., KIRKWOOD, J. K., CHANTREY, J., . . . CUNNINGHAM, A. A. 2010. Emerging infectious disease leads to rapid population declines of common British birds. *PLOS ONE,* 5(8)**,** e12215.

ROBINSON, R. A., SIRIWARDENA, G. M. & CRICK, H. Q. P. 2005. Size and trends of the house sparrow *Passer domesticus* population in Great Britain. *Ibis,* 147(3)**,** 552-562.

ROTH, T. C., COX, J. G. & LIMA, S. L. 2008. Can foraging birds assess predation risk by scent? *Animal Behaviour,* 76(6)**,** 2021-2027.

ROWLAND, C. S., MORTON, R. D., CARRASCO, L., MCSHANE, G., O'NEIL, A. W. & WOOD, C. M. 2017. *Land Cover Map 2015 (1km Dominant Aggregate Class, GB).* [Online]. NERC Environmental Information Data Centre. Available: https://doi.org/10.5285/711c8dc1-0f4e-42ad-a703-8b5d19c92247 [Accessed 05.08.2023].

RSPB. 2022. *Identify a Bird* [Online]. Available: https://www.rspb.org.uk/birds-and-wildlife/wildlife-guides/identify-a-bird/ [Accessed 18.04.2022].

RSPB. 2023. *Big Garden Birdwatch 2023: UK Top 10* [Online]. Available: https://www.rspb.org.uk/globalassets/downloads/25821_resultstop10_a4_uk-v4.pdf [Accessed 25.08.2023].

RUXTON, G. D., THOMAS, S. & WRIGHT, J. W. 2002. Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of Zoology,* 25681-83.

SALINAS-RAMOS, V. B., MORI, E., BOSSO, L., ANCILLOTTO, L. & RUSSO, D. 2021. Zoonotic risk: one more good reason why cats should be kept away from bats. *Pathogens,* 10(3)**,** e304.

SÁNCHEZ-SOTOMAYOR, D., MARTÍN-HIGUERA, A., GIL-DELGADO, J. A., GÁLVEZ, Á. & BERNAT-PONCE, E. 2023. Artificial grass in parks as a potential new threat for urban bird communities. *Bird Conservation International,* 33e16.

SCHULZ, M., ROBINSON, S. & GALES, R. 2005. Breeding of the grey petrel (*Procellaria cinerea*) on Macquarie Island: population size and nesting habitat. *Emu - Austral Ornithology,* 105(4)**,** 323-329.

SCOTT, K. C., LEVY, J. K., GORMAN, S. P. & NEIDHART, S. M. N. 2002. Body condition of feral cats and the effect of neutering. *Journal of Applied Animal Welfare Science,* 5(3)**,** 203-213.

SERESS, G., SÁNDOR, K., VINCZE, E., PIPOLY, I., BUKOR, B., ÁGH, N. & LIKER, A. 2021. Contrasting effects of the COVID-19 lockdown on urban birds' reproductive success in two cities. *Scientific Reports,* 11(1)**,** e17649.

SEYMOUR, C. L., SIMMONS, R. E., MORLING, F., GEORGE, S. T., PETERS, K. & O'RIAIN, M. J. 2020. Caught on camera: the impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. *Global Ecology and Conservation,* 23(2020)**,** e01198.

SHERWIN, H. A., MONTGOMERY, W. I. & LUNDY, M. G. 2013. The impact and implications of climate change for bats. *Mammal Review,* 43(3)**,** 171-182.

SHIONOSAKI, K., YAMADA, F., ISHIKAWA, T. & SHIBATA, S. 2015. Feral cat diet and predation on endangered endemic mammals on a biodiversity hot spot (Amami-Ohshima Island, Japan). *Wildlife Research,* 42(4)**,** 343-352.

SHORE, R. F., BIRKS, J. D. S., AFSAR, A., WIENBURG, C. L. & KITCHENER, A. C. 2003. Spatial and temporal analysis of second-generation anticoagulant rodenticide residues in polecats (Mustela putorius) from throughout their range in Britain, 1992–1999. *Environmental Pollution,* 122(2)**,** 183-193.

SHUTT, J. D., CABELLO, I. B., KEOGAN, K., LEECH, D. I., SAMPLONIUS, J. M., WHITTLE, L., . . . PHILLIMORE, A. B. 2019. The environmental predictors of spatio-temporal variation in the breeding phenology of a passerine bird. *Proceedings of the Royal Society B: Biological Sciences,* 286(1908)**,** e20190952.

SILVA-RODRIGUEZ, E. A. & SIEVING, K. E. 2011. Influence of care of domestic carnivores on their predation on vertebrates. *Conservation Biology,* 25(4)**,** 808-815.

SIMS, V., EVANS, K. L., NEWSON, S. E., TRATALOS, J. A. & GASTON, K. J. 2008. Avian assemblage structure and domestic cat densities in urban environments. *Diversity and Distributions,* 14(2)**,** 387-399.

SMIT, M., CORNER-THOMAS, R. A., WEIDGRAAF, K. & THOMAS, D. G. 2022. Association of age and body condition with physical activity of domestic cats (Felis catus). *Applied Animal Behaviour Science,* 248e105584.

SMITH, C. & WARREN, M. 2019. *GLMs in R for Ecology,* UK, Independent Publisher.

SOH, M. C. K., PANG, R. Y. T., NG, B. X. K., LEE, B. P. Y. H., LOO, A. H. B. & ER, K. B. H. 2021. Restricted human activities shift the foraging strategies of feral pigeons (*Columba livia*) and three other commensal bird species. *Biological Conservation,* 253e108927.

SPARKS, T., WHITTLE, L. & GARFORTH, J. 2021. The value and importance of historical phenology in the UK. *British Wildlife,* 32(5)**,** 345-349.

STANBURY, A., EATON, M., AEBISCHER, N., BALMER, D., BROWN, A., DOUSE, A., . . . WIN, I. 2021. The status of our bird populations: the fifth Birds of Conservation Concern in the United Kingdom, Channel Islands and Isle of Man and second IUCN Red List assessment of extinction risk for Great Britain. *British Birds,* 114(12)**,** 723-747.

STEPHENS, P. A., MASON, L. R., GREEN, R. E., GREGORY, R. D., SAUER, J. R., ALISON, J., . . . WILLIS, S. G. 2016. Consistent response of bird populations to climate change on two continents. *Science,* 352(6281)**,** 84-87.

STOKELD, D., FISHER, A., GENTLES, T., HILL, B. M., WOINARSKI, J. C. Z., YOUNG, S. & GILLESPIE, G. R. 2018. Rapid increase of Australian tropical savanna reptile abundance following exclusion of feral cats. *Biological Conservation,* 225213-221.

STROKAL, M., BAI, Z., FRANSSEN, W., HOFSTRA, N., KOELMANS, A. A., LUDWIG, F., . . . KROEZE, C. 2021. Urbanization: an increasing source of multiple pollutants to rivers in the 21st century. *npj Urban Sustainability,* 1(1)**,** e24.

SU, Y.-S. & YAJIMA, M. 2020. R2jags: Using R to Run 'JAGS'. R package version 0.7-1.

SWALLOW, B., BUCKLAND, S. T., KING, R. & TOMS, M. P. 2019. Assessing factors associated with changes in the numbers of birds visiting gardens in winter: Are predators partly to blame? *Ecology and Evolution,* 9(21)**,** 12182-12192.

TALLAMY, D. W. & SHRIVER, W. G. 2021. Are declines in insects and insectivorous birds related? *Ornithological Applications,* 123(1)**,** e59.

THE CONSERVATION OF HABITATS AND SPECIES REGULATIONS 2010. The Conservation of Habitats and Species Regulations 2010. UK Government.

THE HABITATS DIRECTIVE 1992. The Habitats Directive 1992. European Union.

THOMAS, R. L., FELLOWES, M. D. E. & BAKER, P. J. 2012. Spatio-temporal variation in predation by urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. *Plos One,* 7(11)**,** e49369.

TIDEMANN, C. R., YORKSTON, H. D. & RUSSACK, A. J. 1994. The diet of cats, *Felis catus*, on Christmas Island, Indian Ocean. *Wildlife Research,* 21(3)**,** 279-286.

TILGAR, V., MOKS, K. & SAAG, P. 2011. Predator-induced stress changes parental feeding behavior in pied flycatchers. *Behavioral Ecology,* 22(1)**,** 23-28.

TONER, G. C. 1956. House cat predation on small animals. *Journal of Mammalogy,* 37(1)**,** 119-119.

TRYJANOWSKI, P., ANTCZAK, M., HROMADA, M., KUCZYŃSKI, L. & SKORACKI, M. 2002. Winter feeding ecology of male and female European wildcats *Felis silvestris* in Slovakia. *Zeitschrift für Jagdwissenschaft,* 48(1)**,** 49-54.

TSCHANZ, B., HEGGLIN, D., GLOOR, S. & BONTADINA, F. 2011. Hunters and non-hunters: skewed predation rate by domestic cats in a rural village. *European Journal of Wildlife Research,* 57(3)**,** 597-602.

TURNER, D. & BATESON, P. 2000. *The Domestic Cat: The Biology of its Behaviour,* Cambridge, UK, Cambridge University Press.

TUYTTENS, F. A. M., DELAHAY, R. J., MACDONALD, D. W., CHEESEMAN, C. L., LONG, B. & DONNELLY, C. A. 2000. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology,* 69(5)**,** 815-828.

TWIGG, L. E., LOWE, T. J., MARTIN, G. R. & GRAY, G. S. 1999. *A Review of the Anticoagulant Pesticide Pindone,* Perth, Department of Agriculture Western Australia.

VAN HEEZIK, Y., SMYTH, A., ADAMS, A. & GORDON, J. 2010. Do domestic cats impose an unsustainable harvest on urban bird populations? *Biological Conservation,* 143(1)**,** 121-130.

VIRKKALA, R. & LEHIKOINEN, A. 2017. Birds on the move in the face of climate change: High species turnover in northern Europe. *Ecology and Evolution,* 7(20)**,** 8201-8209.

WARRINGTON, M. H., SCHRIMPF, M. B., DES BRISAY, P., TAYLOR, M. E. & KOPER, N. 2022. Avian behaviour changes in response to human activity during the COVID-19 lockdown in the United Kingdom. *Proceedings of the Royal Society B: Biological Sciences,* 289(1983)**,** e20212740.

WICKHAM, H. 2016. ggplot2: Elegant Graphics for Data Analysis. New York: Springer-Verlag.

WILLIAMS, D. R., CHILD, M. F., DICKS, L. V., OCKENDON, N., POPLE, R. G., SHOWLER, D. A., . . . SUTHERLAND, W. J. 2020. Bird Conservation. *In:* SUTHERLAND, W. J., DICKS, L. V., PETROVAN, S. O. & SMITH, R. K. (eds.) *What Works in Conservation 2020.* Cambridge, UK: Open Book Publishers.

WILLSON, S. K., OKUNLOLA, I. A. & NOVAK, J. A. 2015. Birds be safe: can a novel cat collar reduce avian mortality by domestic cats (*Felis catus*)? *Global Ecology and Conservation,* 3(2015)**,** 359-366.

WOINARSKI, J. C. Z., MURPHY, B. P., LEGGE, S. M., GARNETT, S. T., LAWES, M. J., COMER, S., . . . WOOLLEY, L. A. 2017. How many birds are killed by cats in Australia? *Biological Conservation,* 21476-87.

WOINARSKI, J. C. Z., SOUTH, S. L., DRUMMOND, P., JOHNSTON, G. R. & NANKIVELL, A. 2018. The diet of the feral cat (*Felis catus*), red fox (*Vulpes vulpes*) and dog (*Canis familiaris*) over a three-year period at Witchelina Reserve, in arid South Australia. *Australian Mammalogy,* 40(2)**,** 204-213.

WOODS, M., MCDONALD, R. A. & HARRIS, S. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review,* 33(2)**,** 174-188.

WOODWARD, I. D., MASSIMINO, D., HAMMOND, M. J., HARRIS, S. J., LEECH, D. I., NOBLE, D. G., . . . ROBINSON, R. A. 2018. BirdTrends 2018: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds. *Research Report 708.* Thetford: BTO.

YIP, S. J. S., DICKMAN, C. R., DENNY, E. A. & CRONIN, G. M. 2014. Diet of the feral cat, *Felis catus*, in central Australian grassland habitats: do cat attributes influence what they eat? *Acta Theriologica,* 59(2)**,** 263-270.

YIP, S. J. S., RICH, M. A. & DICKMAN, C. R. 2015. Diet of the feral cat, *Felis catus*, in central Australian grassland habitats during population cycles of its principal prey. *Mammal Research,* 60(1)**,** 39-50.

ZAGER, P. & BEECHAM, J. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus,* 17(2)**,** 95-108.

ZUUR, A. F. & IENO, E. N. 2016. *Beginner's Guide to Zero-Inflated Models with R,* Newburgh, UK, Highland Statistics Ltd.

Appendices

Appendix 2. 1. Numerical output of Shapiro-Wilk and Fligner-Killeen tests on all species groups.

Taxon	Shapiro-Wilk		Fligner-Killeen	
	W	***p***	**Med chi^2**	***p***
Rodents	0.9807	0.983	0.0349	0.852
Insectivores	0.9148	0.214	0.0238	0.877
Med. mammals	0.6561	<0.001	0.0446	0.833
Birds	0.9585	0.731	0.0799	0.777
Reptiles	0.7682	0.003	1.4795	0.224
Amphibians	0.7578	0.002	0.0191	0.89
Fish	0.4457	<0.001	1.8701	0.172

Appendix 2. 2. Principal Component Analysis (PCA) loadings for all species, as illustrated in Figure 2. 6 (biplot).

Species	**PC1**	**PC2**	**PC3**	**PC4**
Mammals	2.6631	1.6613	-0.8099	0.5219
Birds	1.0987	-3.7475	1.0963	-0.2622
Reptiles	-2.6115	0.3737	-0.2350	-2.2721
Amphibians	-1.9290	-0.3253	-0.1090	3.6495
Fish	0.0312	1.3387	4.1130	0.1396

Appendix 2. 3. All species found in the diet of *Felis catus*, showing whether each prey item was recorded by return surveys, consumption studies, or capture studies (marked with an X). Data collection is also sorted by island or mainland (marked with an X).

Group	Species	Returned	Consumed	Caught	Island	Mainland
Mammals	*Acomys russatus*	X				X
Mammals	*Antechinomys laniger*		X			X
Mammals	*Apodemus agrarius*	X	X			X
Mammals	*Apodemus alpicola*	X				X
Mammals	*Apodemus flavicollis*	X	X			X
Mammals	*Apodemus mystacinus*	X	X			X
Mammals	*Apodemus sylvaticus*	X	X		X	X
Mammals	*Arvicola amphibius*	X				X
Mammals	*Atelerix algirus*		X			
Mammals	*Atlantoxerus getulus*		X		X	
Mammals	*Austronomus australis*		X			X
Mammals	*Blarina brevicauda*	X		X		X
Mammals	*Bos taurus*		X			X
Mammals	*Callosciurus finlaysonii*	X				X
Mammals	*Calomys tener*		X			X
Mammals	*Cavia porcellus*	X				X
Mammals	*Chalinolobus gouldii*		X			X
Mammals	*Chionomys nivalis*	X				X
Mammals	*Clethrionomys gapperi*	X				X
Mammals	*Coendou prehensilis*		X			X
Mammals	*Condylura cristata*	X				X
Mammals	*Cricetus cricetus*		X			X
Mammals	*Crocidura leucodon*	X				X
Mammals	*Crocidura pachyura*	X				X
Mammals	*crocidura russula*	X				X
Mammals	*Crocidura sicula*	X				X
Mammals	*Crocidura suaveolens*	X				X
Mammals	*Cryptotis parva*	X				X
Mammals	*Dasyurus hallucatus*		X			X
Mammals	*Delomys dorsalis*		X			X
Mammals	*Didelphis aurita*		X			X
Mammals	*Diplothrix legata*		X		X	
Mammals	*Dromiciops gliroides*		X			X
Mammals	*Dryomys nitedula*	X				X
Mammals	*Eliomys quercinus*	X				X
Mammals	*Eptesicus serotinus*	X				X
Mammals	*Erinaceus europaeus*	X				X
Mammals	*Euryoryzomys russatus*		X			X
Mammals	*Eutamias sibiricus*	X				X
Mammals	*Felis catus*		X			X

Mammals	*Gerbillus allenbyi*	X				X
Mammals	*Glaucomys sabrinus*	X				X
Mammals	*Glaucomys volans*	X				X
Mammals	*Glis glis*	X				X
Mammals	*Hydromys chrysogaster*	X				X
Mammals	*Hypsugo savii*	X				X
Mammals	*Irenomys tarsalis*		X			X
Mammals	*Isoodon macrourus*		X			X
Mammals	*Isoodon obesulus*	X				X
Mammals	*Kannabatemys amblyonyx*		X			X
Mammals	*Lagorchestes hirsutus*		X			X
Mammals	*Lasiurus cinereus semotus*		X		X	
Mammals	*Leggadina forresti*		X			X
Mammals	*Leggadina lakedownensis*		X			X
Mammals	*Lepus europaeus*	X	X			X
Mammals	*Macropus giganteus*		X			X
Mammals	*Macropus rufus*		X			X
Mammals	*Martes martes*	X				X
Mammals	*Melomys burtoni*		X			X
Mammals	*Meriones tristrami*	X	X			X
Mammals	*Mesembriomys gouldii*		X			X
Mammals	*Mesocricetus auratus*	X				X
Mammals	*Micromys minutus*	X				X
Mammals	*Microtus agrestis*	X				X
Mammals	*Microtus arvalis*	X	X			X
Mammals	*Microtus pennsylvanicus*	X		X	X	X
Mammals	*Microtus pinetorum*	X		X		X
Mammals	*Microtus savii*	X				X
Mammals	*Microtus socialis*	X	X			X
Mammals	*Microtus subterraneus*		X			X
Mammals	*Miniopterus schreibersii*	X				X
Mammals	*Mus musculus*	X	X	X	X	X
Mammals	*Muscardinus avellanarius*	X				X
Mammals	*Mustela erminea*	X				X
Mammals	*Mustela nivalis*	X				X
Mammals	*Myocastor coypus*	X				X
Mammals	*Myodes glareolus*	X	X			X
Mammals	*Myotis mystacinus*	X				X
Mammals	*Myotis nattereri*	X				X
Mammals	*Napaeozapus insignis*	X				X

Mammals	*Neomys fodiens*	X				X
Mammals	*Neotoma floridana*		X			X
Mammals	*Notamacropus agilis*		X			X
Mammals	*Notomys alexis*		X			X
Mammals	*Nyctalus leisleri*	X				X
Mammals	*Nyctophilus geoffroyi*	X	X			X
Mammals	*Oligoryzomys longicaudatus*		X			X
Mammals	*Oryctolagus cuniculus*	X	X		X	X
Mammals	*Ovis aries*		X			X
Mammals	*Pentalagus furnessi*		X		X	
Mammals	*Peromyscus gossypinus*			X	X	
Mammals	*Peromyscus leucopus*	X				X
Mammals	*Petaurus breviceps*	X	X			X
Mammals	*Petrogale lateralis*		X			X
Mammals	*Phodopus sungorus*	X				X
Mammals	*Pipistrellus kuhlii*	X				X
Mammals	*Pipistrellus pipistrellus*	X				X
Mammals	*Pipistrelus nathusii*	X				X
Mammals	*Planigale gilesi*		X			X
Mammals	*Planigale ingrami*		X			X
Mammals	*Planigale tenuirostris*		X			X
Mammals	*Plecotus auritus*	X				X
Mammals	*Precotus auritus*	X				X
Mammals	*Pseudantechinus macdonnellensis*		X			X
Mammals	*Pseudomys bolami*		X			X
Mammals	*Pseudomys calabyi*		X			X
Mammals	*Pseudomys delicatulus*		X			X
Mammals	*Pseudomys desertor*		X			X
Mammals	*Pseudomys hermannsburgensis*		X			X
Mammals	*Pseudomys nanus*			X		X
Mammals	*Ptermys volans*	X				X
Mammals	*Pteropus melanotus*		X		X	
Mammals	*Pteropus ornatus*		X		X	
Mammals	*Pteropus tonganus*		X		X	
Mammals	*Pteropus vetulus*		X		X	
Mammals	*Rattus exulans*		X		X	
Mammals	*Rattus fuscipes*	X				X
Mammals	*Rattus norvegicus*	X	X		X	X
Mammals	*Rattus rattus*	X	X		X	X
Mammals	*Rattus villosissimus*		X			X
Mammals	*Rattus villossisimus*		X			X
Mammals	*Rhinolophus ferrumequinum*	X				X

Mammals	*Rhinolophus hipposideros*	X				X
Mammals	*Rousettus aegyptiacus*	X				X
Mammals	*Scalopus aquaticus*	X		X	X	
Mammals	*Sciurus carolinensis*	X		X	X	X
Mammals	*Sciurus vulgaris*	X				X
Mammals	*Sigmodon hispidus*		X			X
Mammals	*Sminthopsis bindi*		X			X
Mammals	*Sminthopsis crassicaudata*		X			X
Mammals	*Sminthopsis douglasi*		X			X
Mammals	*Sminthopsis macroura*		X			X
Mammals	*Sminthopsis ooldea*		X			X
Mammals	*Sminthopsis youngsoni*		X			X
Mammals	*Sooretamys angouya*		X			X
Mammals	*Sorex antinorii*	X				X
Mammals	*Sorex araneus*	X				X
Mammals	*Sorex cinereus*	X				X
Mammals	*Sorex minutissimus*	X				X
Mammals	*Sorex minutus*	X				X
Mammals	*Sorex samniticus*	X				X
Mammals	*Spalax leucodon*	X				X
Mammals	*Spermophilus citellus*		X			X
Mammals	*Suncus etruscus*	X				X
Mammals	*Suncus murinus*		X		X	
Mammals	*Sus scrofa*		X			X
Mammals	*Sylvilagus floridanus*	X				X
Mammals	*Sylvilagus palustris*			X	X	
Mammals	*Tadarida teniotis*	X				X
Mammals	*Talpa caeca*	X				X
Mammals	*Talpa europea*	X	X			X
Mammals	*Talpa romana*	X				X
Mammals	*Tamias striatus*	X		X		X
Mammals	*Tenrec ecaudatus*		X		X	
Mammals	*Tokudaia osimensis*		X		X	
Mammals	*Trichosurus vulpecula*	X	X		X	X
Mammals	*Zapus hudsonius*	X				X
Mammals	*Zyzomys argurus*			X		X
Birds	*Acanthis flammea*		X		X	
Birds	*Acanthiza chrysorrhea*	X				X
Birds	*Acanthiza pusilla*	X				X
Birds	*Acanthorhynchus tenuirostris*	X				X
Birds	*Acridotheres tristis*	X				X
Birds	*Acrocephalus melanopogon*	X				X

Birds	*Acrocephalus schoenobaenus*	X				X
Birds	*Acrrocephalus scirpaceus*	X				X
Birds	*Aegithalos caudatus*	X				X
Birds	*Agapornis fischeri*	X				X
Birds	*Alauda arvensis*	X				X
Birds	*Alectoris rufa*	X				X
Birds	*Alisterus scapularis*	X				X
Birds	*Ammopersix heyi*	X				X
Birds	*Amytornis modestus*		X			X
Birds	*Amytornis purnelli*		X			X
Birds	*Anas crecca*	X				X
Birds	*Anas gibberifrons*		X			X
Birds	*Anas platyryhnchos*	X				X
Birds	*Anas rhynchotis*		X			X
Birds	*Anthochaera carunculata*	X				X
Birds	*Anthochaera lunulata*	X				X
Birds	*Anthornis melanura*	X	X		X	
Birds	*Anthus bertheloti*		X		X	
Birds	*Anthus novaeseelandiae*		X		X	X
Birds	*Anthus pratensis*	X				X
Birds	*Anthus trivialis*	X				X
Birds	*Apus apus*	X				X
Birds	*Ardenna pacifica*		X		X	
Birds	*Ardeola ralloides*	X				X
Birds	*Artamus cinereus*		X			X
Birds	*Artamus minor*		X			X
Birds	*Asio flammeus*	X				X
Birds	*Asio otus*	X				X
Birds	*Athene noctua*	X				X
Birds	*Aythya ferina*	X				X
Birds	*Baeolophus bicolor*	X				X
Birds	*Barnadius zonarius*		X			X
Birds	*Bombycilla garrulus*	X				X
Birds	*Cacatua roseicapilla*	X	X			X
Birds	*Callocephalon fimbriatum*	X				X
Birds	*Calonectris diomedea*	X	X		X	X
Birds	*Caprimulgus europaeus*		X		X	
Birds	*Cardinalis cardinalis*	X		X		X
Birds	*Carduelis barbata*		X			X
Birds	*Carduelis cannabina*	X				X
Birds	*Carduelis carduelis*	X				X

Birds	*Carduelis chloris*	X	X			X
Birds	*Carduelis corsicana*	X				X
Birds	*Carduelis flammea*	X				X
Birds	*Carduelis spinus*	X	X	X		X
Birds	*Carduelis tristis*			X		X
Birds	*Carpodacus mexicanus*			X		X
Birds	*Catharus guttatus*			X		X
Birds	*Certhia familiaris*	X				X
Birds	*Cettia cetti*	X				X
Birds	*Chalcophaps indica*		X		X	
Birds	*Chenonetta jubata*	X				X
Birds	*Chlamydera guttata*		X			X
Birds	*Chloephaga hybrida*		X		X	
Birds	*Chloephaga picta*		X		X	
Birds	*Chrysococcyx lucidus*	X	X		X	X
Birds	*Cinclus cinclus*	X				X
Birds	*Cisticola juncidis*	X				X
Birds	*Clincoramphus cruralis*		X			X
Birds	*Coccothraustes coccothraustes*	X				X
Birds	*Collocalia esculenta*		X		X	
Birds	*Columba livia*	X	X		X	X
Birds	*Columba palumbus*	X				X
Birds	*Cortunix cortunix*	X	X		X	X
Birds	*Cortunix ypsilophora*			X		X
Birds	*Corturnix ypsilophora*		X			X
Birds	*Corvus corone*	X				X
Birds	*Corvus coronoides*	X	X			X
Birds	*Corvus frugilegus*	X				X
Birds	*Corvus monedula*	X				X
Birds	*Coturnix coturnix*		X			X
Birds	*Coturnix novaezealandiae*	X				X
Birds	*Cracticus nigrogularis*		X			X
Birds	*Cracticus tibicen*	X				X
Birds	*Cracticus torquatus*	X				X
Birds	*Crex crex*	X				X
Birds	*Cuculus canorus*	X				X
Birds	*Cyanecula svecica*	X				X
Birds	*Cyanistes caeruleus*	X				X
Birds	*Cyanoramphus saisseti*		X		X	
Birds	*Delichon urbica*	X				X
Birds	*Dendrocopos major*	X				X
Birds	*Ducula whartoni*		X		X	
Birds	*Dumetella carolinensis*	X				X
Birds	*Emberiza cia*	X				X

Birds	*Emberiza cirlus*	X				X
Birds	*Emberiza citrinella*	X				X
Birds	*Emberiza schoeniclus*	X				X
Birds	*Emblema temporalis*	X				X
Birds	*Eopsaltria australis*	X				X
Birds	*Ephthianura tricolor*		X			X
Birds	*Epthianura tricolor*		X			X
Birds	*Erithacus rubecula*	X	X		X	X
Birds	*Eudyptes chrysocome*		X		X	
Birds	*Eudyptes minor*		X		X	
Birds	*Eudyptes pachyrhynchus*		X		X	
Birds	*Eunymphicus uvaeensis*		X		X	
Birds	*Eurostopodus argus*		X			X
Birds	*Falco cenchroides*		X			X
Birds	*Falco columbarius*	X				X
Birds	*Ficedula hypoleuca*	X				X
Birds	*Flavicola nengeta*		X			X
Birds	*Fluica atra*	X				X
Birds	*Foudia madagascariensis*		X		X	
Birds	*Fringilla coelebs*	X	X		X	X
Birds	*Fringilla montifringilla*	X				X
Birds	*Fulica atra*	X				X
Birds	*Galerida cristata*	X				X
Birds	*Gallinula chloropus*	X				X
Birds	*Gallinula ventralis*		X			X
Birds	*Gallus domesticus*		X		X	
Birds	*Garrulus glandarius*	X				X
Birds	*Garrulus lidthi*		X		X	
Birds	*Geopelia cuneata*	X	X			X
Birds	*Grallina cyanoleuca*	X				X
Birds	*Greygone igata*	X				X
Birds	*Gymnorhina tibicen*	X				X
Birds	*Halcyon sancta*	X				X
Birds	*Hemiphaga novaeseelandiae*	X				X
Birds	*Hirundo neoxena*	X	X			X
Birds	*Hirundo rustica*	X				X
Birds	*Hoplopterus spinosus*	X				X
Birds	*Hylocichla mustelina*	X		X	X	
Birds	*Junco hyemalis*	X		X		X
Birds	*Jynx torquilla*	X	X		X	X
Birds	*Lagopus lagopus scoticus*	X				X
Birds	*Lanius collurio*	X				X

Birds	*Lanius nubicus*	X			X
Birds	*Larus argentatus*	X			X
Birds	*Larus michahellis*	X			X
Birds	*Leiothrix lutea*	X	X	X	X
Birds	*Lichenostomus chrysops*	X			X
Birds	*Lichenostomus pencillatus*	X	X		X
Birds	*Lichenostomus virescens*	X			X
Birds	*Lichmera indistincta*	X			X
Birds	*Lullula arborea*	X			X
Birds	*Luscinia megarhynchos*	X	X	X	X
Birds	*Luscinia svecica*	X			X
Birds	*Malurus cyaneus*	X	X		X
Birds	*Malurus lamberti*		X		X
Birds	*Manorina flavigula*		X		X
Birds	*Manorina melanocephala*	X	X		X
Birds	*Melopsittacus undulatus*	X	X		X
Birds	*Microeca flaviventris*		X	X	
Birds	*Mirafra javanica*		X		X
Birds	*Molothrus bonariensis*		X		X
Birds	*Motacilla alba*	X			X
Birds	*Motacilla capensis*		X	X	
Birds	*Motacilla cinerea*	X			X
Birds	*Motacilla flava*	X			X
Birds	*Muscicapa striata*	X	X	X	X
Birds	*Myadestes obscurus*		X	X	
Birds	*Myiopsitta monachus*	X			X
Birds	*Nectrainia osea*	X			X
Birds	*Neophema pulchella*	X			X
Birds	*Ninox novaeseelandiae*		X	X	
Birds	*Nothoptrocta perdicaria*		X		X
Birds	*Nucifraga caryocatactes*	X			X
Birds	*Numida meleagris*		X	X	
Birds	*Nymphicus hollandicus*		X		X
Birds	*Ocyphaps lophotes*	X	X		X
Birds	*Onychoprion fuscatus*		X	X	
Birds	*Oreoica gutturalis*		X		X
Birds	*Oriolus oriolus*	X			X
Birds	*Otus scops*	X			X

Birds	*Pachycephala nifiventris*	X				X
Birds	*Pachycephala pectoralis*	X				X
Birds	*Pachyptila belcheri*		X		X	
Birds	*Pardalotus punctatus*	X				X
Birds	*Pardalotus striatus*	X				X
Birds	*Parus major*	X	X		X	X
Birds	*Parus palustris*	X				X
Birds	*Passer domesticus*	X		X		X
Birds	*Passer italiae*	X				X
Birds	*Passer montanus*	X				X
Birds	*Peltohyas australis*		X			X
Birds	*Perdix perdix*	X				X
Birds	*Periparus ater*	X				X
Birds	*Petroica macrocephala*		X		X	
Birds	*Petroica multicolor*	X				X
Birds	*Petroica phoenicea*	X				X
Birds	*Petronia petronia*	X				X
Birds	*Phalacrocorax capensis*		X		X	
Birds	*Phaps chalcoptera*	X	X			X
Birds	*Phasianus colchicus*	X	X			X
Birds	*Philemon corniculatus*	X				X
Birds	*Phoenicurus ochruros*	X				X
Birds	*Phoenicurus phoenicurus*	X	X		X	X
Birds	*Phylidonyris novahollandiae*	X				X
Birds	*Phylloscopus collybita*	X	X		X	X
Birds	*Phylloscopus trochilus*	X				X
Birds	*Pica pica*	X				X
Birds	*Picus viridis*	X				X
Birds	*Platycercus elegans*	X				X
Birds	*Platycercus eximus*	X				X
Birds	*Platycercus zonarius*	X				X
Birds	*Plectrophenax nivalis*	X				X
Birds	*Podargus strigoides*		X			X
Birds	*Poecile carolinensis*	X				X
Birds	*Poephila bichenovii*	X				X
Birds	*Poephila guttata*		X			X
Birds	*Polytelis anthepeplus*	X				X
Birds	*Prinia gracilis*	X				X
Birds	*Prosthemadera novaeseelandiae*	X	X		X	X
Birds	*Prunella collaris*	X				X

Birds	*Prunella modularis*	X	X		X	X
Birds	*Psephotus haematonotus*	X				X
Birds	*Psephotus varius*		X			X
Birds	*Pseudobulweria rostrata*		X		X	
Birds	*Psittacula krameri*	X				X
Birds	*Pterodroma baraui*		X		X	
Birds	*Pterodroma leucoptera*		X		X	
Birds	*Ptilonorhynchus violaceus*	X				X
Birds	*Ptyonoprogne rupestris*	X				X
Birds	*Puffinus assimilis Gould*		X		X	
Birds	*Puffinus griseus*		X		X	
Birds	*Puffinus tenuirostris*		X		X	
Birds	*Puffinus yelkouan*		X		X	
Birds	*Pycnonotus barbatus*	X				X
Birds	*Pyrrhula pyrrhula*	X				X
Birds	*Rallus aquaticus*	X				X
Birds	*Regulus calendula*	X				X
Birds	*Regulus ignicapillus*	X				X
Birds	*Regulus regulus*	X				X
Birds	*Rhipidura fuliginosa*	X	X		X	X
Birds	*Rhipidura leucophrys*	X	X			X
Birds	*Rhipidura rufifrons*	X				X
Birds	*Saxicola rubicola*	X	X		X	X
Birds	*Sayornis phoebe*			X		X
Birds	*Scolopax rusticola*	X	X			X
Birds	*Seiurus aurocapillus*	X				X
Birds	*Sephanoides sephanoides*		X			X
Birds	*Sericornis frontalis*	X				X
Birds	*Serinus canaria*		X		X	
Birds	*Serinus serinus*	X				X
Birds	*Sinosuthora webbiana*	X				X
Birds	*Sitta europaea*	X				X
Birds	*Spheniscus demerus*		X		X	
Birds	*Spinus tristis*	X				X
Birds	*Sterna fuscata*		X		X	
Birds	*Stiltia isabella*		X			X
Birds	*Streptopelia decaocto*	X	X		X	X
Birds	*Streptopelia senegalensis*	X				X
Birds	*Streptopelia turtur*	X				X
Birds	*Strigops habroptilus*		X		X	

Birds	*Struthidea cinerea*		X			X
Birds	*Sturnella loyca*		X		X	
Birds	*Sturnus vulgaris*	X	X		X	X
Birds	*Sylvia atricapilla*	X	X		X	X
Birds	*Sylvia borin*	X				X
Birds	*Sylvia communis*	X				X
Birds	*Sylvia conspicillata*	X				X
Birds	*Sylvia curruca*	X				X
Birds	*Sylvia melanocephala*	X	X		X	X
Birds	*Sylvia sarda*	X				X
Birds	*Sylvia subalpina*	X				X
Birds	*Sylvia undata*	X				X
Birds	*Taeniopygia guttata*	X	X			X
Birds	*Tarsiger cyanurus*	X				X
Birds	*Thraupis palmarum*		X			X
Birds	*Thryothorus ludovicianus*	X				X
Birds	*Thyrothorus ludovicianus*	X				X
Birds	*Tringa erythropus*	X				X
Birds	*Troglodytes aedon*	X	X			X
Birds	*Troglodytes musculus*		X			X
Birds	*Troglodytes troglodytes*	X			X	X
Birds	*Turdus falklandii*		X		X	
Birds	*Turdus iliacus*	X				X
Birds	*Turdus merula*	X	X		X	X
Birds	*Turdus migratorius*	X		X		X
Birds	*Turdus pallidus*		X		X	
Birds	*Turdus philomelos*	X	X		X	X
Birds	*Turdus pilaris*	X				X
Birds	*Turdus poliocephalus*		X		X	
Birds	*Turdus viscivorus*	X				X
Birds	*Turnix pyrrhothorax*		X			X
Birds	*Turnix varius*		X			X
Birds	*Turnix velox*		X			X
Birds	*Tyto alba*	X				X
Birds	*Upupa epops*	X				X
Birds	*Vanellus chilensis*		X			X
Birds	*Vestiaria coccinea*		X		X	
Birds	*Zenaida macroura*			X		X
Birds	*Zonotrichia albicollis*	X				X
Birds	*Zonotrichia capensis*		X			X
Birds	*Zoothera dauma*	X				X
Birds	*Zosterops japonicus*		X		X	
Birds	*Zosterops lateralis*	X	X		X	X
Birds	*Zosterops natalis*		X		X	

Reptiles	*Acritoscincus trilineata*	X				X
Reptiles	*Agama stellio*	X				X
Reptiles	*Agyroides fitzingeri*	X				X
Reptiles	*Amphibolurus burnsi*		X			X
Reptiles	*Amphibolurus gilberti*		X			X
Reptiles	*Amphibolurus muricatus*	X				X
Reptiles	*Anguis fragilis*	X				X
Reptiles	*Anguis veronensis*	X				X
Reptiles	*Anolis carolinensis*			X	X	X
Reptiles	*Antaresia stimsoni*		X			X
Reptiles	*Archaeolacerta bedriagae*	X				X
Reptiles	*Brachyurophis roperi*			X		X
Reptiles	*Caesoris novocaledoniae*		X		X	
Reptiles	*Caledoniscincus aqilonius*		X		X	
Reptiles	*Caledoniscincus atropunctatus*		X		X	
Reptiles	*Caledoniscincus auratus*		X		X	
Reptiles	*Caledoniscincus austocaledonicus*		X		X	
Reptiles	*Caledoniscincus bodoi*		X		X	
Reptiles	*Caledoniscincus festivus*		X		X	
Reptiles	*Caledoniscincus haplorhinus*		X		X	
Reptiles	*Caledoniscincus notialis*		X		X	
Reptiles	*Caledoniscincus orestes*		X		X	
Reptiles	*Carphophis amoenus amoenus*	X				X
Reptiles	*Celatiscincus similis*		X		X	
Reptiles	*Chalcides chalcides*	X				X
Reptiles	*Chalcides ocellatus*	X				X
Reptiles	*Chalcides viridanus viridanus*		X		X	
Reptiles	*Chamaeleo chamaeleon*	X	X			X
Reptiles	*Christinus marmoratus*	X				X
Reptiles	*Coluber constrictor*	X				X
Reptiles	*Coluber jugularis*	X				X
Reptiles	*Coluber rhodorhachis*	X				X
Reptiles	*Coluber Rogersi*	X				X
Reptiles	*Coluber rubriceps*	X				X
Reptiles	*Coronella austriaca*	X				X

Reptiles	*Coronella girondica*	X			X
Reptiles	*Cryptoblepharus boutonii*		X	X	
Reptiles	*Cryptoblepharus egeriae*		X	X	
Reptiles	*Cryptoblepharus novocaledonicus*		X	X	
Reptiles	*Cryptoblepharus plagiocephalus*	X			X
Reptiles	*Ctenophorus fordi*		X		X
Reptiles	*Ctenophorus gibba*		X		X
Reptiles	*Ctenophorus nuchalis*		X		X
Reptiles	*Ctenophorus pictus*		X		X
Reptiles	*Ctenophorus vadnappa*		X		X
Reptiles	*Ctenotus alacer*		X		X
Reptiles	*Ctenotus australis*	X			X
Reptiles	*Ctenotus fallens*	X			X
Reptiles	*Ctenotus helenae*		X		X
Reptiles	*Ctenotus joanae*		X		X
Reptiles	*Ctenotus leonhardii*		X		X
Reptiles	*Ctenotus olympicus*		X		X
Reptiles	*Ctenotus pantherinus*		X		X
Reptiles	*Ctenotus quatturodecimlineatus*		X		X
Reptiles	*Ctenotus regius*		X		X
Reptiles	*Ctenotus robustus*	X	X		X
Reptiles	*Ctenotus saxatilis*		X		X
Reptiles	*Ctenotus schomburgkii*		X		X
Reptiles	*Ctenotus strauchii*		X		X
Reptiles	*Ctenotus taeniatus*		X		X
Reptiles	*Ctenotus uber*		X		X
Reptiles	*Ctenous brooksi*		X		X
Reptiles	*Ctenous leae*		X		X
Reptiles	*Ctenous olympicus*		X		X
Reptiles	*Ctenous regius*		X		X
Reptiles	*Ctenous schomburgkii*		X		X
Reptiles	*Ctenous strauchii*		X		X
Reptiles	*Cyclodina aenea*	X			X
Reptiles	*Cyclodomorphus branchialis*		X		X
Reptiles	*Cyclodomorphus melanops*		X		X
Reptiles	*Cycophiops semicarinatus*		X	X	
Reptiles	*Delma nasuta*		X		X
Reptiles	*Delma tincta*		X		X

Reptiles	*Demansia psammophis*		X			X	
Reptiles	*Denisonia devisi*		X			X	
Reptiles	*Diadophis punctatus*	X				X	
Reptiles	*Diplodactylus ciliaris*		X			X	
Reptiles	*Diplodactylus conspicillatus*		X			X	
Reptiles	*Diplodactylus damaeus*		X			X	
Reptiles	*Diplodactylus steindachneri*		X			X	
Reptiles	*Diplodactylus stenodactylus*		X			X	
Reptiles	*Diplodactylus tessellatus*		X			X	
Reptiles	*Drysdalia coronoides*		X		X		
Reptiles	*Egernia inornata*		X			X	
Reptiles	*Egernia stokesii*		X			X	
Reptiles	*Egernia striata*		X			X	
Reptiles	*Egernia striolata*		X			X	
Reptiles	*Eirenis decemlineatus*	X				X	
Reptiles	*Elaphe quatuorlineata*	X				X	
Reptiles	*Emoia atrocostata*		X		X		
Reptiles	*Emoia cyanura*		X		X		
Reptiles	*Emoia loyaltiensis*		X		X		
Reptiles	*Emoia nativitatis*		X		X		
Reptiles	*Epibator nigrofasciolatus*		X		X		
Reptiles	*Eremiascincus fasciolatus*		X			X	
Reptiles	*Eremiascincus richardsonii*		X			X	
Reptiles	*Eumeces fasciatus*			X		X	
Reptiles	*Eumeces schneideri*		X			X	
Reptiles	*Furina diadema*		X			X	
Reptiles	*Furina ornata*		X			X	
Reptiles	*Gallotia atlantica*		X		X		
Reptiles	*Gallotia galloti caesaris*		X		X		
Reptiles	*Gehyra catenata*		X			X	
Reptiles	*Gehyra variegata*		X			X	
Reptiles	*Graciliscincus shonae*		X		X		
Reptiles	*Hemidactylus frenatus*		X		X		
Reptiles	*Hemidactylus mabouia*		X		X		
Reptiles	*Hemidactylus turcicus*	X	X	X	X	X	
Reptiles	*Heteronotia binoei*		X			X	
Reptiles	*Hierophis carbonarius*	X				X	
Reptiles	*Hierophis viridiflavus*	X				X	

Reptiles	*Hoplocephalus bitorquatus*		X			X
Reptiles	*Kanakysaurus viviparus*		X		X	
Reptiles	*Kanakysaurus zebratus*		X		X	
Reptiles	*Lacerta agilis*	X	X			X
Reptiles	*Lacerta bilineata*	X				X
Reptiles	*Lacerta laevis*	X				
Reptiles	*Lacerta trilineata*	X				
Reptiles	*Lacerta virdis*	X				X
Reptiles	*Lacerta vivipara*	X				X
Reptiles	*Leiolopisma zealandica*		X		X	
Reptiles	*Lerista bipes*		X			X
Reptiles	*Lerista bougainvillii*		X		X	
Reptiles	*Lerista desertorum*		X			X
Reptiles	*Lerista labialis*		X			X
Reptiles	*Lerista punctatovittata*		X			X
Reptiles	*Lialis burtonis*		X			X
Reptiles	*Liopholis inornata*		X			X
Reptiles	*Lioscincus steindachneri*		X		X	
Reptiles	*Lioscincus vivae*		X		X	
Reptiles	*Lothognathus gilberti*			X		X
Reptiles	*Lucasium byrnei*		X			X
Reptiles	*Lucasium damaeum*		X			X
Reptiles	*Lucasium immaculatum*		X			X
Reptiles	*Lucasium stenodactylum*		X			X
Reptiles	*Lygosoma bowringii*		X		X	
Reptiles	*Mabuya vittata*	X	X			X
Reptiles	*Malpolon monspessulanus*	X				X
Reptiles	*Marmorosphax taom*		X		X	
Reptiles	*Marmorosphax tricolor*		X		X	
Reptiles	*Mediodactylus kotschyi*	X				X
Reptiles	*Menetia greyii*		X			X
Reptiles	*Micrelaps mulleri*	X				X
Reptiles	*Microlophus bivittatus*		X		X	
Reptiles	*Moloch horridus*		X			X
Reptiles	*Morethia adelaidensis*		X			X
Reptiles	*Morethia boulengeri*		X			X
Reptiles	*Morethia taenioleura*		X			X
Reptiles	*Nannoscincus exos*		X		X	

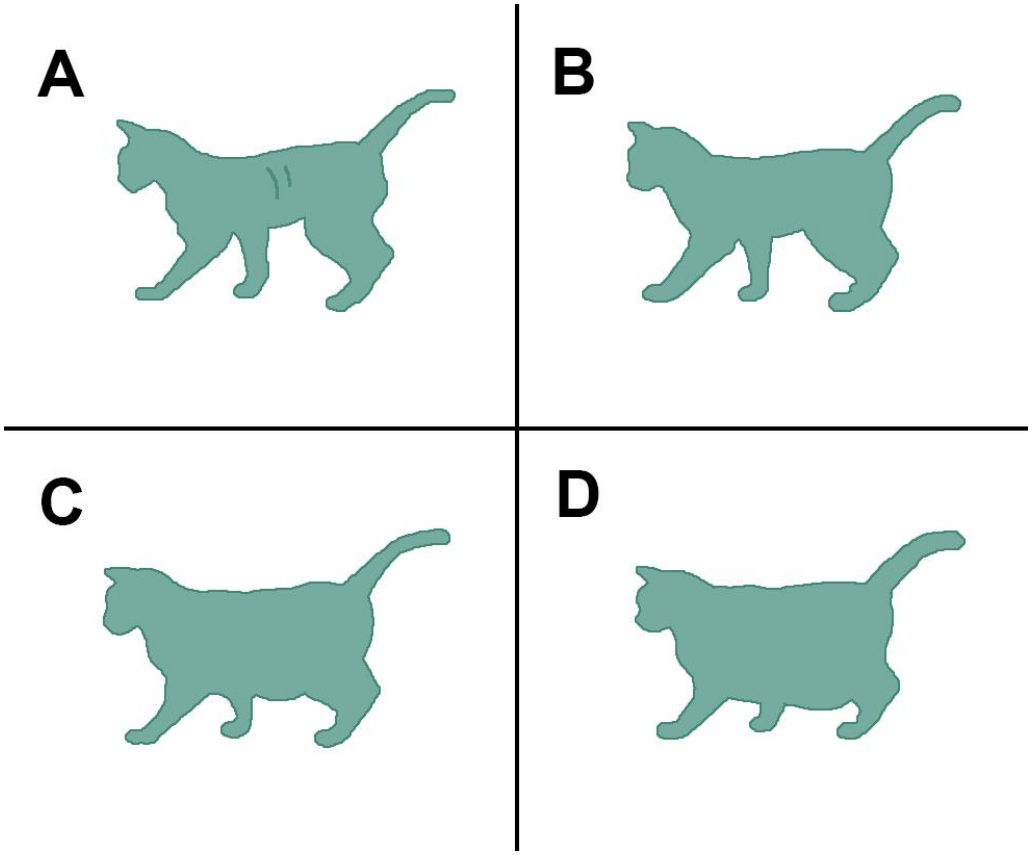
Reptiles	*Nannoscincus hanchisteus*		X		X		
Reptiles	*Nannoscincus manautei*		X		X		
Reptiles	*Nannoscincus slevini*		X		X		
Reptiles	*Natrix natrix*	X				X	
Reptiles	*Natrix tessellata*	X	X			X	
Reptiles	*Naultinus elegans*	X				X	
Reptiles	*Nephrurus asper*		X			X	
Reptiles	*Nephrurus levis*		X			X	
Reptiles	*Nephrurus milli*		X			X	
Reptiles	*Niveoscincus metallicus*		X		X		
Reptiles	*Niveoscincus ocelatus*		X		X		
Reptiles	*Notechis ater*		X		X		
Reptiles	*Oedura marmorata*		X			X	
Reptiles	*Oedura rhombifer*		X			X	
Reptiles	*Oligosoma nigriplantare polychroma*	X				X	
Reptiles	*Opheodrys aestivus*	X				X	
Reptiles	*Ophisaurus ventralis*			X	X		
Reptiles	*Pantherophis obsoletus*	X				X	
Reptiles	*Phasmasaurus maruia*		X		X		
Reptiles	*Phasmasaurus tillieri*		X		X		
Reptiles	*Phoboscincus garnieri*		X		X		
Reptiles	*Plestiodon fasciatus*	X		X	X		
Reptiles	*Plestiodon laticeps*	X		X	X		
Reptiles	*Podarcis filfolensis*	X	X		X	X	
Reptiles	*Podarcis muralis*	X	X		X	X	
Reptiles	*Podarcis siculus*	X				X	
Reptiles	*Podarcis tiliguerta*	X				X	
Reptiles	*Pogona barbata*	X				X	
Reptiles	*Pogona minor*	X	X			X	
Reptiles	*Pogona vitticeps*		X			X	
Reptiles	*Pseudechis australis*		X			X	
Reptiles	*Pseudonaja aspidorhyncha*		X			X	
Reptiles	*Pseudonaja ingrami*		X			X	
Reptiles	*Pseudonaja modesta*		X			X	
Reptiles	*Pseudonaja nuchalis*			X		X	
Reptiles	*Pseudonofa textilis*	X				X	
Reptiles	*Ptyodactylus guttatus*	X				X	
Reptiles	*Pygopus nigriceps*		X			X	
Reptiles	*Pygopus schraderi*		X			X	
Reptiles	*Ramphotyphlops bituberculatus*		X			X	

Reptiles	*Ramphotyphlops endoterus*		X			X
Reptiles	*Rhacodactylus auriculatus*		X		X	
Reptiles	*Rhacodactylus leachianus*		X		X	
Reptiles	*Rhinoplocephalus boschmai*		X			X
Reptiles	*Rhynchoedura eyrensis*		X			X
Reptiles	*Rhynchoedura ornata*		X			X
Reptiles	*Sceloporus undulatus*	X				X
Reptiles	*Scincella lateralis*	X				X
Reptiles	*Sigalooseps deplanchei*		X		X	
Reptiles	*Simoselaps anomalus*		X			X
Reptiles	*Simoselaps australis*		X			X
Reptiles	*Simoselaps bertholdi*		X			X
Reptiles	*Simoselaps fasciolatus*		X			X
Reptiles	*Simoselaps incinctus*		X			X
Reptiles	*Spalerosophis diadema*	X				X
Reptiles	*Storeria dekayi*			X		X
Reptiles	*Storeria occipitomaculata*	X				X
Reptiles	*Strophrurus cilliaris*		X			X
Reptiles	*Strophurus ciliaris*		X			X
Reptiles	*Suta monachis*		X			X
Reptiles	*Suta suta*		X			X
Reptiles	*Tarentola angustimentalis*		X		X	
Reptiles	*Tarentola boettgeri hierrensis*		X		X	
Reptiles	*Tarentola mauritanica*	X				X
Reptiles	*Testudo hermanni*	X				X
Reptiles	*Thamnophis sauritus sauritus*	X				X
Reptiles	*Tiliqua rugosa*	X	X			X
Reptiles	*Tiliqua scinocoides*	X	X			X
Reptiles	*Tropidoscincus boreus*		X		X	
Reptiles	*Tropidoscincus variabilis*		X		X	
Reptiles	*Tympanocryptis centralis*		X			X
Reptiles	*Tympanocryptis intima*		X			X
Reptiles	*Tympanocryptis lineata*		X			X
Reptiles	*Tympanocryptis tetraporophora*		X			X

Reptiles	*Typhlops vermicularis*	X				X
Reptiles	*Underwoodisaurus milii*	X	X			X
Reptiles	*Varanus giganteus*		X			X
Reptiles	*Varanus gouldii*		X			X
Reptiles	*Varanus panoptes*		X			X
Reptiles	*Varanus spenceri*		X			X
Reptiles	*Varanus tristis*		X			X
Reptiles	*Vipera aspis*	X				X
Reptiles	*Vipera berus*	X				X
Reptiles	*Vipera palaestinae*	X				X
Reptiles	*Virginia valeriae*	X				X
Reptiles	*Zamenis lineatus*	X				X
Reptiles	*Zamenis longissimus*	X				X
Reptiles	*Zootoca vivipara*	X				X
Amphibians	*Anaxyrus fowleri*	X				X
Amphibians	*Bufo balearicus*	X				X
Amphibians	*Bufo bufo*	X				X
Amphibians	*Cyclorana alboguttata*		X			X
Amphibians	*Cyclorana australis*			X		X
Amphibians	*Cyclorana novaehollandiae*		X			X
Amphibians	*Hyla arborea*	X				X
Amphibians	*Hyla cinerea*			X	X	
Amphibians	*Limnodynastes dumerilii*	X				X
Amphibians	*Limnodynastes ornatus*		X			X
Amphibians	*Limnodynastes spenceri*		X			X
Amphibians	*Limnodynastes terraereginae*		X			X
Amphibians	*Lithobates clamitans*	X				X
Amphibians	*Lithobates sphenocephalus*			X	X	
Amphibians	*Litoria adelaidensis*	X				X
Amphibians	*Litoria caerulea*		X	X		X
Amphibians	*Litoria ewingii*	X				X
Amphibians	*Litoria latopalmata*		X			X
Amphibians	*Litoria moorei*	X				X
Amphibians	*Litoria nasuta*			X		X
Amphibians	*Litoria peronii*	X				X
Amphibians	*Litoria rubella*		X			X
Amphibians	*Neobatrachus centralis*		X			X
Amphibians	*Neobatrachus sudelli*		X			X
Amphibians	*Pelophylax synklepton esculentus*	X				X

Amphibians	*Pseudacris crucifer*			X	X	
Amphibians	*Rana dalmatina*	X				X
Amphibians	*Rana italica*	X				X
Amphibians	*Rana latastei*	X				X
Amphibians	*Rana ridibunda*		X			X
Amphibians	*Rana temporaria*	X				X
Amphibians	*Salamandra salamandra*	X				X
Amphibians	*Triturus vulgaris*	X				X
Fish	*Carassius auratus*	X				X
Fish	*Cyprinus carpio*	X				X
Invertebrates	*Agonum haasti*		X		X	
Invertebrates	*Amphipsalta zelandica*		X		X	
Invertebrates	*Anax imperator*		X		X	
Invertebrates	*Anisolabis maxima*		X		X	
Invertebrates	*Anthocharis cardamines*	X				X
Invertebrates	*Apotrechus ambulans*		X		X	
Invertebrates	*Australomyia rostrata*		X		X	
Invertebrates	*Brachytrupes megacephalus*		X			X
Invertebrates	*Calliphora vicina*		X		X	
Invertebrates	*Calosoma oceanicum*		X			X
Invertebrates	*Cercophanius squama*		X		X	
Invertebrates	*Cherax destructor*		X			X
Invertebrates	*Chortoicetes terminifera*		X			X
Invertebrates	*Coenomantis kraussiana*		X			X
Invertebrates	*Concorhynchus conicirostris*		X		X	
Invertebrates	*Coniocleonus excoriatus*		X		X	
Invertebrates	*Dericorys lobata*		X		X	
Invertebrates	*Diestrammena gigas*		X		X	
Invertebrates	*Giniopsis cruentata*		X			X
Invertebrates	*Gryllotalpa australis*		X		X	
Invertebrates	*Gymnoplectron edwardsii*		X		X	
Invertebrates	*Hemiandrus furcifer*		X		X	
Invertebrates	*Hemideina thoracica*	X	X		X	X
Invertebrates	*Herpisticus calvus*		X		X	
Invertebrates	*Hippotion celerio*		X			X
Invertebrates	*Hyles livornicoides*		X			X
Invertebrates	*Lasiorhynchus barbicornis*		X		X	
Invertebrates	*Liochoria sorenseni*		X		X	

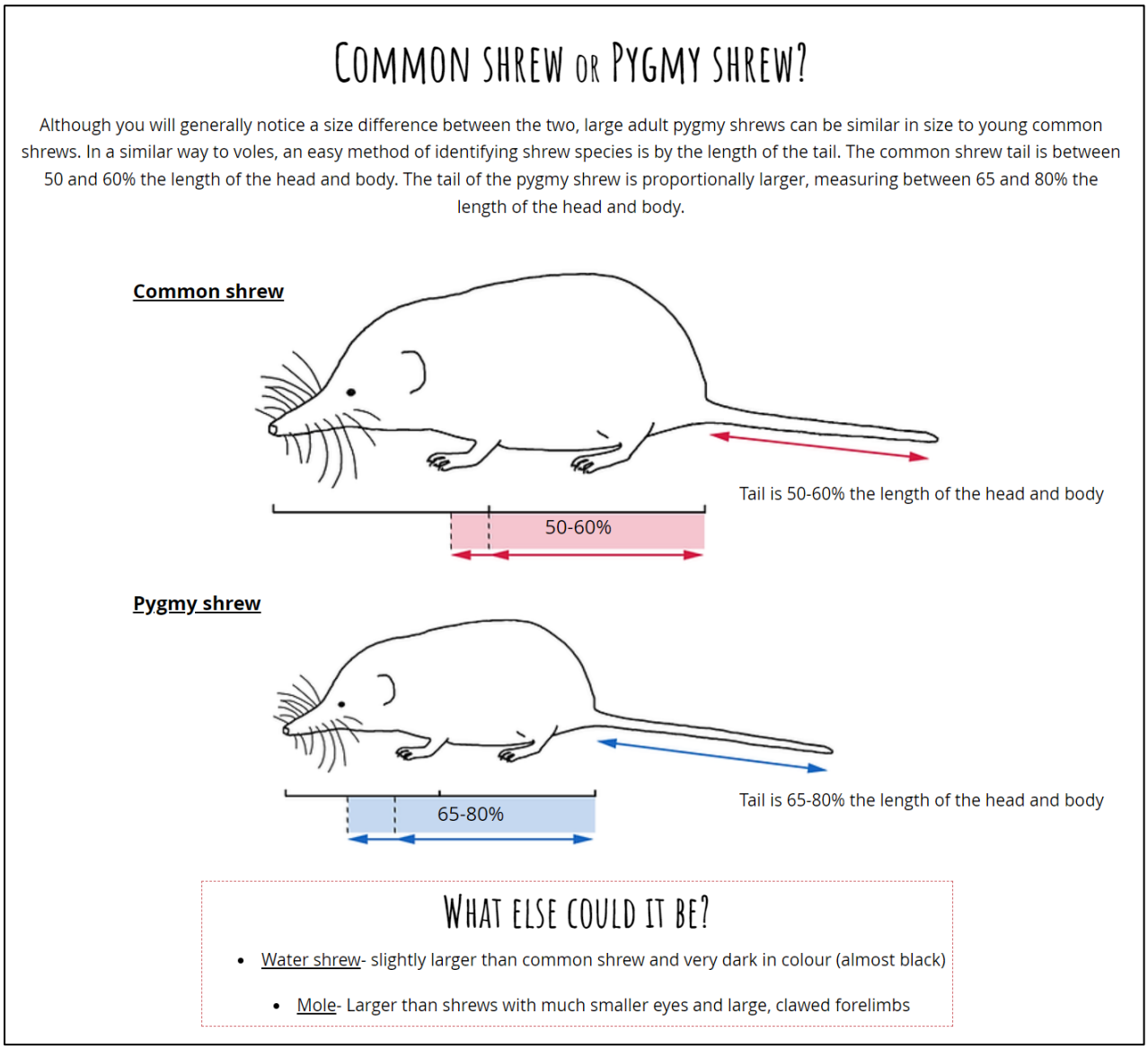
Invertebrates	*Nesomachilus maoricus*		X	X	
Invertebrates	*Nymphalis polychloros*	X			X
Invertebrates	*Oclandius cineveus*		X	X	
Invertebrates	*Ocypode quadrata*		X		X
Invertebrates	*Oryctes nasicornis*		X	X	
Invertebrates	*Oxycanus fuscomaculatus*		X	X	
Invertebrates	*Pachyrhamma longipes*		X	X	
Invertebrates	*Paivaea hispida*		X	X	
Invertebrates	*Persectania ewingii*		X	X	
Invertebrates	*Phaulacridium vittatum*		X	X	
Invertebrates	*Phyllognathus excavatus*		X	X	
Invertebrates	*Pieris brassicae*	X			X
Invertebrates	*Pimelia laevigata costipennis*		X	X	
Invertebrates	*Pimelopus nothus*		X	X	
Invertebrates	*Rumina decollata*		X	X	
Invertebrates	*Saphobius edwardsi*		X	X	
Invertebrates	*Scutigera coleoptera*		X		X
Invertebrates	*Stanwellia pexa*		X	X	
Invertebrates	*Teleogryllus commodus*	X			X
Invertebrates	*Tenodera australasiae*		X	X	
Invertebrates	*Theba geminata*		X	X	
Invertebrates	*Thereupoda clunifera*		X	X	
Invertebrates	*Ucides cordattus*		X		X
Invertebrates	*Urodacus armatus*		X		X
Invertebrates	*Uropetala carovei*		X	X	
Invertebrates	*Vanessa atlanta*	X			X
Invertebrates	*Vanessa cardui*	X			X
Invertebrates	*Zietzia geologa*		X		X



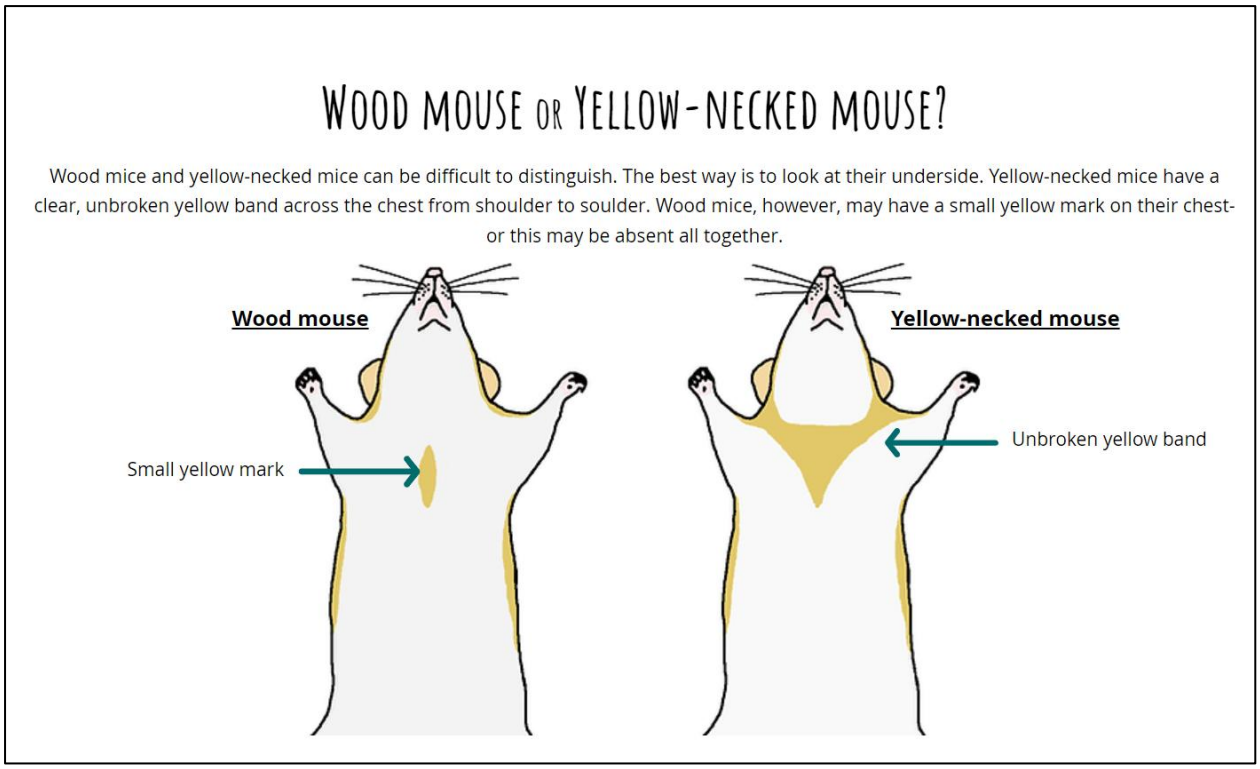
Appendix 3. 1. Body condition visual categories (A, B, C, and D), selected by each cat owner during the registration process.

Appendix 3. 2. The questions asked in the cat registration survey.

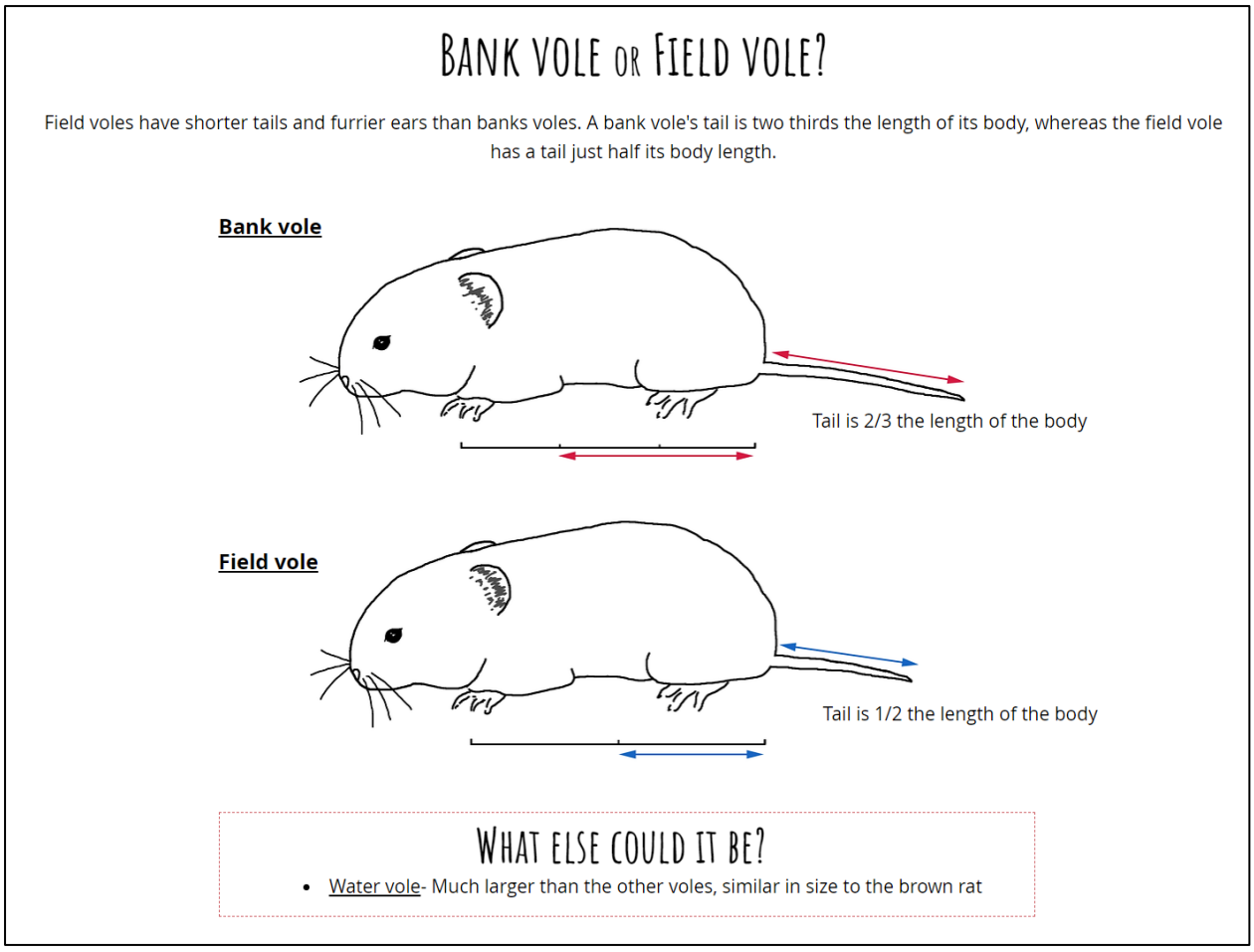
Question no.	Question
1	Your full name
2	Your postcode
3	Your email address
4	How many cats live in your household?
5	Your cat's name
6	How old is your cat?
7	Please tell us the breed or colouration of your cat
8	Sex of cat
9	Has your cat been neutered?
10	IF YES: At what age was your cat neutered?
11	Using the diagram below, how would you categorise your cat's body shape? (See Appendix 1)
12	What food do you provide for your cat?
13	Does your cat have access to a cat-flap?
14	Does your cat wear a collar with a bell on it?
15	Do you regularly provide food for wild birds in your garden?
16a	On average, how many dead small mammals or birds does your cat bring home per month? April- September
16b	On average, how many dead small mammals or birds does your cat bring home per month? October- March
17a	On average, how many living small mammals or birds does your cat bring home per month? April- September
17b	On average, how many living small mammals or birds does your cat bring home per month? October- March
18a	On average, how many hours per day does your cat spend outside? April-September
18b	On average, how many hours per day does your cat spend outside? October-March
19	Please use the space below to tell us about any current health problems which you think may influence your cat's behaviour.
20	Are you interested in taking part in our GPS and/or cat-camera study?



Appendix 3. 3. An example of an illustration found in the prey identification guide provided to participants, showing key identifying features of two shrew species. Guide and illustrations created by the author, based on (Couzens *et al.*, 2017).



Appendix 3. 4. An example of an illustration found in the prey identification guide provided to participants, showing key identifying features between two similar-looking mouse species. Guide and illustrations created by the author, based on (Couzens *et al.*, 2017).



Appendix 3. 5. An example of an illustration found in the prey identification guide provided to participants, showing key identifying features of two vole species. Guide and illustrations created by the author, based on (Couzens *et al.*, 2017).

Appendix 3. 6. Test outputs for normality and homogeneity of differences on square root-transformed data for time spent outdoors by cats in two seasons.

Season	**Test**	**Test statistic**	***p***	**N**
Summer	Shapiro-Wilk	W=0.97	<0.001	553 cats
Winter	Shapiro-Wilk	W=0.94	<0.001	553 cats
Summer & Winter	Fligner-Killeen	Med χ^2= 3.48	0.062	553 cats

Appendix 3. 7. Table containing all prey return records, by species. Where a broader taxonomic group is given (e.g. Muridae sp.), identification to species level was not achieved. Totals for each taxon are given in bold, following the species names, as is a total of all prey recorded.

Class	Latin name	Common name	Total	% of all prey
Mammalia		Small mammal	897	12.79
	Muridae sp.	(Mouse)	874	12.46
	Apodemus sylvaticus	Wood mouse	1446	20.62
	Apodemus flavicollis	Yellow-necked mouse	27	0.39
	Mus musculus	House mouse	274	3.91
	Micromys minutus	Harvest mouse	16	0.23
	Rattus norvegicus	Brown rat	228	3.25
	Cricetidae sp.	(Vole)	203	2.90
	Myodes glareolus	Bank vole	551	7.86
	Microtus agrestis	Field vole	680	9.70
	Muscardinus avellanarius	Hazel dormouse	6	0.09
	Sciurus carolinensis	Grey squirrel	12	0.17
	Talpa europaea	European mole	13	0.19
	Soricidae sp.	(shrew)	125	1.78
	Sorex araneus	Common shrew	141	2.01
	Sorex minutus	Pygmy shrew	107	1.53
	Neomys fodiens	Water shrew	6	0.09
	Chiroptera sp.	(Bat)	4	0.06
	Pipistrellus sp.	(Pipistrelle bat)	3	0.04
	Plecotus auritus	Brown long-eared bat	1	0.01
	Myotis nattereri	Natterer's bat	1	0.01
	Oryctolagus cuniculus	European rabbit	217	3.09
	Erinaceus europaeus	Hedgehog	1	0.01
	Mustela erminea	Stoat	1	0.01
	Mustela nivalis	Weasel	1	0.01
		Mammals	**5835**	**83.21**
Aves		Bird	187	2.67
	Paridae sp.	(Tit)	6	0.09
	Cyanistes caeruleus	Blue tit	75	1.07
	Parus major	Great tit	29	0.41
	Aegithalos caudatus	Long-tailed tit	9	0.13
	Poecile palustris	Marsh tit	1	0.01
	Periparus ater	Coal tit	4	0.06
	Prunella modularis	Dunnock	72	1.03
	Troglodytes troglodytes	Wren	66	0.94
	Sturnus vulgaris	Starling	17	0.24
	Turdidae sp.	(Thrush)	6	0.09
	Turdus merula	Blackbird	102	1.45
	Turdus iliacus	Redwing	1	0.01
	Turdus philomelos	Song thrush	4	0.06

	Erithacus rubecula	Robin	100	1.43
	Sylvia atricapilla	Black cap	4	0.06
	Regulus regulus	Goldcrest	3	0.04
	Passer domesticus	House sparrow	207	2.95
	Fringillidae sp.	(Finch)	5	0.07
	Chloris chloris	Greenfinch	14	0.20
	Fringilla coelebs	Chaffinch	25	0.36
	Carduelis carduelis	Goldfinch	35	0.50
	Pyrrhula pyrrhula	Bullfinch	7	0.10
	Linaria cannabina	Linnet	1	0.01
	Carduelis spinus	Siskin	2	0.03
	Columbidae Sp.	(Pigeon/dove)	31	0.44
	Streptopelia decaocto	Collared dove	9	0.13
	Columba palumbus	Wood pigeon	58	0.83
	Columba livia	Feral pigeon	17	0.24
	Corvidae Sp.	(Corvid)	1	0.01
	Corvus monedula	Jackdaw	2	0.03
	Pica pica	Magpie	4	0.06
	Dendrocopos major	Great spotted woodpecker	4	0.06
	Sitta europaea	Nuthatch	2	0.03
	Certhia familiaris	Treecreeper	3	0.04
	Delichon urbicum	House martin	2	0.03
	Apus apus	Swift	1	0.01
	Motacilla cinerea	Grey wagtail	1	0.01
	Psittacula krameri	Ring-necked parakeet	2	0.03
	Laridae sp.	(Gull)	1	0.01
	Anatidae sp.	(Duck)	1	0.01
	Anas platyrhynchos	Mallard	3	0.04
		Birds	**1124**	**16.03**
Reptilia	*Anguis fragilis*	Slow worm	6	0.09
	Zootoca vivipara	Common lizard	4	0.06
		Reptiles	**10**	**0.14**
Amphibia	*Rana temporaria*	Common frog	37	0.53
	Pelophylax ridibundus	Marsh frog	1	0.01
	Bufonidae sp.	(Toad)	2	0.03
	Bufo bufo	Common toad	3	0.04
		Amphibians	**43**	**0.61**
		Total prey	**7012**	

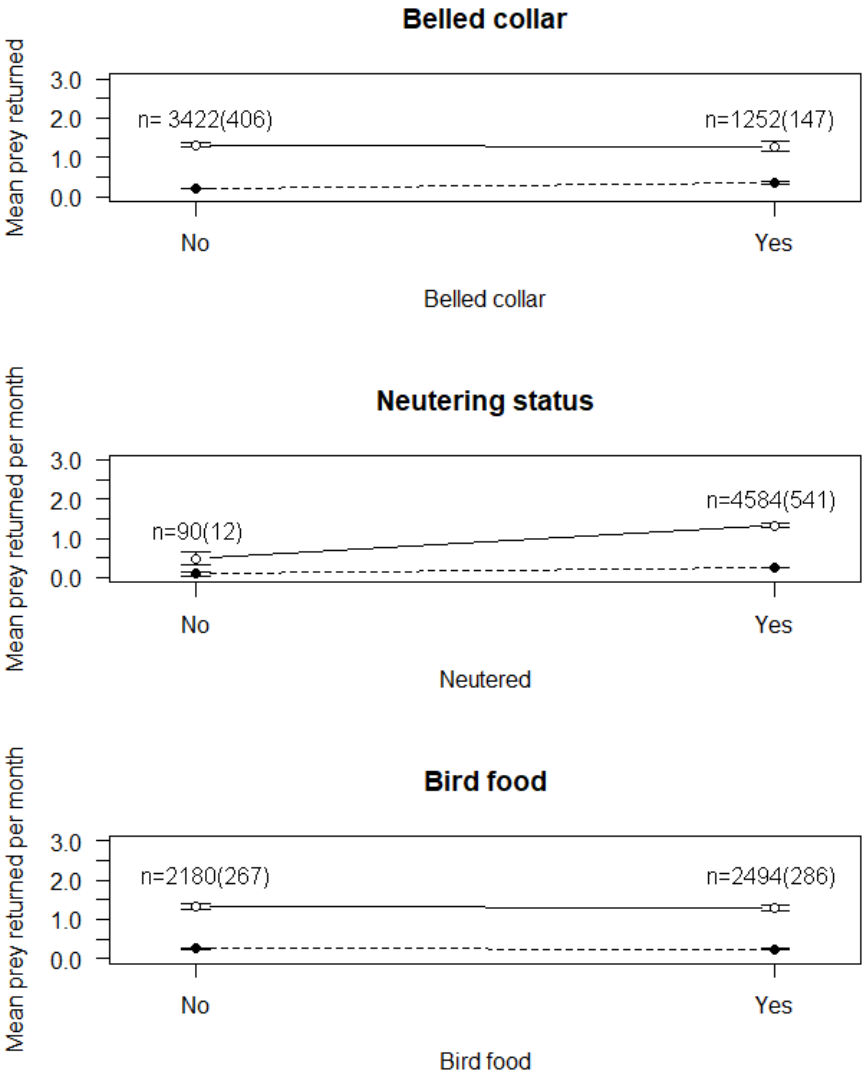
Appendix 3. 8. Table of misidentified species, as detected through photographic records, by corrected 'Prey ID'. 'Identified as' shows the cat owners' original description, followed by the number of cases in which this occurred. Prey are ordered first by taxon, followed by the most misidentified species or group.

Taxon	Prey ID	Identified as	No. of occurrences
Mammals	Bank vole	Mouse sp.	42
		Wood mouse	15
		House mouse	11
		Field vole	10
		Shrew sp.	1
	Field vole	Bank vole	28
		Mouse sp.	9
		Wood mouse	6
		House mouse	6
	Wood mouse	House mouse	32
		Harvest mouse	6
		Hazel dormouse	3
		Field vole	1
		Common shrew	1
	Brown rat	House mouse	9
		Wood mouse	2
		Yellow-necked mouse	1
		Mouse sp.	1
	Vole sp.	Mouse sp.	11
		Wood mouse	1
		House mouse	1
	House mouse	Harvest mouse	3
		Wood mouse	1
		Brown rat	1
		Bank vole	1
	Common shrew	House mouse	3
		Pygmy shrew	2
		Wood mouse	1
	Harvest mouse	wood mouse	1
	Pygmy shrew	Mouse sp.	1
	Water shrew	Common shrew	1
	Yellow-necked mouse	House mouse	1
Birds	Dunnock	House sparrow	3
		Tree sparrow	2
	Goldfinch	Siskin	3
	Robin	House sparrow	3
	Great tit	Blue tit	2
	House sparrow	Tree sparrow	1

		Thrush sp.	1
	Starling	House sparrow	1
	Wren	House sparrow	1
	Blue tit	Greenfinch	1

Appendix 3. 9. Numerical outputs of Bayesian negative binomial GLMM, testing for inclusion or exclusion in the final model. Posterior mean (P mean), standard error (SE), and the 2.5% and 97.5% credible intervals are given. Where credible intervals do not cross zero, a statistically important result is observed. Results in bold show important differences, and those bold variables were selected for inclusion in the final model.

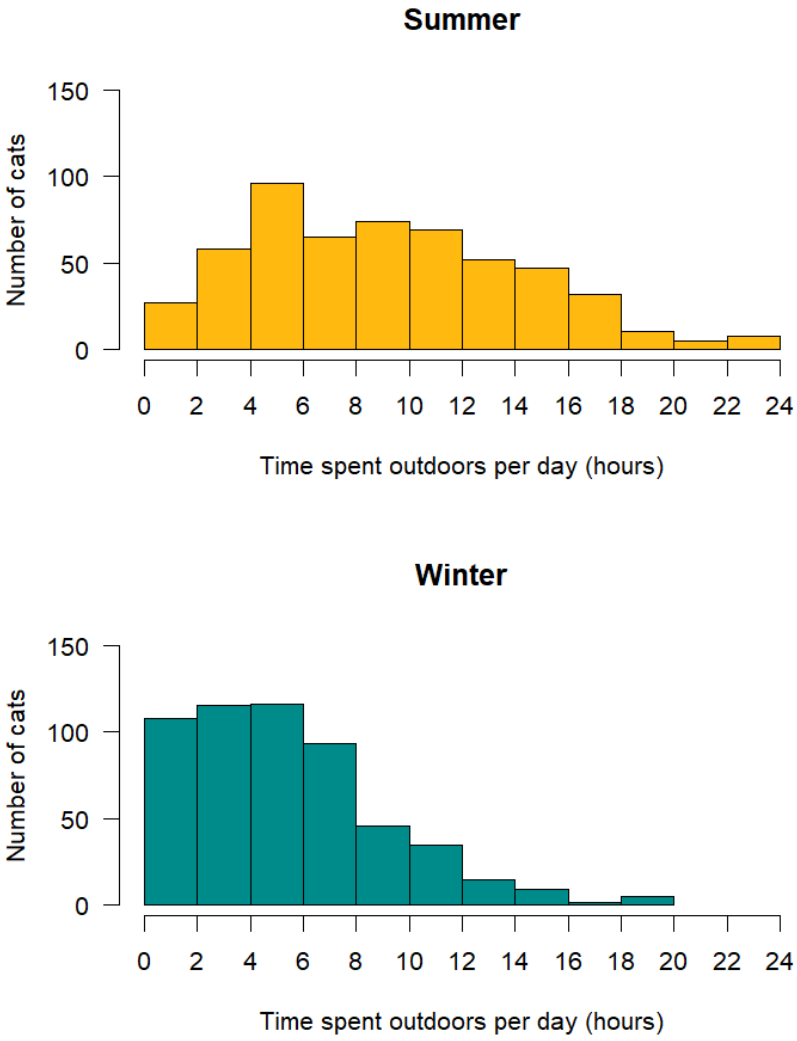
Variable	P mean	SE	2.5%	97.5%
Taxon: Birds < Mammals	**1.3**	**0.25**	**0.90**	**1.69**
Sex: Female < Male	**0.6**	**0.19**	**0.21**	**0.95**
Age: Kitten < Young adult	**1.2**	**0.29**	**0.43**	**1.55**
Kitten = Old adult	0.1	0.33	-0.70	0.46
Kitten > Old	**-1.1**	**0.48**	**-2.30**	**-0.45**
Body condition: A > B	**-0.6**	**0.29**	**-1.13**	**-0.03**
A > C	**-1.2**	**0.29**	**-2.05**	**-0.74**
A > D	**-1.1**	**0.40**	**-2.18**	**-0.38**
Belled collar: No = Yes	0.3	0.35	-0.31	0.87
Season: Winter < Spring	**0.7**	**0.11**	**0.49**	**0.88**
Winter < Summer	**1.3**	**0.08**	**1.16**	**1.48**
Winter = Autumn	0.01	0.09	-0.18	0.18
Year: 2018 > 2019	**-0.5**	**0.18**	**-0.78**	**-0.17**
2018 > 2020	**-0.6**	**0.25**	**-1.04**	**-0.30**
2018 > 2021	**-0.7**	**0.24**	**-1.09**	**-0.31**
Neutered: No = Yes	1.04	0.94	-0.11	2.51
Bird food: No = Yes	-0.5	0.42	-1.34	0.16
Cat flap: No < Yes	**0.8**	**0.25**	**0.22**	**1.28**



Appendix 3. 10. Interaction plots showing the variation in mean prey returned (per month) by different groups of cats (all found not to be important to the model) for both mammals and birds, along with Standard Error (SE) bars. Solid line represents mammals, and broken line indicates birds. Sample sizes given represent the number of recording months for which there are data in each category, followed by the number of cats in parentheses.

Appendix 3. 11. Time of day, grouped into three-hour categories and the number of mammals and birds recorded at that hour (of 3598 mammals and 696 birds, for which time was recorded).

Time category	Number of mammals	Number of birds
00:00 – 02:59	241	15
03:00 – 05:59	292	33
06:00 – 08:59	622	151
09:00 – 11:59	488	183
12:00 – 14:59	426	104
15:00 – 17:59	398	111
18:00 – 20:59	568	70
21:00 – 23:59	563	29



Appendix 3. 12. Frequency distributions of cats and how long they spend outdoors per day, on average (based on owner estimates) during the summer (April-September) and winter months (October-March).

Appendix 4. 1. Test outputs for normality (Shapiro-Wilk) and homogeneity (Fligner-Killeen) testing for the estimated time spend outdoors per day by cats in the warm (April-September) and cold (October-March) seasons.

Data	Test	Test statistic	*p*
Time outdoors- warm	Shapiro-Wilk	*W*= 0.9816	<0.001
	Fligner-Killeen	Med χ^2= 2.5255	0.1120
Time outdoors- cold	Shapiro-Wilk	*W*= 0.9487	<0.001
	Fligner-Killeen	Med χ^2= 0.0739	0.7858

Appendix 4. 2. Test outputs for normality (Shapiro-Wilk) and homogeneity (Fligner-Killeen) testing for the mean number of prey returned per month by cats in the warm (April-September) and cold (October-March) seasons.

Data	Test	Test statistic	*p*
Prey returned- warm	Shapiro-Wilk	*W*= 0.5530	<0.001
	Fligner-Killeen	Med χ^2= 0.6911	0.4058
Prey returned- cold	Shapiro-Wilk	*W*= 0.6100	<0.001
	Fligner-Killeen	Med χ^2= 1.0323	0.3096

Appendix 4. 3. Time taken to record the first predation event for the six cats found to predate whilst wearing the cat camera. Predation rate is given for each individual, along with the return rate (per month), for comparison.

Cat name	Total outdoor recording time (hours)	Time to first predation (hours)	Predation rate (per hour of video)	Mean prey returned per month (Chapter 3)
Benji	11.36	11.30	0.09	4.53
Joey	1.47	0.56	0.68*	0.10
Darling	8.17	0.51	0.37	7.85
Rocky	31.32	19.37	0.03	5.85
Treacle	51.72	10.06	0.04	2.90
Leyhausen	19.24	4.16	0.21	4.69

*No vertebrates caught, one invertebrate only

Appendix 4. 4. Twenty-seven occasions when prey items were reported to be returned home by the owner on the same day as camera recording took place, but were not observed in the footage retrieved. Prey common name is given, along with the time (or approximate time) of return, and the time that video recording began that day. Where timings were known, it is noted whether the camera was used either before or after the reported prey return.

Cat name	Prey	Return time	Time camera switched on	Camera: before/after return
Benji	Brown rat	'Morning'	19:41	After
	Dunnock	'Day'	07:33 & 23:33	Before & after
Rascal	Wood mouse	'Early'	20:15	After
Rocky	European rabbit	Unknown	08:00	-
	Bank vole	13:30	07:10	Before
	Bank vole	19:00	08:00	Before
Treacle	Bird sp.	18:00	09:08	Before
	House sparrow	14:00	09:11	Before
	Blackbird	07:00	07:03	After
	Vole sp.	23:30	22:10	Before
	Wood mouse	03:50	04:10	After
	Wood mouse	01:00	21:53	After
	Wood mouse	17:15	22:00	After
	Wood mouse	21:45	22:00	After
	Wood mouse	23:00	23:00	After
	Wood mouse	20:10	21:43	After
	Wood mouse	21:35	21:43	After
	Wood mouse	05:00	05:30	After
	Wood mouse	05:25	05:30	After
	Wood mouse	'Day'	19:50	After
	Brown rat	Unknown	19:00	-
Leyhausen	Wren	09:20	13:55	After
	Common shrew	11:10	13:55	After
	Common shrew	19:08	13:55	Before
	Bank vole	13:55	13:55	After
	Bank vole	07:30	14:50	After
	Small mammal sp.	Unknown	14:05	-

Appendix 5. 1. Common names (in British English) and scientific Latin names of the top 10 most commonly returned bird species (as found in Chapter 3).

Common name (British English)	**Latin name**
House sparrow	*Passer domesticus*
Blackbird	*Turdus merula*
Robin	*Erithacus rubecula*
Blue tit	*Cyanistes caeruleus*
Dunnock	*Prunella modularis*
Wren	*Troglodytes troglodytes*
Woodpigeon	*Columba palumbus*
Goldfinch	*Carduelis carduelis*
Great tit	*Parus major*
Chaffinch	*Fringilla coelebs*

Appendix 5. 2. Common names (in British English) and scientific Latin names of the top 10 most commonly returned mammal species (as found in Chapter 3).

Common name (British English)	**Latin name**
Wood mouse	*Apodemus sylvaticus*
Field vole	*Microtus agrestis*
Bank vole	*Myodes glareolus*
House mouse	*Mus musculus*
Brown rat	*Rattus norvegicus*
European rabbit	*Oryctolagus cuniculus*
Common shrew	*Sorex araneus*
Pygmy shrew	*Sorex minutus*
Yellow-necked mouse	*Apodemus flavicollis*
Harvest mouse	*Micromys minutus*

Appendix 5. 3. Land cover classifications (habitats) used in analyses, adapted from CEH (2017).

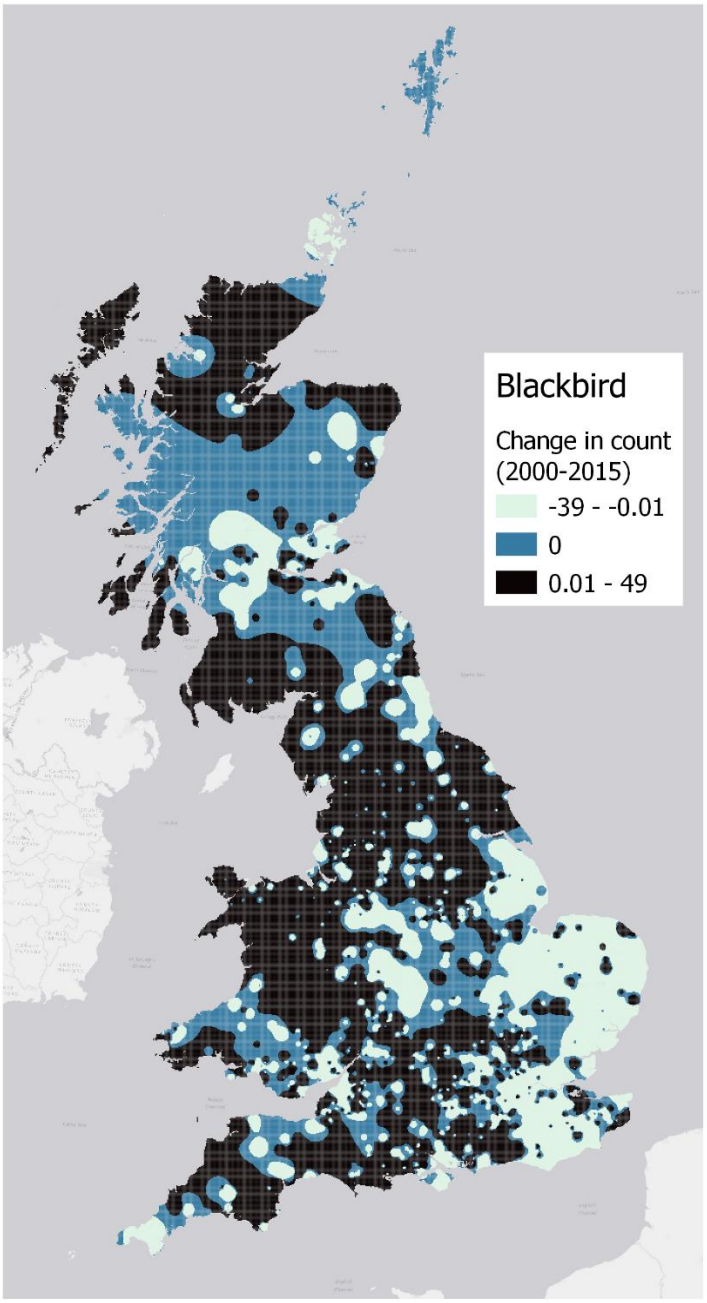
No.	Land type	Description
1	Broadleaf woodland	Broadleaved, mixed, and yew woodland
2	Coniferous woodland	Coniferous woodland
3	Arable	Arable and horticulture
4	Improved grassland	Improved grassland
5	Semi-natural grassland	Neutral, calcareous, and acid grassland. Fen, marsh, and swamp.
6	Mountain, heath, bog	Dwarf shrub heath, bog, and inland rock
7	Saltwater	Saltwater
8	Freshwater	Freshwater
9	Coastal	Supra-littoral rock and sediment, littoral rock and sediment
10	Built-up and gardens	Built-up areas and gardens

Appendix 5. 4. GLM test output showing the results of the models including the full dataset for all cat densities which best fit the data (n=988 km squares). Under 'Variable', * denotes an interaction between two variables. Significant effects are highlighted in bold. Land classifications are: A = remained arable, BU = remained built-up, G = remained improved grassland, W = remained broadleaved woodland. When interpreting the 'estimate' values, it should be noted that the x and y coordinates are in meters.

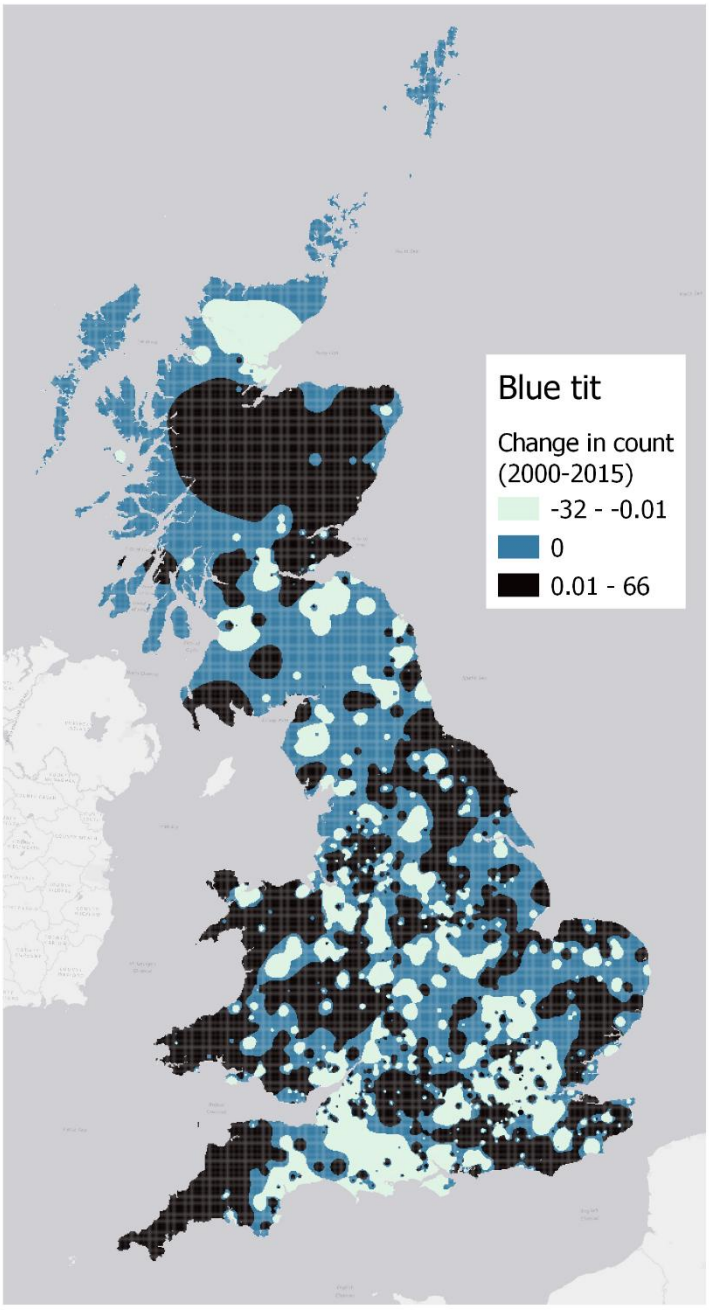
Species	Variable	Estimate	t value	*p* value
Blackbird	Cat density	$-3*10^{-3}$	-0.69	0.493
	Temperature (ave)	16.29	0.53	0.595
	Temperature (min)	-7.14	-0.48	0.633
	Temperature (max)	-8.64	0.57	0.571
	x coordinate (W-E)	**$-9*10^{-6}$**	**-2.31**	**0.021**
	Land: A > BU	**-3.06**	**-2.81**	**0.005**
	A = G	-0.04	-0.06	0.955
	A = W	0.80	0.66	0.510
	BU < G	**3.02**	**2.75**	**0.006**
	BU < W	**3.86**	**2.57**	**0.010**
	G = W	0.84	0.67	0.502
	Cat density * Temperature (ave)	**-0.45**	**-2.20**	**0.028**
	Cat density * Temperature (min)	**0.22**	**2.19**	**0.029**
	Cat density * Temperature (max)	**0.23**	**2.24**	**0.025**
Blue tit	y coordinate (S-N)	$2*10^{-6}$	1.49	0.138
	Land: A > BU	**-1.92**	**-2.67**	**0.008**
	A = G	0.18	0.31	0.756
	A = W	1.03	0.92	0.358
	BU < G	**2.01**	**2.84**	**0.005**
	BU < W	**2.95**	**2.44**	**0.015**
	G = W	0.85	0.75	0.452
Dunnock	Cat density	$2*10^{-3}$	0.85	0.397
	Temperature (ave)	12.86	0.98	0.329
	Temperature (min)	-6.42	-1.00	0.317
	Temperature (max)	-6.81	-1.04	0.298
	Cat density * Temperature (ave)	-0.15	-1.75	0.080
	Cat density * Temperature (min)	0.08	1.89	0.060
	Cat density * Temperature (max)	0.07	1.72	0.086
House sparrow	**Cat density**	**0.02**	**1.99**	**0.046**
	x coordinate (W-E)	**$-2*10^{-5}$**	**-3.67**	**<0.001**
	Land: A > BU	**-6.95**	**-4.12**	**<0.001**
	A = G	-1.61	-1.45	0.148
	A = W	-0.44	-0.23	0.815
	BU < G	**5.34**	**3.10**	**0.002**
	BU < W	**6.51**	**2.77**	**0.006**
	G = W	1.17	0.60	0.552
	Cat density * x coordinate	$-4*10^{-8}$	-1.81	0.071
Robin	Cat density	$-2*10^{-3}$	-0.67	0.502
	Temperature (max)	-1.25	-1.01	0.313
	Cat density * Temperature (max)	$8*10^{-3}$	1.45	0.147

Appendix 5. 5. The mean error values generated through k-fold cross validation (10 folds) for each of the two datasets and five bird species. Cross validation was conducted on the best fitting model for each species (identified through stepwise simplification). Lower error values signify the better-fitting models.

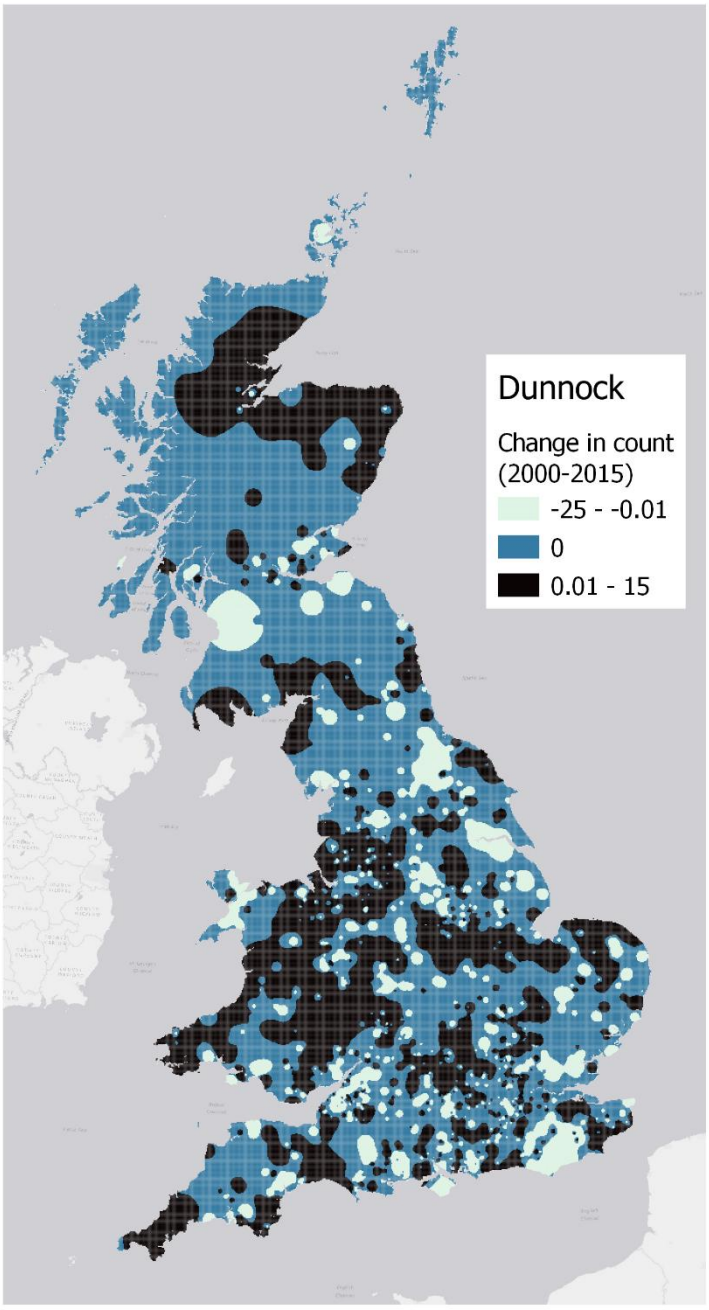
Data	Species	10-fold cross validation error
All data points	Blackbird	68.94
	Blue tit	62.15
	Dunnock	13.42
	House sparrow	179.35
	Robin	32.03
<500 cats per km^2	Blackbird	69.02
	Blue tit	59.75
	Dunnock	13.17
	House sparrow	153.40
	Robin	31.05



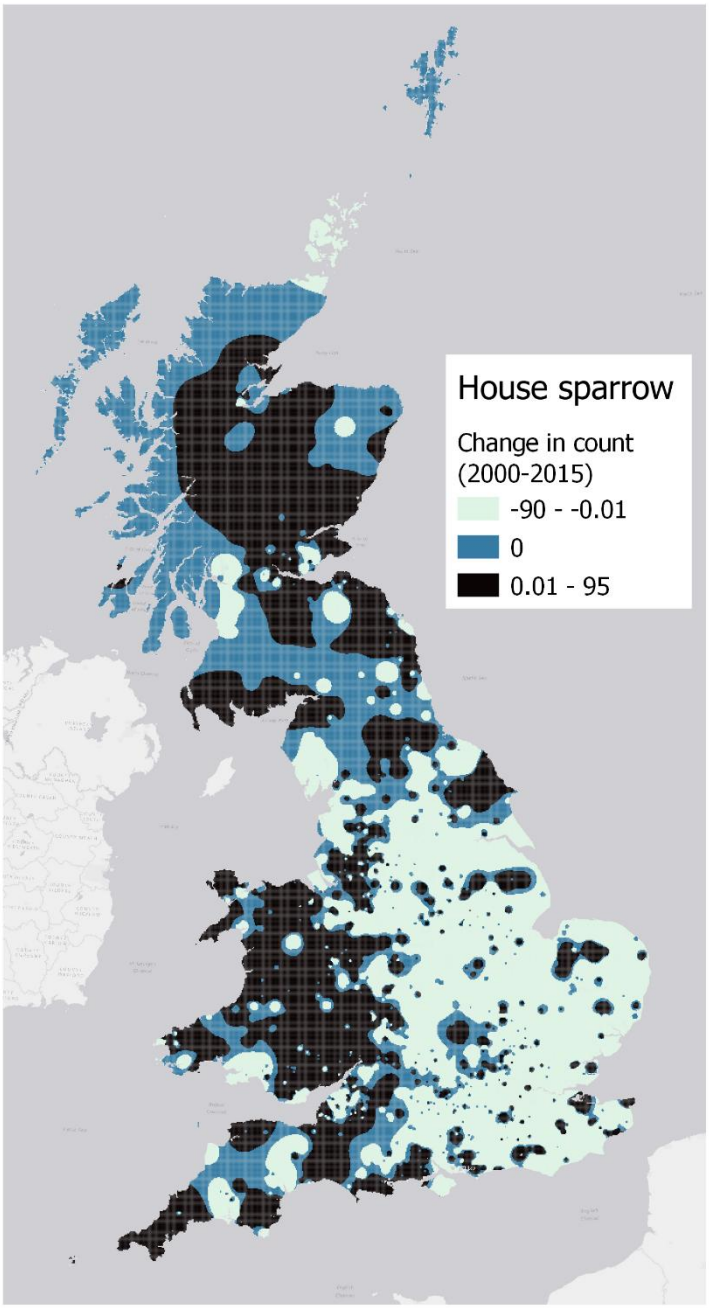
Appendix 5. 6. Interpolated spatial data representing the change in count for blackbirds between 2000 and 2015. Inverse-Distance Weighted (IDW) interpolation predicted values across Britain from 1,445 actual 1km grid squares, using a distance coefficient (P) of two (the inverse distance square weighted approach).



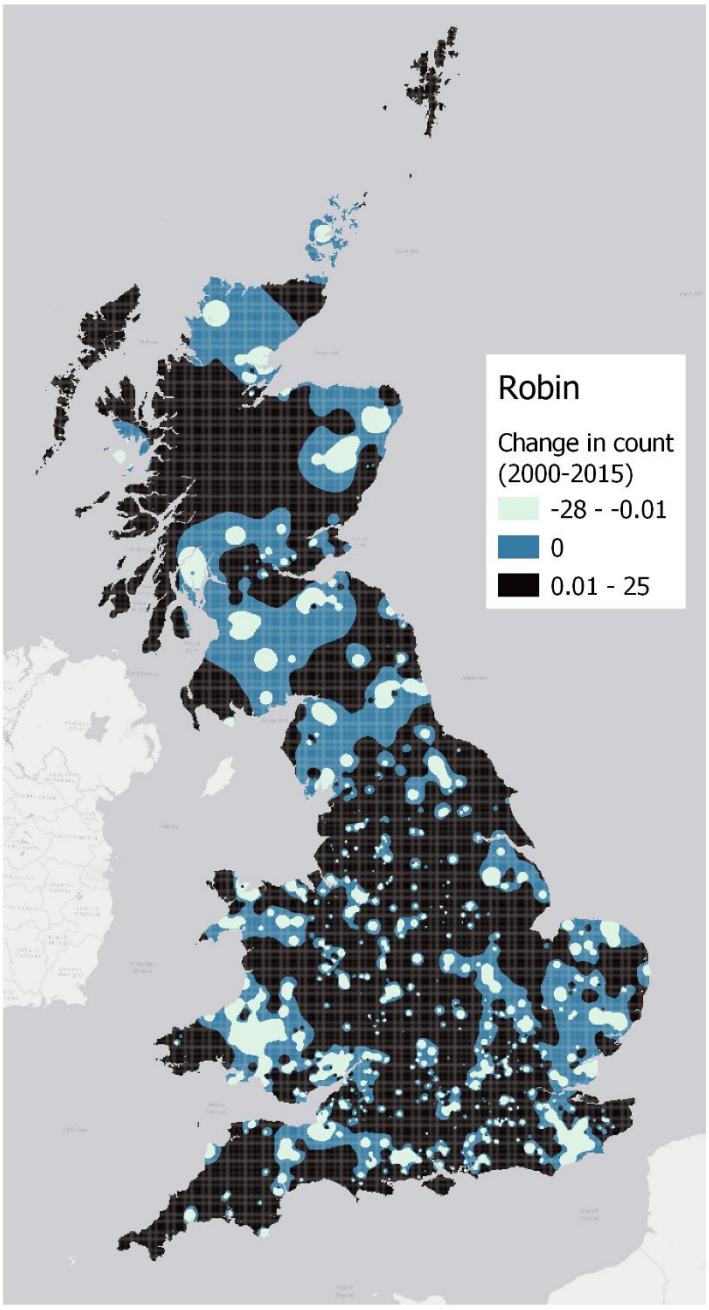
Appendix 5. 7. Interpolated spatial data representing the change in count for blue tits between 2000 and 2015. Inverse-Distance Weighted (IDW) interpolation predicted values across Britain from 1,445 actual 1km grid squares, using a distance coefficient (P) of two (the inverse distance square weighted approach).



Appendix 5. 8. Interpolated spatial data representing the change in count for dunnocks between 2000 and 2015. Inverse-Distance Weighted (IDW) interpolation predicted values across Britain from 1,445 actual 1km grid squares, using a distance coefficient (P) of two (the inverse distance square weighted approach).



Appendix 5. 9. Interpolated spatial data representing the change in count for house sparrows between 2000 and 2015. Inverse-Distance Weighted (IDW) interpolation predicted values across Britain from 1,445 actual 1km grid squares, using a distance coefficient (P) of two (the inverse distance square weighted approach).



Appendix 5. 10. Interpolated spatial data representing the change in count for robins between 2000 and 2015. Inverse-Distance Weighted (IDW) interpolation predicted values across Britain from 1,445 actual 1km grid squares, using a distance coefficient (P) of two (the inverse distance square weighted approach).

Ethical approval

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Request for ethical approval for research undertaken by staff, post-graduate research and post-graduate professional students

Please submit your completed form to the chair of your college research ethics committee (CREC)

Your Name	**Hannah Lockwood**
College	**Life and Natural Sciences**
College Research Ethics Committee	
Staff ID	**STF3839**
Student ID	**100463912**
Unimail address	**h.lockwood@derby.ac.uk**
Programme name / code	**PhD**
Name of supervisor(s)	**Dr Maren Huck, Prof Karim Vahed, Debbie Alston**

Title of proposed research study

The impact of domestic cats (Felis silvestris catus) on British wildlife populations

Background information

Has this research been funded by an external organisation (e.g. a research council or public sector body) or internally (such as the RLTF fund)? If yes, please provide details.	No
Have you submitted previous requests for ethical approval to the Committee that relate to this research project? If yes please provide details.	No
Are other research partners involved in the proposed research? If yes please provide details.	No

Signatures

The information supplied is, to the best of my knowledge and belief, accurate. I clearly understand my obligations and the rights of the participants. I agree to act at all times in accordance with University of Derby Policy and Code of Practice on Research Ethics:
http://www.derby.ac.uk/research/uod/ethics/

Signature of applicant	**H Lockwood**
Date of submission by applicant	17/05/2018
Signature of supervisor (if applicable)	
Date of signature by supervisor (if applicable)	17th May 2018

For Committee Use *Reference Number (Subject area initials/year/ID number)* Bio/2018/01

Date received 17 May 2018 Date considered 20 May 2018

Committee decision Approved (following revision) Signed

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1. What is the aim of your study? What are the objectives for your study?

Aim

- To assess whether predation by domestic cats is impacting prey populations.

Objectives

- To quantify predation
- To assess effects of cats on prey species densities
- To examine whether predation by cats removes healthy, breeding adults from prey populations
- To establish whether cats are negatively affecting prey populations

2. Explain the rationale for this study (refer to relevant research literature in your response).

As an introduced species occurring in far greater densities than any natural predator, the domestic cat (*Felis silvestris catus*; hereafter 'cat') has been implicated in a number of vertebrate extinctions and population declines, globally. While a number of studies have investigated the impacts of cats on native wildlife, the majority give focus to vulnerable small island populations. The impacts on British wildlife however, having co-evolved with similar predators such as the European wildcat (*Felis silvestris*), have not yet been fully assessed (Fitzgerald & Turner 2000). This topic is of great interest to wildlife groups, along with members of the public who take a keen interest in the natural world.

Unlike many other carnivores, cats are opportunistic, solitary hunters, taking small prey items whenever available. This trophic strategy means that hunting behaviour is not driven by hunger, and therefore, pet cats predate on wildlife despite adequate food provision by owners. Although prey items may regularly be returned to the owners' home, it is not known what proportion of total predation this represents. Previously, a study by Kays and DeWan (2004) in the USA suggested that returned items represent just 30.3% of all wild kills, with the remaining prey animals being either discarded elsewhere or consumed. While a number of studies have used this estimate as a basis for their own conclusions (Baker *et al.* 2005, 2008), it is not likely representative of the wider population due to the methodology used. The estimate comes from comparing the number of prey returned home by individuals (n=12 cats) with behavioural observations when outdoors (n=11 cats). As well as involving a small sample size, these two recording methods were used on different cats, 11 years apart, and for just three months out of the year (May-July). Although providing an insight into total predation rates, its use may result in vast over- or under-estimation of predation and potential impacts on wildlife when used in further studies.

In more recent years, researchers have used camera technology to quantify total predation by cats in the USA (Loyd *et al.* 2013) and Australia (McGregor *et al.* 2015). However, this information alone does not reveal anything about the ecological impacts of free-ranging cats, or the vulnerability of prey populations. Therefore, it is also necessary to survey local bird and small mammal assemblages to assess whether the presence of cats is indeed having a negative effect on populations. Previously, studies have examined prey body condition (Baker *et al.* 2008), compared species productivity with total predation rates (Baker *et*

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al. 2005), and compared population density of prey with that of cats (Kays & DeWan 2004, Baker *et al.* 2008). There are, however, a number of limitations associated with the experimental design of each of these studies, including low sample size, inefficient methods of sampling prey populations, and short-term surveying. The methodology proposed here addresses these limitations, producing a reliable estimate of predation rates and the potential impact on a range of prey species in the UK.

Baker, P.J., Bentley, A.J., Ansell, R.J., Harris, S., 2005. Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, 35(3&4), pp. 302-312.

Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C., Harris, S., 2008. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? *Ibis*, 150(s1), pp. 86-99.

Fitzgerald, B.M., Turner, D.C., 2000. Hunting behaviour of domestic cats and their impact on prey populations. In: Turner, D.C., Bateson, P., (eds). *The Domestic Cat: the Biology of its Behaviour*. 2nd ed. Cambridge University Press: Cambridge.

Kays, R.W., DeWan, A.A., 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. *Animal Conservation*, 7(3), pp. 273-283.

Loyd, K.A.T., Hernandez, S.M., Carroll, J.P., Abernathy, K.J., Marshall, G.J., 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation*, 160(2013), pp. 183-189.

McGregor, H., Legge, S., Jones, M.E., Johnson, C.N., 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS One*, 10(8), e0133915.

3. Provide an outline of your study design and methods.

This project employs a range of techniques to first discover whether cats are impacting prey populations, and second, to establish the proportion of prey returned home, informing future works.

The first part of this study measures cat density and compares this with that of local prey populations. For this, six study sites are to be selected around Derbyshire. All sites are to be built-up areas of around 0.3-0.5km^2, and will be selected such that each site contains hedgerow and woodland habitat of similar quality and plant species composition. This ensures that all areas used to survey prey populations have the same potential. Using a total of six sites allows three sites per year to be surveyed in close succession, limiting seasonal variability between survey areas.

Initial questionnaires will be delivered to houses within the six pre-determined study sites in order to establish cat density. Small mammal traps will then be used to sample three hedgerow transects at each

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site (n=18). Captured animals will be fur-clipped for identification and measurements taken. All live trapping and fur-clipping work will be conducted under the terms of the General Licence to Take Shrews (Natural England licence GL01). These data will be used to estimate small mammal density using the mark-recapture method. Bird surveys will be conducted at each site using point counts and distance sampling, again producing density estimates. Ten cats at each site will be fitted with a GPS unit to monitor their spatial activity. Prey populations will then be compared between areas of high and low cat density.

The second part of this study is a nation-wide distributed questionnaire and 12 month 'cat diary' to monitor the prey items returned home. Here, cat owners will be asked to record all kills brought home and, where possible, to retain those suitable for further analysis. This will allow assessment of body condition to determine whether predation by cats is removing healthy and reproductively active individuals from the wider population. For this, body measurements will be taken and compared to those of small mammals caught in traps, and to published bird measurements. For cats which use an indoor litter tray, faecal samples can also be retained for dietary analysis, where bones and hair can be identified. A website will be set up, along with dedicated social media pages in order to reach a large number of cat owners for participation in the cat diary.

Collar-mounted video cameras will be deployed (n=30), for use on cats also taking part in the 12 month cat diary. The resulting footage will show all predation events, including those which are consumed or discarded. As with the cat diaries, these data will be collected over a 12 month period. These data can then be combined with questionnaire data and faecal analysis to give total predation rates. Further comparing these data with known species productivity, along with body condition and life stage data will give us a greater understanding of the true predatory impact of domestic cats.

4. If appropriate, please provide a detailed description of the study sample, covering selection, sample profile, recruitment and inclusion and exclusion criteria.

Participants of the 12-month 'cat diary' will be recruited continuously for 1 year, and will begin recording data the following month. For example, a person registering mid-August will begin the cat diary on the 1st September. Registration will be open between the end of May 2018 and June 2019. Those registering in 2019 will still be asked to participate for 12 months, and so data collection will end in June 2020.

The two inclusion criteria for participation are that participants are resident in the UK, and own a cat with access to outdoor space. Therefore, owners of indoor cats would not be accepted onto the study. Access to the internet is required for registration and data submission, but this would only exclude a relatively small number of people from participating.

Participants can register through the website (www.whatthecatdraggedin.org) and the project will be publicised through social media, posters and leaflets, adverts in publications, and newsletters (e.g. Mammal Society E-bulletin).

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5. Are payments or rewards/incentives going to be made to the participants? Yes ☐ No ☒
If so, please give details.

6. Please indicate how you intend to address each of the following ethical considerations in your study. If you consider that they do not relate to your study please say so.
Guidance to completing this section of the form is provided at the end of the document.

a. Consent

Questionnaire & Cat Diary

Prior to completing the initial questionnaire, participants will be provided with the following information:

- The purpose of this research
- Who is conducting this research
- Participation is voluntary and participants can withdraw at any time
- Where data is stored and how long for
- How long this questionnaire should take to complete

A copy of this information is provided as Appendix 1.

Participants are then asked to electronically sign this form, giving their consent. By doing this they confirm that they are at least 18 years old and agree to participate as a volunteer.

Cameras & GPS

A second consent form will be emailed to participants of the camera and/or GPS part of the study. This will provide the same information as above (Appendix 2).

Prey surveys

Thirdly, as small mammal trapping is to take place on private land, signed consent is required from landowners. Again, they will be provided with information regarding the project itself and data usage. Landowners will also be told how long data collection will take and which areas of their land will be used. By signing this, they confirm that they own the land, are at least 18 years of age, and that they give permission for access to their land for the purposes outlined. A copy of this can be found in Appendix 3.

In the event that permission may be required from homeowners to trap in their garden, a re-worded version of this can be found in Appendix 4.

b. Deception

All relevant information will be available to participants prior to registration for the project. Participants will be informed through email of any alterations to the planned methodology.

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c. Debriefing

Owners of cats who participate in the GPS part of this study will be provided with a map of their cat's range.

Residents who have had small mammal traps in their garden will be told what was caught. This information will also be communicated through village newsletters/announcements, along with the results of local bird surveys, informing all residents and thanking those who participated.

Due to publishing embargos, key findings will not be released prior to publication.

d. Withdrawal from the investigation

Participants are free to withdraw from this study at any time. Any data collected before this point will be included in analyses, unless requested otherwise by the participant (in line with the GDPR, coming into effect on 25/05/2018). Participants are made aware of this in the consent form (Appendix 1).

e. Confidentiality

Although participants are not anonymous in this study, none of the data collected is considered 'sensitive'. Contact information will never be shared with a third party.

f. Protection of participants

There is no risk of harm to participants.

g. Observation research

Cameras

Video footage obtained from cat-mounted cameras may include images recorded within the home. Cat owners are encouraged to review footage before sending it to us, and are free to withhold any footage which they do not wish to release to us. These cameras are very easy to use, and footage can easily be transferred onto the participant's computer using a USB cable (provided). Videos are saved as AVI files, which can be easily viewed on computer programmes such as Windows Media Player.

Third parties may also be filmed by cats in this study, although people will rarely be identifiable, due to the position of the camera itself (low to the ground). This footage will never be passed to third parties, with the exception of the police if potentially incriminating. Any footage which may be considered to be sensitive will be destroyed.

These cameras are commercially available and therefore, there are no legal restrictions on their use in the UK.

h. Giving advice

No advice will be given.

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i. Research undertaken in public places

Prey surveys

Bird surveys will be conducted in public areas, although no harm or distress will be caused to any people or wildlife.

j. Data protection

Questionnaire data will be collected using 'LimeSurvey' via survey.derby.ac.uk. This is considered to be a secure system which adheres to the University of Derby's data protection policy and the GDPR. Data collected here will be stored on two encrypted external hard drives.

Footage from cat-borne video cameras will be reviewed by the owner before being uploaded to Microsoft OneDrive, ensuring that they are aware of and agree to share footage which may be considered sensitive (e.g. video within the home).

When contacting multiple participants via email, the blind copy (Bcc) function will be used to protect the contact information of individuals.

All contact information will be destroyed using crypto-shredding, ensuring permanent deletion.

k. Animal Rights

Cameras & GPS: Cat welfare:

- Cameras and GPS units will weigh less than 5% of each cat's body weight
- Collars will have a quick-release breakaway clip to ensure that no cat becomes entangled in anything
- Care will be taken to ensure that devices used on cats do not negatively impact the behaviour or welfare of any cat. Owners are instructed to remove devices if it is apparent that they are causing distress to the cat.

Prey surveys: Small mammal welfare:

- Small mammals will be trapped in Longworth traps with substantial bedding, food and drainage.
- Traps will be checked regularly, in accordance with the General Licence (Natural England licence GL01), as shrews are likely captures.
- All handling and fur-clipping will be conducted by trained persons.
- Trapping will not take place in extremely poor weather conditions.
- All captured individuals will be processed quickly and efficiently, and released at the site of capture, minimising stress.
- Traps will be well hidden and camouflaged from the public, avoiding interference and unnecessary stress to captured animals.

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I. Environmental protection

Lab work

Due to infection risks, wild animal carcasses will be collected by the University of Derby's chemical waste contractors (Ward) and incinerated. Smaller carcasses may be disposed of by the University's burying beetle colony.

Similarly, cat faeces will be autoclaved and collected by Ward for incineration.

Are there other ethical implications that are additional to this list? Yes ☐ No ☒

7. Have / do you intend to request ethical approval from any other body/organisation? Yes ☐ No ☒
If 'Yes' – please give details

8. Do you intend to publish your research? Yes ☒ No ☐.
If 'Yes', what are your publication plans?

Please see the following table:

Type of publication*	Authors	Proposed date of submission	Date of submission	Proposed title of Publication
Journal article	Lockwood, H., Huck, M.	Oct 2018		Impact of predation by domestic cats (*Felis silvestris catus*) on British wildlife populations: a systematic review
Journal article	Lockwood, H., Huck, M.	Oct 2019		Factors influencing the predation of wildlife by domestic cats (*Felis silvestris catus*)
Journal article	Lockwood, H., Huck, M.	Oct 2020		Predatory behaviour of the domestic cat (*Felis silvestris catus*) in the UK
Journal article	Lockwood, H., Huck, M.	Oct 2020		Is predation by domestic cats (*Felis silvestris catus*) negatively impacting wildlife populations?

9. Have you secured access and permissions to use any resources that you may require?
(e.g. psychometric scales, equipment, software, laboratory space). Yes ☒ No ☐.
If Yes, please provide details.

I have access to the questionnaire software, LimeSurvey. I have also set up a website and social media pages for the project.

The lab technicians at Kedleston Road are aware of the space and equipment requirements of this project and are able to accommodate this.

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I have not yet secured landowner permission to conduct prey surveys (rural hedgerows).
10. Have the activities associated with this research project been risk-assessed? Yes ☒ No ☐ Risk assessment has been completed, but not yet signed off.

Which of the following have you appended to this application?

❑ Focus group questions	❑ Psychometric scales
☒ Self-completion questionnaire	❑ Interview questions
❑ Other debriefing material	❑ Covering letter for participants
❑ Information sheet about your research study	☒ Informed consent forms for participants
❑ Location consent form	❑ Other (please describe)

PLEASE SUBMIT THIS APPLICATION WITH ALL APPROPRIATE DOCUMENTATION

Advice on completing the ethical considerations aspects of a programme of research

Consent
Informed consent must be obtained for all participants before they take part in your project. The form should clearly state what they will be doing, drawing attention to anything they could conceivably object to subsequently. It should be in language that the person signing it will understand. It should also state that they can withdraw from the study at any time and the measures you are taking to ensure the confidentiality of data. If children are recruited from schools you will require the permission, depending on the school, of the head teacher, and of parents. Children over 14 years should also sign an individual consent form themselves. If conducting research with children or vulnerable adults you will normally also require Disclosure and Barring Service (DBS) clearance. Research to be carried out in any institution (prison, hospital, etc.) will require permission from the appropriate authority.

Covert or Deceptive Research
Research involving any form of deception can be particularly problematical, and you should provide a full explanation of why a covert or deceptive approach is necessary, why there are no acceptable alternative approaches not involving deception, and the scientific justification for deception.

Debriefing
Debriefing is a process of reflection once the research intervention is complete, for example at the end of an interview session. How will participants be debriefed (written or spoken feedback)? If they will not be debriefed, give reasons. Please attach the written debrief or transcript for the oral debrief. This can be particularly important if covert or deceptive research methods are used.

Withdrawal from investigation
Participants should be told explicitly that they are free to leave the study at any time without jeopardy. It is important that you clarify exactly how and when this will be explained to participants. Participants also have the right to withdraw their data in retrospect, after you have received it. You will need to clarify how they will do this and at what point they will not be able to withdraw (i.e. after the data has been analysed and disseminated).

Protection of participants
Are the participants at risk of physical, psychological or emotional harm greater than encountered ordinary life? If yes, describe the nature of the risk and steps taken to minimise it.

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Observational research
If observational research is to be conducted without prior consent, please describe the situations in which observations will take place and say how local cultural values and privacy of individuals and/or institutions will be taken into account.

Giving advice
Students should not put themselves in a position of authority from which to provide advice and should in all cases refer participants to suitably qualified and appropriate professionals.

Research in public places
You should pay particular attention to the implications of research undertaken in public places. The impact on the social environment will be a key issue. You must observe the laws of obscenity and public decency. You should also have due regard to religious and cultural sensitivities.

Confidentiality/Data Protection
You must comply with the Data Protection Act and the University's Good Scientific Practice http://www.derby.ac.uk/research/policy-and-strategy This means:

- It is very important that the Participant Information Sheet includes information on what the research is for, who will conduct the research, how the personal information will be used, who will have access to the information and how long the information will be kept for. This is known as a 'fair processing statement.'
- You must not do anything with the personal information you collect over and above that for which you have consent.
- You can only make audio or visual recordings of participants with their consent (this should be stated on the Participant Information sheet)
- Identifiable personal information should only be conveyed to others within the framework of the act and with the participant's permission.
- You must store data securely. Consent forms and data should be stored separately and securely.
- You should only collect data that is relevant to the study being undertaken.
- Data may be kept indefinitely providing its sole use is for research purposes and meets the following conditions:
- The data is not being used to take decisions in respect of any living individual.
- The data is not being used in any which is, or is likely to, cause damage and/or distress to any living individual.
- You should always protect a participant's anonymity unless they have given their permission to be identified (if they do so, this should be stated on the Informed Consent Form).
- All data should be returned to participants or destroyed if consent is not given after the fact, or if a participant withdraws.

Animal rights.
Research which might involve the study of animals at the University is not likely to involve intrusive or invasive procedures. However, you should avoid animal suffering of any kind and should ensure that proper animal husbandry practices are followed. You should show respect for animals as fellow sentient beings.

Environmental protection

The negative impacts of your research on the natural environment and animal welfare, must be minimised and must be compliant to current legislation. Your research should appropriately weigh longer-term research benefit against short-term environmental harm needed to achieve research goals.